

Order PROCELLARIIFORMES

A rather distinct group of some 80–100 species of pelagic seabirds, ranging in size from huge to tiny and in habits from aerial (feeding in flight) to aquatic (pursuit-diving for food), but otherwise with similar biology. About three-quarters of the species occur or have been recorded in our region. They are found throughout the oceans and most come ashore voluntarily only to breed. They are distinguished by their hooked bills, covered in horny plates with raised tubular nostrils (hence the name Tubinares). Their olfactory systems are unusually well developed (Bang 1966) and they have a distinctly musky odour, which suggest that they may locate one another and their breeding places by smell; they are attracted to biogenic oils at sea, also no doubt by smell. Probably they are most closely related to penguins and more remotely to other shorebirds and waterbirds such as Charadriiformes and Pelecaniiformes. Their diversity and abundance in the s. hemisphere suggest that the group originated there, though some important groups occurred in the northern hemisphere by middle Tertiary (Brodkorb 1963; Olson 1975).

Structurally, the wings may be long in aerial species and shorter in divers of the genera *Puffinus* and *Pelecanoides*, with 11 primaries, the outermost minute, and 10–40 secondaries in the Oceanitinae and great albatrosses respectively. The tail varies in length, being forked in *Oceanodroma*, forked to pointed in other forms, usually with 12 rectrices but up to 16 in fulmars. The tarsi are light and cylindrical in aerial forms; strong and laterally compressed with legs set far back in aquatic ones. The front toes are webbed; hind toe small or absent. The proventriculus is long and glandular; the gizzard small and twisted; and the small intestine often spiral in *Pterodroma*, presumably to aid absorption of the unusual lipids in their food. Chicks are helpless and covered in down, with two coats except in some Oceanitinae. Some larger species have a darker immature plumage, and the female is often darker than the male in the great albatrosses. The male is usually larger than the female, though smaller in the Oceanitinae and some other small species. Otherwise there is little difference in appearance with sex or age, except that young birds may have more pronounced pale or dark edges to the feathers. Many have simple counter-shaded markings that often appear to have given rise to uniformly dark or, less often, to pale derivatives; some species in most groups are dimorphic or polymorphic. The more complex groups have often developed distinctive markings of the extremities.

Breed more or less colonially on offshore islands, coastal cliffs, or on hills and deserts inland, where they perform complex vocal and aerial displays. The nest is a simple scrape or cup in a burrow or natural hole, sometimes under vegetation. The s. albatrosses build large cone-shaped nests in the open; may be lined with any debris available in the area. Smaller species visit it only at night, though larger ones and those breeding on remote islands may come to nests in the open by day. Parents incubate for spells of several days in turn and generally leave the chick alone soon after it hatches, only returning at long intervals to feed it by regurgitation. In consequence the chick is vulnerable to introduced predators and some species are now greatly reduced and at least two are now extinct. Some species also periodically liable to have unsuccessful breeding seasons. Many young or even old birds may be wrecked ashore and die when they meet bad weather or suffer shortage of food on migration or in the winter. Though it has been claimed that they are also vulnerable to all sorts of pollution, the evidence is weak (Bourne 1976). There is at present anxiety about the effect of some fishing methods, such as long-lining, which may be endangering species such as the great albatrosses.

All species feed at sea on a variety of fish, cephalopods and small marine invertebrates, either socially or alone; larger species may scavenge all sorts of offal or prey on other birds. Most, except perhaps *Pelecanoides*, can digest the complex lipids formed by some marine animals (Clarke & Prince 1976), and may eject them to soil the plumage of their enemies with lethal results (Swennen 1974). Some species can digest wax (Obst 1986). Many now take wastes from whaling and fishing operations (Fisher 1952). All have long life-cycles in proportion to their size; they disperse on fledging and then prospect for nest-sites for 2–12 years in their youth. They usually lay a single large white egg annually; though a successful breeding cycle may be completed in less than a year in at least one tropical species, *Puffinus lherminieri*, it may take 2 years in larger southern ones. Before laying, the birds court for weeks or months, then go to sea for feeding. Incubation lasts 6–8 weeks, and fledging 2–9 months. Once the fat chick fledges it fends for itself, even in species that immediately make a long migration, sometimes to the opposite hemisphere.

Tendency for failed breeders and non-breeders to begin moult before successful breeders. Five strategies of wing-moult in breeding adults: (1) In albatrosses, remiges replaced in staffelmauser interrupted while breeding; in nearly all other species, primaries moulted outwards; possibly simultaneously in some diving-petrels. (2) In most subantarctic and temperate species, moult begins soon after breeding and is completed shortly before next breeding season. (3) In most tropical species, moult aseasonal, between breeding attempts; resumption of breeding apparently depends on when moult completed. (4) In trans-equatorial migrants, wing-moult delayed until they reach non-breeding quarters, where it is completed; moult rapid but no satisfactory evidence for flightlessness. In

some species, body-moult also in winter quarters; in others, at breeding grounds. (5) In some species of high latitudes, rapid moult completed in summer when they breed; some begin moult long before breeding finished.

The history of the classification of the Order is very confused, as is seen by comparing Timmermann's (1965) discussion of their Mallophagan parasites with that by Klemm (1969) of their leg muscles and that by Harper (1978) of their proteins, but it is now widely agreed that the Order is best divided into four families: Diomedidae or large to huge aerial albatrosses; Procellariidae or medium-sized, mainly aerial but sometimes aquatic, petrels, shearwaters and prions; Hydrobatidae or small to tiny, aerial storm-petrels; and Pelecanoididae or small aquatic diving-petrels.

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Family PROCELLARIIDAE fulmars, petrels, prions, shearwaters

The family Procellariidae represents the main radiation of medium-sized 'true petrels', characterized by having united nostrils with a median septum and the outer functional primary at least as long as the next. It tends to be dominant among the birds of the Southern Ocean, though in the n. hemisphere the Charadriiformes are more numerous. The giant-petrels *Macronectes* have also developed as large scavengers and predators, showing some convergence in appearance and behaviour with the Diomedidae. The Procellariidae may be divided into four main groups with some intermediate species, which makes it hard to draw distinctions between them.

(1) The fulmars *Macronectes*, *Fulmarus*, *Thalassoica*, *Daption* and *Pagodroma* consist of seven species of surface predators and filter-feeders of rather varying structure and appearance (Voous 1949) that breed in high latitudes but may migrate along cool currents into much lower ones. *Fulmarus* appears to have colonized the n. hemisphere in the Tertiary. Six of the seven species are essentially confined to our region.

(2) The gadfly-petrels *Pterodroma* are a large series of some 30 agile species; 16 breed in our region and another six occur rarely or rather rarely. Their short sturdy bills are adapted for seizing soft prey at the surface, and their twisted intestines, for digesting marine animals with an unusual biochemistry, which are also found throughout the warmer oceans (Imber 1985). They show complex markings of face and wings that must serve as interspecific recognition-marks (Murphy & Pennoyer 1952). Some species placed in this group have an intermediate structure and intergrade with all other groups distinguished here: *Pterodroma (Lugensa) brevirostris*, which moves S in winter, has distinctly big eyes like *Pagodroma*; *Halobaena caerulea* has a plumage similar to that of prions; *Bulweria* has some structural resemblance to shearwaters. At present it is difficult to determine their precise relationships.

(3) The prions *Pachyptila* are a specialized group of six (perhaps five) very numerous species, all in our region, that show a progressive adaptation of a small, agile, cryptically coloured, fulmarine form for filter-feeding on zooplankton. There has been dispute over their classification (Cox 1980; Harper 1980) but the arrangement discussed by Fleming (1941) seems best except that the Broad-billed Prion *P. vittata* appears to intergrade with Salvin's Prion *P. salvini* through *macgillivrayi* of Ile St Paul; so they may be better treated as subspecies of the same species.

(4) The shearwaters *Procellaria*, *Calonectris* and *Puffinus* include some 20 agile species with long bills adapted to catch prey more or less under water throughout the warmer seas (Kuroda 1954); 13 species breed in our region, some migrating into the n. hemisphere; six others are chance or perhaps regular visitors. From the fossil record (Brodkorb 1963; Olson 1975); they seem to have been particularly common in the great Tethys Ocean of the middle latitudes of the n. hemisphere in the Tertiary, so this development of aquatic habits may have occurred there without competition from penguins with a subsequent return S by the more successful forms.

General features of the family are: body, ovate, or elongate in shearwaters; wings, long and narrow, 11 primaries, p10 longest, p11 minute; 20-29 secondaries, short, diastataxic; tail, short, 12 feathers; bill, heavy (*Macronectes*), slender (shearwaters), broad (prions) or stubby (gadfly-petrels), hooked, formed of several horny plates; nostrils in dorsal tube of varying length; legs set far back, laterally flattened but round in gadfly-petrels; three toes, webbed, hind toe vestigial, raised. Oil-gland feathered. Peculiar musky odour. Sexes similar, male usually larger than female. Plumage, black or grey above, white below, or all dark; light and dark morphs in some species. Juveniles and immatures usually like adults.

Cosmopolitan throughout the oceans, essentially pelagic; more abundant in cool or cold waters rich in plankton and mostly away from ice. Swim well but usually aerial except when feeding or resting. Fly with alternate swooping and flapping action close to the surface but often arcing high in some gadfly-petrels. Gait on land, a shuffling crouch, being unable to walk properly with feet set so far back; generally avoid open areas on land, being thus vulnerable to predators. Nest colonially; for the most part in burrows and cavities in all sorts of terrain, sometimes far from the sea and in mountainous areas but some species, e.g. *Macronectes*, nest on open ground. Hole-nesters usually nocturnal at colonies, when often extremely vocal, though generally silent at sea. Migratory and dispersive. Some species divide the year between s. and n. hemisphere, often migrating in large flocks that may settle on the sea in huge dense rafts. Feed mostly on fish, cephalopods and crustaceans obtained by flight-feeding, plunge-diving, surface feeding, surface-diving and underwater pursuit; hydroplaning (Murphy) is a characteristic method used particularly by prions.

Probably all defend small nesting territories to which they return regularly while undisturbed; certainly so in some hole- and burrow-nesting forms. Agonistic and sexual behaviour of nocturnal, hole-nesting species very poorly known but generally seem to have little specialization for visual displays. Tactile actions such as allopreening and billing used but olfactory and vocal communication is probably important. Breeding is usually seasonal, generally with synchronized laying, often after a pre-laying exodus but some may not nest annually; some have shorter

cycles or nest continually. For the most part, little attempt to make substantial nests. Eggs, ovate, mat, white. Clutch-size, invariably one; single-brooded; no replacement laying. Incubation by both sexes in alternate spells of 1–11 days. Single median brood-patch. Incubation period, 45–55 days. Eggshells probably always trampled in nest. Young, semi-altricial, nidicolous; hatched in down. Rarely left alone in nest for first 1–2 weeks. Cared for and fed by incomplete regurgitation by both parents. Nestling period generally shorter in cliff- and ledge-nesting species than in hole-nesters. Young attain greatest weight, often well above that of adult, some days before fledging, by which time weight has been reduced to about the same as an adult, but no clear evidence that young are totally deserted for last few days in nest. Adults and young of most species liable to eject stomach-oil in defence. Young independent at fledging. Maturity reached at minimum of 3–4 years, in some 6–12 years.

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Puffinus carneipes **Flesh-footed Shearwater**

Puffinus carneipes Gould 1844, *Ann. Mag. Nat. Hist.* 13:365 — small islands off Cape Leeuwin, Western Australia.

The specific name is compounded of the Latin *caro*, *carnis* (flesh) and *pes* (foot) and refers to the legs and feet but ambiguously as regards to colour or nature.

OTHER ENGLISH NAMES **Fleshy-footed Petrel** or **Shearwater**, **Big** or **Lord Howe Island Muttonbird**, **Pale-footed Shearwater**.

All English names are awkward or unsatisfactory, perhaps because the Latin specific name is originally ambiguous. The feet are no more fleshy by nature than those of other shearwaters but are strikingly flesh-coloured, which the Latin name does not imply. **Fleshy-footed** inappropriately implies a fleshy nature; **Flesh-footed**, though ambiguous, has less of this imputation. **Pale-footed** (previous US usage) is really more acceptable but has been dropped from the AOU Checklist.

MONOTYPIC

FIELD IDENTIFICATION Length: 40–45 cm; wing-span: 99–107 cm; weight: 580–750 g. Large bulky all-dark shearwater of the Pacific and Indian Oceans. Recalls a small *Procellaria* petrel, especially **Black Petrel** *P. parkinsoni* but smaller and less bulky with more slender bill and plumage somewhat paler. Bill more robust than other *Puffinus* spp (except **Pink-footed Shearwater** *P. creatopus*); appears larger-headed and with more bulky body than other dark shearwaters of genus. Diagnostic combination of dark-tipped pale horn-coloured bill and pink legs and feet. Sexes alike. No seasonal plumages. Immatures resemble adults.

DESCRIPTION ADULT. Upperparts, blackish brown, darkest on head and primaries; feathers of back, scapulars and wing-coverts have brown margins, becoming paler with wear. Tail, blackish, gently wedged or rounded; feet do not extend beyond tail in flight. Underparts, dark brown; underwing, greyish brown, underprimaries show silvery reflection and pale shaft-bases in good light. Bill more robust than other *Puffinus* shearwaters, with nostril tubes more prominently raised above base of culmen. Bill much less robust than *Procellaria* petrels, which have longer and deeper bills with nostril tubes even more conspicuously raised, and massive unguis. Most of latericorn, ramicorn and nostril tubes, pale horn with pinkish tinge; unguis and distal tip of nostril tubes, blackish brown. Iris, brown. Legs and feet, flesh-pink tending to pale brown distally.

SIMILAR SPECIES Readily distinguished from other all-dark *Puffinus* shearwaters by large pale bill. **Sooty** *P. griseus* and **Short-tailed** *P. tenuirostris* **Shearwaters**, smaller with slender dark bills, dark legs and feet, narrower wings and faster flight. **Wedge-tailed Shearwater** *P. pacificus* (dark morph) shares pink legs and feet and broad wings with **Flesh-footed**, but **Wedge-tailed** has slender dark bill, is more lightly built, has longer tail and holds wings bowed and well forward. Most easily confused with **Black Petrel**, especially where ranges overlap round n. NZ and in Tasman Sea. **Black Petrel** larger and bulkier, with larger head, thicker neck and longer broader wings. **Black feet** of **Black Petrel** trail slightly beyond tip of short wedge-shaped tail. Bill of **Flesh-footed** appears pale with small dark tip at sea, whereas bill of adult **Black Petrel** appears bicoloured yellowish and black, with more ex-

tensive black tip, culmen and sulcus. (See **Black Petrel** for more details.) **Westland Petrel** *Procellaria westlandica* and **White-chinned Petrel** *P. aequinoctialis*, much larger and bulkier, with massive bills and black feet; bill of **White-chinned** appears entirely pale at sea, without dark tip of **Flesh-footed Shearwater**. **Great-winged Petrel** *Pterodroma macroptera* has stubby black bill, black feet and (usually) grey face. Silhouette and flight-style of **Great-winged Petrel** differ markedly from **Flesh-footed Shearwater**; **Great-winged** has high forehead, bull-neck and long, narrow wings held forward and swept back at carpal joint; flight fast and bounding, with high arcs and little low gliding. **Great-winged Petrel** more oceanic, and spends less time resting on surface.

Mainly frequent seas over continental shelves and slopes except on migration. Commonly occur in inshore waters. Breed on islands off n. NZ and in Cook Strait, Lord Howe I., islands off sw. Aust. and Ile St Paul. Colonies often dense, but may be mixed with other burrowing petrels. Gait on land less awkward than other shearwaters, can run well without spreading wings for balance. Swim buoyantly, although not so high in water as *Procellaria* petrels. Can dive well (especially in pursuit of scraps and bait from boats) but do not dive so often as typical diving shearwaters e.g. **Sooty** and **Short-tailed**. Use partially folded wings for propulsion under water. Flight: in calm conditions, flap wings more slowly and effortlessly than diving shearwaters; progress slowly and gracefully in long glides with one wing-tip near sea-surface interspersed with deep lazy wing-beats; in higher winds, bank more, with more shearwatering and less flapping, but never as impetuous as **Sooty** and **Short-tailed Shearwaters**. Feed during day, facing into wind and running along surface between shallow belly-flop dives; also dive deeply from surface. Often solitary, but occasionally form flocks of hundreds, especially round trawlers and when rafting off breeding islands in late afternoon. Often occur among mixed species feeding flocks of other shearwater species, gulls, terns and gannets. Regularly approach ships, especially fishing vessels; can be a nuisance when diving after baits. Usually silent at sea, but feeding birds occasionally emit high-pitched squeal. Nocturnal at breeding colonies. On ground, main call short repeated *gug-gug-gug* followed by hoarse, crooning *ku-koo-ah* repeated 3–6 times,

becoming increasingly hysterical until *koo* becomes scream. This call occasionally given in flight over colony. Other calls include quiet cackles.

HABITAT Marine, pelagic; mainly in subtropical waters. Occur mainly over continental shelves and slopes (Hindwood 1945; Norris 1965; Cox 1976; Barton 1977); occasionally inshore (Gibson & Sefton 1958; Marchant 1977). In NZ, concentrate where tidal movement strong (Norris 1965), and observed feeding at edge of shoals of fish on down-current side of tidal streams (Jenkins 1974). In n. hemisphere, occur mainly in coastal waters, particularly over upwellings; observed over waters of surface-temperature 11–16 °C off California and Japan (Kuroda 1955; Bailey 1966; Ainley 1976).

Breed on islands in A'asian region, and in Indian Ocean. Nest under forest, scrubland, shrubland, grassland or succulents (Hindwood 1940; Warham 1958; Lane 1982a,b; Robinson *et al.* 1986), where burrowing not restricted by deep litter, dense vegetation or bare rock (Lane 1982a,b). Need clear, elevated places close to colony for take-off (Hindwood 1940).

Feed mainly from surface, but dive occasionally; observed retrieving scraps at 2 m depth (Milledge 1977) and following baited hooks to 3–5 m (Falla 1934). Loaf and sleep on sea surface.

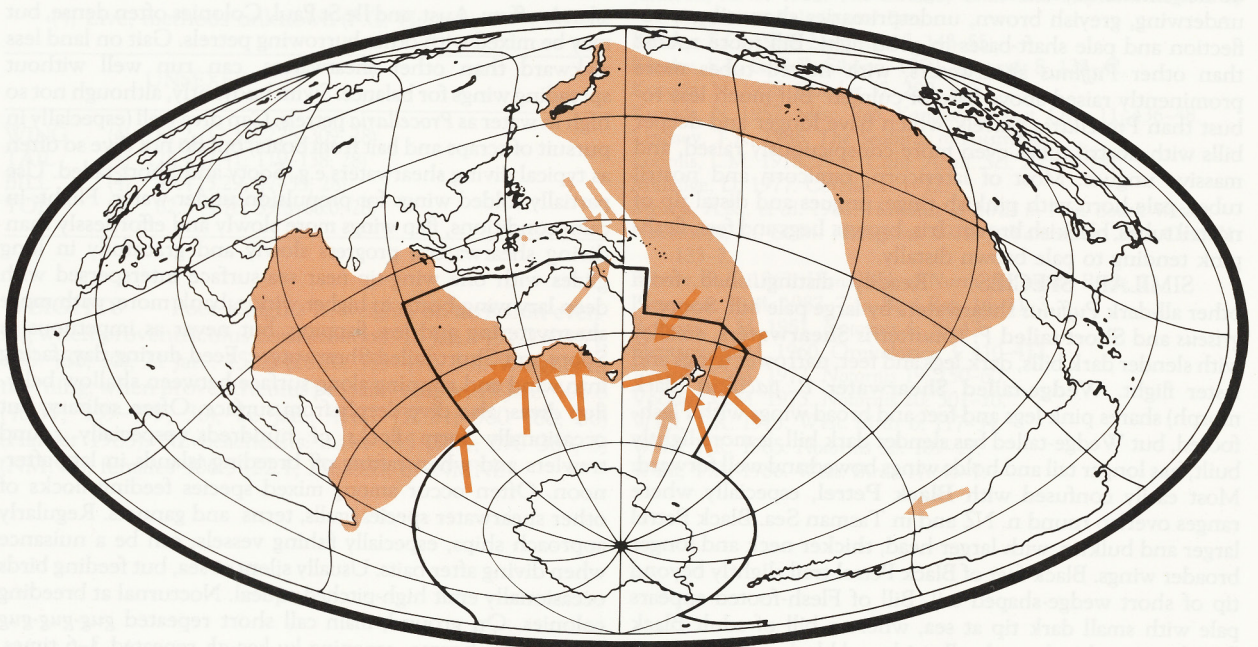
Breeding colonies susceptible to introduced predators; foxes probably responsible for destruction of colonies on WA mainland (Warham 1958). Colonies on Eclipse I., WA, disrupted by construction of lighthouse and tracks, but restoration has been carried out, and they may recover (Fullagar 1978).

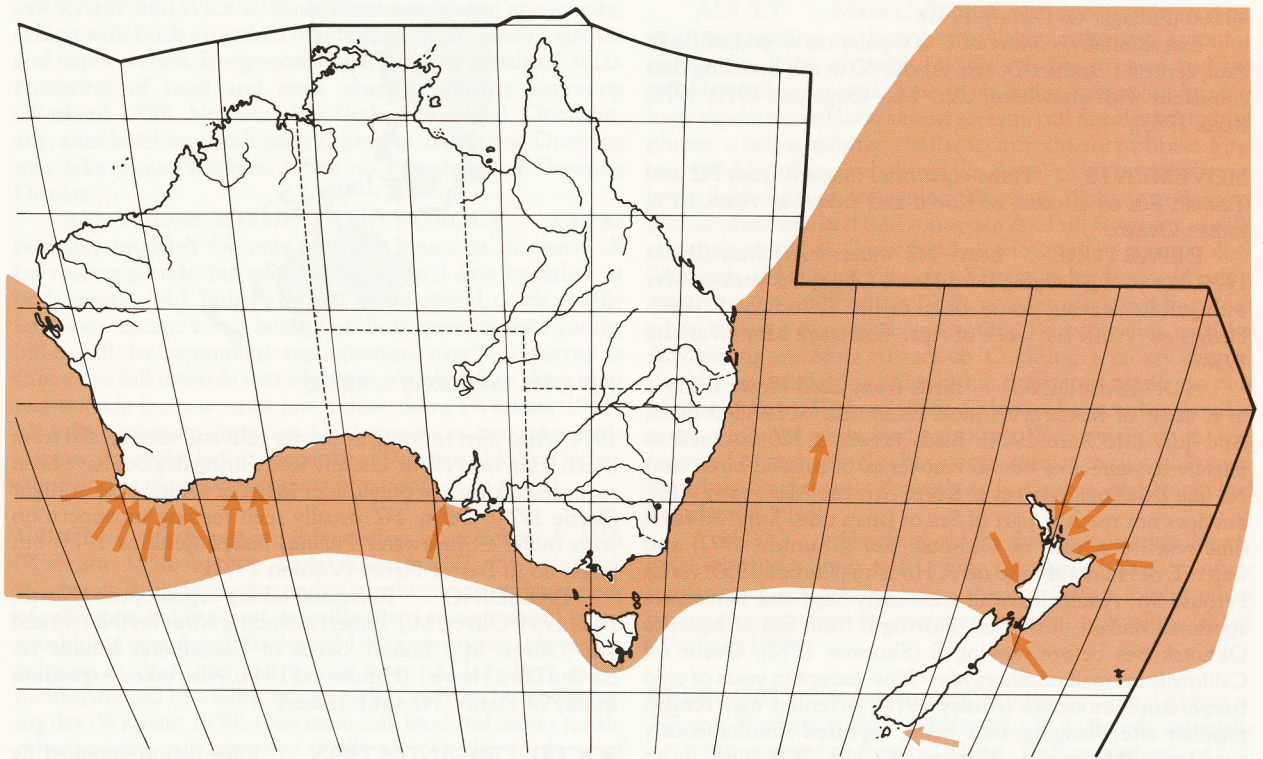
DISTRIBUTION AND POPULATION Pelagic; trans-equatorial migrant; widely distributed across s. Indian and sw. Pacific Oceans in breeding season. Central and n. Pacific Ocean to N of Subtropical Convergence and, in Indian Ocean, NW to Arabian Sea, SE past Maldives and Sri Lanka; also recorded at sea off Ile Amsterdam and Ile St Paul (where

small colony) (Segonzac 1970, 1972; Watson 1975). Breed Ile Saint-Paul, islands off w. and central coast of s. Aust., islands off coast of NI, NZ and Lord Howe I. (Peters).

AUST. Locally common breeding and non-breeding visitor to coastal and pelagic waters of s. Aust., present all months, with smaller numbers migrating and wandering birds recorded at least as far N as 16°S. **Qld.** Passage migrant well E of Qld, with some wandering into Qld seas N to 16°47'S, recorded May, Sept.–Oct., summer reports from se. Qld, Nov.–Feb. of breeding birds foraging from Lord Howe I. (Palliser 1985; Stewart 1984; Storr 1973, 1984). **NSW.** Fairly common, Sept.–May, most records ne. NSW, including breeding birds foraging from Lord Howe I., Nov.–Feb., scarcer se. NSW and other months (NSW Bird Rep. 1982; McGill 1961; Morris 1975; Morris *et al.* 1981; Smith & Chafer 1987; Aust. Atlas). **Vic.** Uncommon June, Sept., Nov.–Apr., some beachcast after storms; single record from Queenscliff 1884, but scattered records since 1956, including Portland, Barwon Heads, Phillip I., Wilsons Promontory and Port Fairy (Cooper 1974; Learmonth 1966; Vic. Bird Rep. 1981; Wheeler 1967, 1981; Aust. Atlas; Vic. Atlas). **Tas.** Uncommon summer visitor, rare other months, most records s. Tas. (Sharland 1981; White 1985). **SA.** Common se. SA, Oct.–May, scarce other months; breeding birds from WA may wander in some numbers into SA waters in summer; commonest shearwater in waters N of Kangaroo I. during summer, there largely replacing Short-tailed Shearwater, which forages farther out to sea; small colony found at Smith I. near se. tip of Eyre Pen., Nov. 1982 (Condon 1969; Parker *et al.* 1979; Robinson *et al.* 1986; Aust. Atlas). **WA.** Common, breeding confined to s. coast, Nov.–Apr., common visitor se. WA waters Oct.–Apr., rarely May, w. coast passage migrant Apr.–May and Aug.–Oct. N to c. 25°S (Serventy & Whittell 1976; Storr 1987; Storr & Johnstone 1988; Aust. Atlas).

NZ Breeds Hen and Chickens, Mercury and Alderman Is, Karewa I. and possibly others in Hauraki Gulf and Bay of Plenty, East I. (off East C.), main Sugar Loaf I. (off New Plymouth), Trio and Titi Is (Cook Str.) and islets off Taranaki





coast, Sep.–May, also ranging around NI, S to Foveaux Str. and E to Chatham Is, rare or absent other months (Falla *et al.* 1981; NZCL).

LORD HOWE I. Only breeding locality of e. Aust. and presence not confirmed until 1911; colonies formerly more extensive. Non-breeding birds also present in some numbers, recorded Sept.–May; banding returns have demonstrated that during summer, breeding birds forage as far as seas of se. Qld and ne. NSW (Fullagar *et al.* 1974; Hindwood 1940; McKean 1963; McKean & Hindwood 1965).

NORFOLK I. Vagrant: first recorded Nov. 1975 and one found ashore among Wedge-tailed Shearwaters *P. pacificus*, 16 Nov. 1979; may be regular summer visitor from breeding sites on Lord Howe I. and NZ, where absent from more southerly waters Apr.–Sept. (McKean *et al.* 1976; Moore 1985; Schodde *et al.* 1983).

BREEDING Important known breeding stations:

AUST.

SA
Smith I., near se. tip of Eyre Pen., small colony, found Nov. 1982

WA
Islet off C. Hamelin ('Cosy Corner')
Seal I. (off C. Leeuwin)
Sandy I. (near Pt D'Entrecasteaux)
Chatham I.
Saddle I.
Stanley I.

Mutton-bird I.
Eclipse I.
Breaksea I.
Michaelmas I.
Doubtful Is
Recherche Arch.

(largest colonies: Charley, Long, Remark, Frederick, Mondrain, Barrier, Gulch, Wickham and Daw Is)

NZ Information supplied by G.A. Taylor, D.V. Merton and D.J. Butler.

NI — ne. coast:

Chickens (Marotiri) Is

Lady Alice I.

Whatupuke I.

Coppermine I.: 10s of 1000s; largest population in this group.

Hen (Taranga) I.: 100s pairs

Mercury Is

Middle I.: 1000s pairs

Green I.

Stanley I.: possible; 1 pair on stack off Stanley

Double I.: few pairs

Red Mercury I.: possibly

Korapuki I.: several 100s

Alderman Is

Ohinau I. (Ohena)

Little Ohinau I.: possibly.

Karewa I.: many 1000s pairs.

East I. (off East C.).

NI — w. coast

Kauwahaia I., Bethell's Beach: few pairs.

Motumahunga I., New Plymouth: 100s pairs.

Main Sugarloaf I.

COOK STR.

Main I., Trio Is: few pairs

Titi I.: 220 pairs.

LORD HOWE I. Now restricted to lowland forest areas round settlement, mostly in palm forests along e. side from Ned's Beach, S to Transit Hill; also Old Settlement Bay. Colonies cover 46 ha; breeding population estimated as 20 000-

40 000 (Fullager & Disney 1981).

Extraliminally, colony of c. 600 pairs on n. end of Ile St Paul, central s. Indian Ocean. About 30 m asl, breeding data consistent with elsewhere; Oct.-May (Segonzac 1970, 1972; Roux 1985).

MOVEMENTS Trans-equatorial migrant from NZ and Tasman Sea to e. coast of Korea and from sw. Aust. to n. Indian Ocean.

DEPARTURE Leave NZ waters early May (Bartle 1974), last young fledging Lord Howe I. by third week in May with adults leaving some days earlier (Hindwood 1940). Fledges sw. Aust. last week of Apr.-first week May (Warham 1958).

NON-BREEDING Birds from Lord Howe I. move to e. coast of Korea with most recoveries of banded birds, Apr.-July (McClure 1974). Birds breeding NZ assumed to migrate to same area but all recoveries of banded birds near NZ (see Banding). Arrives at Korea Str. late Mar.-early Apr., but does not reach n. part of Sea of Japan until June. At same time reaches s. part of Okhotsk Sea (Shuntov 1972) and waters E of Hokkaido and off n. Honshu (Kuroda 1955) via La Perouse Str. Adults leave all areas early Sept. but immatures appear to remain until Oct., moving E from Sea of Japan to Okhotsk Sea before moving S (Shuntov 1972). Occur off California in small numbers May-Nov. except in years of cold temperature anomalies (Ainley 1976). Juveniles may remain together after fledging, four being captured simultaneously near Japan (McKean & Hindwood 1965). WA birds fly to Arabian Sea and Gulf of Oman, where they arrive by 25 May, probably taking direct great-circle route (Bourne & Radford 1961) via s. Indian Ocean where large numbers present mid-late Apr. (D.W. Eades) and passing Laccadive and Maldiva Is (Bailey 1972), rather than clockwise circuit of Indian Ocean postulated by Gibson-Hill (1953). Observations by Shuntov (1972) of large numbers flying S between Sulawesi and Moluccas in Oct. suggest that at least part of WA population also travels to Pacific.

RETURN First arrive Lord Howe I. early Sept. with majority by Oct. (Hindwood 1940); to colonies off NZ about 1 Oct. (M.J. Imber) and to Eclipse I., sw. Aust., by third week Sept. (Serventy & Whittell 1976) though first seen SA waters 8 Aug. (Parker & May 1982). Appear to return to same breeding burrow each year (Warham 1958, n=1).

BREEDING Recoveries during breeding season suggest Lord Howe I. birds feed off e. Aust. coast (McKean & Hindwood 1965) from at least as far N as Stradbroke I., se. Qld (Smyth & Corben 1984) to as far S as Maria I., e. Tas. (D.W. Eades); those from sw. Aust. feed as far N as Bunbury and as far E as SA (Serventy & Whittell 1976). Birds observed off nw. Tas. and w. Vic. Oct.-Jan. and distributed widely across s. Indian Ocean were probably from sw. Aust. (D.W. Eades). Round NZ largely confined to waters off n. SI and NI (Jenkins 1981).

BANDING Returns from Lord Howe I. (ABBBS) summarized Fig. 1. Of returns from birds banded NZ (NZNBS) 18 were > 100 km, all within 645 km, most on NI beaches.

FOOD Poorly known; fish and cephalopods recorded. **BEHAVIOUR.** Food usually taken by pursuit-plunging, some surface-seizing and surface-plunging (Brown *et al.* 1977; Harper *et al.* 1985) and pursuit-diving to 4 m (Falla 1934); often take offal from behind fishing boats (Falla 1934; Bartle

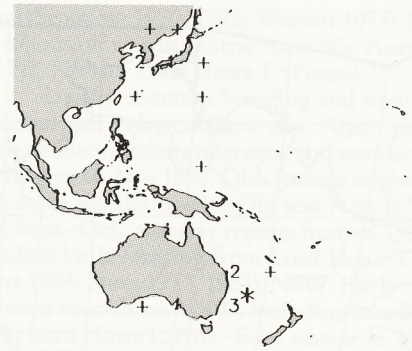


Fig. 1. 31S 159E 10X10 % ABBBS

1974). Also seen running in among gulls and seizing offal from beach (Harrison 1970). Usually feed during day but have been recorded taking live prey under lights of fishing boat at night (Bartle 1974). Off n. NZ usually seen feeding in association with Buller's Shearwater *Puffinus bulleri* (Jenkins 1974) but rarely so in Bay of Plenty (Vooren 1973).

BREEDING Recorded taking cephalopods (North; Falla 1934; Oliver; M.J. Imber) including *Nautilus* (North) and fish (Oliver; M.J. Imber). Seeds of *Caesalpinia bonduc* recorded Lord Howe I. (Hindwood 1946). Also takes *Argonauta* in Bay of Plenty, NZ (M.J. Imber).

SOCIAL ORGANIZATION Information supplied by M.J. Imber. Less gregarious than most other shearwaters; forage singly, but congregate at food, e.g. swarms of euphausiids or small fish driven to surface by predatory fish (M.J. Imber). Form rafts off breeding colonies before flying to colonies at or after sunset (Warham 1958). No information on composition of flocks, but almost certainly of mixed sexes and age classes (M.J. Imber).

BONDS Monogamous; probably long-term or sustained. No information on age at first pairing. No co-operative breeding. Both parents incubate and tend young until fledging.

BREEDING DISPERSION Colonial. No measures of density, but size of colony and distance between nests depend on substrate. Birds defend area round nest-site. No feeding territory.

ROOSTING Nocturnal roosting usual throughout year, probably at sea and certainly in burrows at colonies during breeding season. Arrive at colony at dusk and leave before or at dawn. Diurnal loafing at sea observed throughout year.

SOCIAL BEHAVIOUR Based mainly on Warham (1958). Behaviour difficult to observe because birds nocturnal and mostly in burrows. Displays not conspicuous. Flocks form when feeding, resting, loafing, preening and sleeping; rafting observed in late afternoon off breeding colonies. Possibly forms flocks on migration like other shearwaters.

AGONISTIC BEHAVIOUR No information.

SEXUAL BEHAVIOUR Little information on Advertising, Greeting Displays, Copulation; study in WA, took place after laying and probably after peak of sexual behaviour (Warham 1958). **ADVERTISING.** Breeding colonies very noisy; birds call in flight over colonies and on ground; aerial calling less frequent than from ground (M.J. Imber); calling probably functions in Advertising, Mate Attraction and Greeting.

COURTSHIP BEHAVIOUR. Birds Duet (see Voice) at nest-site, calling with birds crouched beside each other, heads together and napes arched. Reciprocal and apparently ritualized **ALLO-PREENING** of head and neck observed during courtship (Warham 1958). No courtship feeding observed. Occasionally, after hatching, both parents present at nest and Duetting may take place (Warham 1958); no knowledge of Greeting Display.

RELATIONS WITHIN FAMILY GROUP Chicks probably brooded for only first few hours, as in nearly all burrowing petrels, but guarded for up to 3 days by either or both parents (M.J. Imber). In post-guard period, chick usually left alone except when being fed. Both parents feed young, bill-to-bill, by incomplete regurgitation; nestlings *chirrup* as they drive bill towards that of parent. Adults often sleep in or just outside burrow until just before dawn (Warham 1958). No information on desertion. Of three chicks, two sat outside burrow on night before departure (Warham 1958). Fledges alone and is then independent of parents.

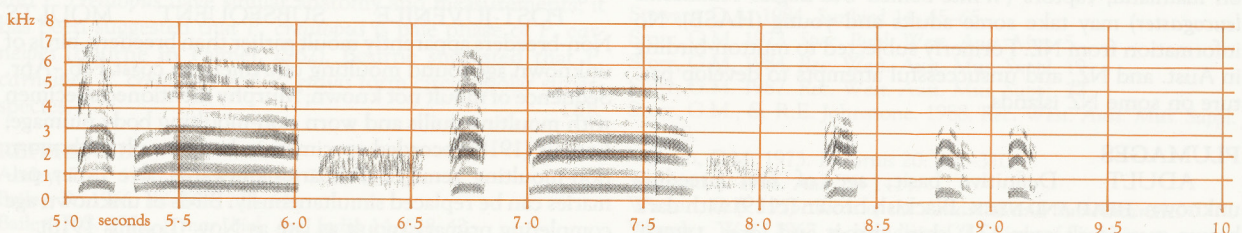
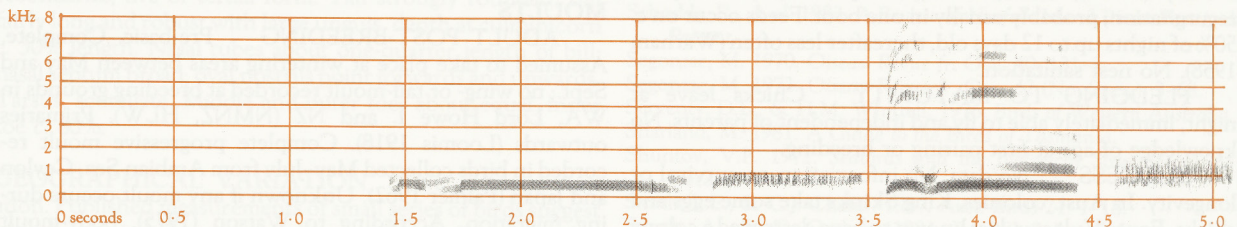
VOICE Little known; information from Eclipse I., WA (Warham 1958) and at Lady Alice I., NZ (M.J. Imber). Warham's study limited to end of incubation period and peak of calling probably past. Generally silent at sea but call when squabbling over food (Hindwood 1945); very noisy at breeding colonies at dusk and just before dawn (M.J. Imber); when incubating and brooding, occasionally call from burrows during day (Warham 1958). One main call, loud and rather harsh; other quieter calls reported. Calls very similar to those of Great Shearwater *P. gravis* and quite similar to those of Sooty Shearwater *P. griseus* (M.J. Imber). Calling restricted to breeding season, over colony and at nest-site. In WA, first birds arrive silently at colony c. 30 min after sunset, quickly followed by large numbers of birds and increasing calling. Indication that aerial activity and calling decrease on moonlit nights (Warham 1958) but statements somewhat contradictory. **Duetting.** Pairs duet using Main Call with no differences between sexes reported; duets infectious, with nearby birds or pairs also calling; calling would peak for a few minutes then die away (Warham 1958). Duetting noted during Courtship and also when both parents at nest tending young. No sexual differences noted. No information on individual or geographical differences. No reports of non-vocal sounds.

ADULT Main Call: brief introductory phrase: *gug, gug, gug* leading to hoarse trisyllabic asthmatic crooning phrase: *ku -kooo -ah*, with middle syllable stressed and last syllable a sob; repeated three to six times, becoming increasingly strident until *kooo* almost scream; call finishes with third phrase: a fading *splutter*, similar to introductory phrase. First two syllables of second phrase (*ku -kooo*) given on exhalation, last syllable (*-ah*) on inhalation (Warham 1958); introductory phrase often omitted (see sonagram A). Full function of calls not clear; noted as Courtship behaviour when given as duet (Warham 1958); probably also Threat as birds would call if disturbed at nest (Warham 1958); occasionally given by parent when arriving at nest to feed young. Probably also used for Advertising and Mate Attraction. **Cackling:** a variety of quiet *Cackles* reported during Courtship Behaviour, similar to calls of broody hen (Warham 1958). **Other calls:** peculiar *gurgling* noises reported when feeding young (Warham 1958). At sea, reported to make single sharp note, similar to that of Pomarine Skua *Stercorarius pomarinus* but more highly pitched (Hindwood 1945).

YOUNG Hatching chicks *cheep* persistently. Newly hatched chicks utter soft *piping*, similar to that of other similar-aged congeners; later, chicks *chirrup* loudly when parent arrives at burrow entrance and continue calling till fed (Warham 1958).

BREEDING Poorly known. Studies by Falla (1934) in n. NZ and Warham (1958) on Eclipse I., WA. Breeds colonially on scrub-covered or forested islands with good depth of soil; associated with Great-winged Petrel in Aust. and NZ (Warham 1958; M.J. Imber), but, having opposed breeding seasons, if one species rears chick, the other is usually prevented from breeding in following season in same burrow (M.J. Imber). Also associated with Sooty and Little *P. assimilis* Shearwaters in NZ. In n. NZ colonies Tuataras *Sphenodon punctatus* frequent burrows (Oliver; M.J. Imber).

SEASON In Aust., from late Sept. to early May (Warham 1958). In NZ, from about 1 Oct. to early May (Falla 1934; M.J. Imber). No precise knowledge of events of breeding cycle but arrival at NZ colonies about 1 Oct.; pre-laying exodus not observed; laying in both Aust. and NZ, last week Nov. to first week Dec.; departure of young, last week Apr. to first week May in Aust. and NZ (Falla 1934; Warham 1958;



Serventy & Whittell 1976; Oliver; M.J. Imber).



SITE In burrows on gentle to steep slopes, rarely on nearly flat ground, in coastal forest or scrub. Burrows 1–2 m long; at Ile St Paul, entrances av. 23.2 cm, 16.4 wide (Roux 1985; n=14). In Aust., sometimes under mats of vegetation (Warham 1958). Same burrows probably used by same birds year after year. Great-winged Petrels, Sooty and Little Shearwaters share area of colony; skinks *Egernia kingii* in Aust. and Tuataras in NZ enter and share burrows (HASB; Oliver). Excavation, density of burrows not recorded.

NEST, MATERIALS In enlarged chamber at end of burrows; entrance of occupied burrows often blocked with plant material. Further details not known except that building occurs at night and that plant material is pulled up and passed over shoulder of building bird (Warham 1958). The same nest or material is used as left by Great-winged Petrels, in burrows previously used by that species.

EGG Elongate ovoid; smooth textured, not glossy; white.

MEASUREMENTS: WA: 69 (60–75; 55) x 46 (38–50) (HASB); 70 (64–76; 46) x 46 (43–50) (Serventy & Whittell 1976).

WEIGHT:

WA: 75 (69–81) (Serventy & Whittell 1976).

LAYING Well synchronized in both Aust. and NZ, most eggs laid within two weeks, last week of Nov., first week of Dec. (Warham 1958; Oliver). No replacement laying. No further information.

INCUBATION By both sexes but share not known. **INCUBATION PERIOD** not determined; HASB gives 60 days, probably overestimated. No further information.

YOUNG Semi-altricial, nidicolous. Hatched with medium-grey protoptile above, light-grey on breast, belly and underwing (HASB). Mesoptile, sooty grey above, whitish below; bill, bluish slate, darker at tip; feet, bluish slate (Oliver). No data on growth or development of feathering. **NESTLING PERIOD:** c. 92 days, without details (Warham 1958). Brooded probably for only first few hours; guarded by both parents for 2–3 days (Warham 1958). Fed by both parents, by incomplete regurgitation, probably usually in one bout. Feeds occur on c. 50% of nights up to 12 days old, thereafter less often (Warham 1958). No nest sanitation.

FLEDGING TO MATURITY Chicks leave at night, immediately able to fly and independent of parents. No knowledge of age at first pairing or breeding.

SUCCESS No data. No information on survival or longevity. In Aust. colonies, King Skinks take some eggs and chicks. Foxes *Vulpes vulpes* known to have destroyed a colony on mainland; raptors (White-bellied Sea-Eagles *Haliaeetus leucogaster*) may take some adults and young (HASB). No information from NZ. Formerly subjected to mutton-birding in Aust. and NZ, and unsuccessful attempts to develop pasture on some NZ islands.

PLUMAGES

ADULT Definitive basic; age of first breeding unknown. **HEAD AND NECK.** Blackish brown (c119) with dark brown-grey (dark grey 121) chin, throat and lores. **UPPER-PARTS.** Feathers blackish brown (c119) with medium-brown (119A-119B) open pennaceous tips. Tips narrow in longest

scapulars, broad elsewhere. Tips get broader with wear, causing scalloped appearance. **TAIL,** black-brown (119). **UPPER-WING.** Alula and all coverts, black-brown (119) with medium-brown (119A-119B) open pennaceous tips. Tips get broader with wear, causing scalloped appearance. Remiges, black-brown (119). **UNDERPARTS,** greyish brown. Feathers, dark grey-brown (greyish 119A) with grey (86) on proximal two-thirds that can be exposed when ruffled. Feathers have very narrow pale grey-brown (119D) tips when fresh; when worn, wider and buff-brown (27–223D). **TAIL,** black-brown (119). **UNDERWING.** Remiges, blackish brown with light-grey (85) gloss in some lights. All under wing-coverts, dark grey-brown (dark 121).

DOWNY YOUNG Protoptile, medium-grey above, light grey on breast, belly and underwing (HASB). Half-grown nestling from Chicken Is, presumably in mesoptile, uniform sooty grey above and below (Falla 1934). Puzzling chick from NZ, with grey-brown (grey 119B) mesoptile on upperparts and head, and traces of brown-white protoptile on hindneck and breast, seems inconsistent with both descriptions.

JUVENILE As adult. None seen this study; assumed to have grey bloom characteristic of dark juvenile shearwaters.

ABERRANT PLUMAGES Partial albinos reported (Hindwood 1940; McKean & Hindwood 1965).

BARE PARTS Based on skins (NMNZ, HLW) and photos in Lindsey (1986), NZRD, and at NZDOC.

ADULT, JUVENILE Iris, dark brown (c21–) to black-brown (119); hazel also recorded (NMNZ). Culminicorn, unguis, and narrow sulcus, dark grey (83) to blackish (82), sometimes with brownish tinge. Rest of bill, pale horn to cream white (c54), sometimes with pale flesh or pink tinge (NMNZ, HLW). Tarsus and feet, fleshy white to pearl-grey (81), usually with dark-grey (c83) or blackish (82) tips to webs and toes; dark tips widest on outer toe. Claws blackish (82), sometimes with light horn or pink bases.

DOWNY YOUNG In protoptile: bill, grey-blue; legs, flesh-grey; webs, flesh coloured (Warham 1958). In mesoptile: bill, fleshy purple, dark at tip; feet, fleshy pink (Falla 1934).

MOULTS

ADULT POST-BREEDING Pre-basic. Complete. Assumed to take place at wintering areas between May and Sept.; no wing- or tail-moult recorded at breeding grounds in WA, Lord Howe I. and NZ (NMNZ, HLW). Primaries outwards (Loomis 1918). Complete progressive moult recorded in birds collected May–July from Arabian Sea, Ceylon and Japan (Palmer 1962). Unknown if any moult occurs during migration. According to Watson (1975), body-moult begins towards end of breeding season.

POST-JUVENILE, SUBSEQUENT MOULTS Non-breeders apparently moult earlier than breeders; birds of unknown age found moulting off American coast Feb.–Apr. Sequence of moult not known; Murphy mentioned specimen with moulting quills and worn non-moulting body plumage; Loomis (1918) recorded specimen in body-moult with worn non-moulting remiges. Primaries outwards, five inner primaries can be replaced simultaneously. Birds of unknown age completing primary moult as late as Nov. (Loomis 1918).

MEASUREMENTS (1) NZ region, definitive, recently

dead (NMNZ). (2) NZ breeding localities, definitive skins (NMNZ).

	MALES	FEMALES
WING	(1) 330 (7.48; 320-338; 3)	327 (7.08; 317-340; 9)
8TH P	(2) 204.3 (3.09; 200-207; 3)	201.9 (4.61; 195-208; 9)
TAIL	(1) 114.2 (3.79; 109-118; 3)	117.0 (3.50; 113-123; 9)
BILL	(1) 41.9 (1.56; 39.9-43.7; 3)	40.6 (1.22; 39.3-43.6; 9)
TARSUS	(1) 56.2 (2.17; 53.5-58.8; 3)	55.6 (1.12; 53.8-57.7; 9)
TOE	(1) 66.5 (1.40; 65.1-67.9; 2)	65.2 (1.28; 63.6-67.9; 9)

(3) WA, definitive skins (HLW). (4) Lord Howe I., definitive skins (Bourne in Palmer 1962). (5) NZ region, definitive skins (Palmer 1962).

	UNSEXED
WING	(3) 321.9 (7.12; 314-335; 9) (4) 314 (309-320; 7) (5) 327 (317-331; 7)
8TH P	(3) 194.1 (4.20; 185-200; 9)
TAIL	(3) 109.0 (1.63; 106-112; 9) (4) 109 (107-112; 7) (5) 115 (108-120; 7)
BILL	(3) 42.0 (1.60; 40.3-44.7; 9) (4) 42.9 (40-49; 7) (5) 41.3 (37-44; 7)
TARSUS	(2) 54.3 (52-58; 7) (3) 54.2 (1.26; 52.5-56.7; 9) (4) 55.1 (53-58; 7)
TOE	(3) 65.3 (1.78; 63.2-68.3; 6)

Additional measurements in Loomis (1918), Hindwood (1945), Segonzac (1970, 1972) and Murphy.

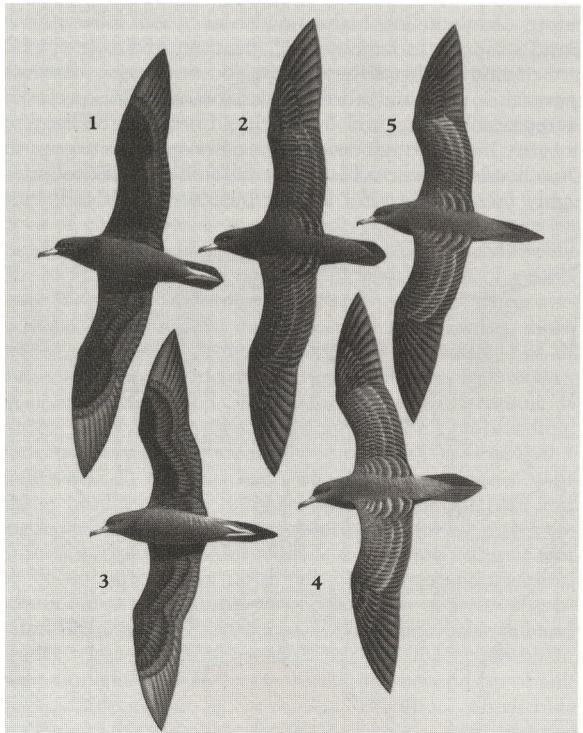
WEIGHTS At NZ breeding colonies 609 g (52.7; 533-692; 9) (NMNZ). At sea in NZ region, Mar.-May 595 (58.3; 561-682; 4) (NMNZ). Male in Arabian Sea, 22 July, 540 g.

STRUCTURE Eleven primaries, p11 minute, p10 longest, p9 0-6, p8 15-22, p7 34-43, p6 57-69, p5 80-92, p4 106-118, p3 130-144, p2 152-167, p1 170-189. Twenty-one secondaries, five of tertial form. Tail strongly rounded. Bill fairly long and robust with large unguis, depth at culminicorn c. 30% length. Nasal tubes about one-quarter length of bill; nasal septum broad; oval nostrils point forwards and upwards. Tarsus, scutellate. Middle and outer toes about equal, inner toe c. 80%.

GEOGRAPHICAL VARIATION No plumage variation. Published measurements of small series of birds suggest birds largest in NZ region, smallest in WA. *Puffinus carneipes* and *P. creatopus* have similar anatomy and measurements; it has been suggested that *P. creatopus* is pale phase of *P. carneipes* (Bourne in Palmer 1962). Bourne suggested that *P. carneipes*, *P. creatopus* and *P. gravis* form circumpolar super-species.

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Volume 1 (Part A), Plate 45

Flesh-footed Shearwater *Puffinus carneipes*

- 1. Adult, ventral
- 2. Adult, dorsal

Wedge-tailed Shearwater *Puffinus pacificus*

- 3. Adult, ventral
- 4. Adult, dorsal, worn
- 5. Adult, dorsal, fresh

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