Marchant, S. & Higgins, P.J. (co-ordinating editors) 1990. Handbook of Australian, New Zealand & Antarctic Birds. Volume 1, Ratites to ducks; Part A, Ratites to petrels. Melbourne, Oxford University Press. Pages 263-264, 355-369; plate 25.

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# 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

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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: Diomedeidae 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.

## References

Bang, B.G. 1966. Acta anat. 65: 305-415.
Bourne, W.R.P. 1976. Pp 403-502. In: Johnston 1976.
Brodkorb, P. 1963. Bull. Flor. St. Mus. biol. Sci. 7: 179-293.
Clarke, A., & P.A. Prince. 1976. J. Exp. mar. Biol. Ecol. 23: 15-30.
Fisher, J. 1952. The Fulmar.
Harper, P.C. 1978. NZ J. Zool. 5: 509-549.

Johnston, R. (Ed.). 1976. Marine Pollution.
Klemm, R.D. 1969. S. Ill. Univ. Monogr. Sci. Ser. 2.
Obst, B.S. 1986. Wilson Bull. 98: 189–95.
Olson, S.L. 1975. Smithson. Contr. Paleobiol. 23.
Swennen, C. 1974. Ardea 62: 111–117.
Timmermann, G. 1965. Abh. Verh. naturwiss. Vereins Hamburg NF 8, Suppl. 1–249.

# 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 Diomedeidae. 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 relation-ships.

(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

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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.

#### REFERENCES

Brodkorb, P. 1963. Bull. Flor. St. Mus. biol. Sci. 7: 179-293. Cox, J.B. 1980. Rec. S. Aust. Mus. 10: 91-121. Fleming, C.A. 1941. Emu 41: 134-55. Harper, P.C. 1980. Notornis 27: 235-86.

Imber, M.J. 1985. Ibis 127: 197-229.

Kuroda, N. 1954. On the classification and phylogeny of the order Tubinares, particularly the shearwaters (Puffinus), with special consideration on their osteology and habit differentiation. Tokyo.

Murphy, R.C., & J.M. Pennoyer. 1952. Am. Mus. Novit. 1580.

Olson, S.L. 1975. Smithson. Contr. Paleobiol. 23. Voous, K.H. 1949. Ardea 37: 113-22.

## Macronectes giganteus Southern Giant-Petrel

COLOUR PLATE FACING PAGE 368

Procellaria gigantea Gmelin, 1789, Syst. Nat. 1: 563; based on 'Giant Petrel' of Latham, 1785, Gen. Synop. Birds 3: 396, Pl. 100 — Staten Island off Tierra del Fuego.

The generic name means the long swimmer ( $\mu\alpha\kappa\rho\delta\zeta$  long +  $\nu\eta\kappa\tau\delta\zeta$  swimming), and the specific, obviously, refers to the bird's size.

OTHER ENGLISH NAMES Giant Fulmar, Glutton, Mollymawk, Mother Carey's or Sea Goose, Nelly, Stinker, Stinkpot, Vulture of the seas, Bone-shaker.

#### MONOTYPIC

FIELD IDENTIFICATION Length 85–100 cm; wingspan 150–210 cm; weight: male 5.0 kg, female 3.8 kg. Very large, fulmarine petrel, size of small albatross, with massive pale yellowish-green bill; in flight, heavy-bodied with hunchbacked jizz, wings held stiff and disproportionately small and narrow; tail short and rounded. Dimorphic; dark grey-brown with whitish head and neck (dark morph) or pure white with scattered black feathers (white morph). Sexes alike in plumage; male markedly larger. No seasonal plumage differences. Dark-morph immatures have distinct plumage stages.

DESCRIPTION ADULT. Dark morph. Head, neck and upper breast, dirty white, freckled grey-brown on crown and nape (head almost pure white in oldest birds), irregularly mottled grey-brown, varyingly mottled on lower breast and flanks; upper- and underwing, grey-brown, except for pale leading-edge of inner wing, and pale silvery-grey bases of inner primaries and some secondaries on underwing. Bill massive, with prominent nasal tube extending over three-fifths of length; yellowish-horn to yellowish-green with nails of both mandibles forming pale-green tip; black marking on ungues varies in extent. Iris, brown, grey-brown or pale grey; becomes paler with age. Legs and feet, blackish, grey-brown or dull blue-grey. White morph (up to 15% in some populations; Shaughnessy 1971). Wholly white except for some dark feathers randomly scattered throughout plumage. Bare parts as dark morph. **Leucistic birds** (0.3%; Conroy *et al.* 1975). Entirely white, lacking dark mottling of white morph. Bill, pink with uniformly horn-coloured nail on upper and lower mandibles. Legs and feet, pink. JUVENILE. **Dark morph**. Entirely glossy sooty black, sometimes with white flecks round head; juvenile plumage soon fades to brownish black and greybrown, particularly on back and wings. With age, head and neck become more mottled and then whiter, starting with cheeks and throat. Birds 7–8 years old normally have mottling round face (Hunter 1983b). Juveniles of white and leucistic morphs similar to adults.

SIMILAR SPECIES Dark morph likely to be confused with Northern Giant-Petrel M. halli. Distinguished at all ages by bill appearing uniformly coloured at distance (green colour of tip visible only at close range), lacking dark tip typical of M. halli. Juvenile and immature plumages similar to those of M. halli. Adult plumage usually distinguished from that of M. halli by whitish head and neck (in M. halli, hindneck and crown often darker than foreneck and upperbreast, giving hooded appearance), contrasting with uniformly dark body (in older M. halli, ventral area often markedly lighter than upperparts). Distinguished from Sooty Phoebetria fusca and Light-mantled Sooty P. palpebrata Albatrosses by massive pale bill, short round tail, much stockier jizz and heavier flight; from juvenile **Wandering Albatross** *Diomedea exulans* by dark, not white, underwing, and jizz. White and leucistic morphs distinguished from **Wandering** and **Royal** *D. epomophora* **Albatrosses** by white, not dark, remiges; white morph also by diagnostic random mottling.

Pelagic, marine and even coastal waters, from Antarctic to Subtropical Zone; range largely overlaps with that of *M. halli.* Flight appears laboured with generally 4–5 flaps followed by stiff-winged glide; approach effortless gliding of albatrosses only in very strong winds. Aggressive scavenger, gathering in numbers at dead cetaceans, seals and seabirds; with *M. halli*, only petrel to feed on land on subantarctic and Antarctic islands. *Contra* Johnstone (1974), regularly follow ships (Devillers & Terschuren 1980; Hunter 1983b; J-C. Stahl), but possibly less persistent follower than *M. halli.* Usually silent at sea.

HABITAT Marine; Antarctic to subtropical waters. Adults present round Antarctic breeding colonies all year (Conroy 1972; Johnstone et al. 1973; Mougin 1975); immatures disperse from breeding colonies, some moving into Subtropical Zone and dispersing E with prevailing winds. In summer, mainly over Antarctic waters, widespread S to packice and Antarctic continent. In Ross Sea, range from Antarctic continent to 3.0 °C sea surface-temperature isotherm: in early summer, most abundant over continental slope; in late summer, uniform distribution from continental slope N to Polar Front; also occur S to Ross Ice Shelf at low densities (Ainley et al. 1984). No preference for pack-ice of particular density (Zink 1981a,b; Ainley et al. 1984); but may avoid crossing extensive ice sheets, which dampen sea swell and inhibit soaring (Ainley et al. 1984). Abundant in pack-ice near penguin colonies (Ainley et al. 1978). In summer, also over subantarctic waters near breeding islands in Atlantic and Indian Oceans (Johnstone 1974; Voisin 1980; J-C. Stahl), subantarctic to s. subtropical waters on Argentinian Shelf (Cooke & Mills 1972; Devillers & Terschuren 1980) and off NZ (McOuaid & Ricketts 1984) and cold eastern boundary current off South America (Downes et al. 1959; Ingham 1959). In winter, range extends from Antarctic to subtropical waters; over pack-ice mainly when conditions mild and leads open in sea-ice (Rootes 1988). Possibly mostly N of 50°S in winter as rare in waters of s. Indian Ocean (J-C. Stahl) while common off South America (Rumboll & Jehl 1977), South Africa (Brooke & Sinclair 1978), Aust. (Aust. Atlas) and NZ (Sibson 1969). Occur in both pelagic and inshore waters (Cox 1976; Marchant 1977; Milledge 1977; Jouventin et al. 1982). Attracted to land at sewage outfalls (Milledge 1977). Scavenge ashore; at Iles Crozet, distribution shifts towards land in summer, when birds frequent penguin and seal colonies (Jouventin et al. 1982).

Breed on Antarctic Continent, Pen. and islands, and on subantarctic islands and South America. In s. Antarctic zone, nest in exposed snow- and ice-free coastal areas; rocky bluffs, outcrops, ridges, slopes, mounds, raised beaches, open flats, edges of plateaux or offshore rocks (Mougin 1968; Voisin 1968; Conroy 1972; Johnstone *et al.* 1973; Cowan 1979); from 5 to 120 m asl (Conroy 1972). Colonies often sited near steep drop or on slope for easy take-off (Mougin 1968; Conroy 1972; Johnstone *et al.* 1973). In Terre Adélie, colony faces prevailing wind; exposure assists take-off and prevents snow drift over nests (Mougin 1968); at Signy I., drifting snow kills chicks in sheltered nests (Conroy 1972). At n. localities, colonies on open vegetated flats, hill sides or ridge tops; avoid tussock-grass at Iles Crozet and S. Georgia (Voisin 1968; Hunter 1984a). Extralimitally, in dense vegetation at Gough I. (Johnstone *et al.* 1976), Isla Noir (Clark *et al.* 1984); on sandy beaches on Falkland Is (Murphy); on rocky open terrain on Isla Ance off Argentina (Humphrey & Livezey 1983).

At sea, feed mainly on surface, occasionally diving to shallow depths. In pack-ice, roost on icebergs and snow slopes at sea edge (Ainley *et al.* 1978).

If colony persistently disturbed, site may be abandoned; establishment of field station and banding activities at Signy I. led to desertion of colony of 200 breeding pairs within 8 years and decrease in breeding population on island (Conroy 1972; Rootes 1988); at Dumont d'Urville, population decreased from 69 pairs in 1969 to two pairs in 1980 after establishment of base, with some pairs moving to nearby island (Jouventin *et al.* 1984); breeding population on this island may be exterminated by construction of airstrip.

**DISTRIBUTION AND POPULATION** Pelagic range circumpolar, from Antarctica to *c*. 20°S (winter); imperfectly known because most records of giant-petrels at sea not separated to species. Breed between 40–60°S on subantarctic and Antarctic islands, Antarctica and South America.

In summer, mostly in Antarctic waters S of 60-63°S in South Pacific (Zink 1981a; Ainley et al. 1984; Wanless & Harris 1988) and se. Indian Oceans (Johnstone 1974; Mochizuki & Kasuga 1985); N to 53°S in Heard I. region (Stahl 1987). Also coastal waters off Iles Crozet (J-C. Stahl), near Macquarie I. (Johnstone 1974), NZ waters (McQuaid & Ricketts 1984), Humboldt Current N to 28°S (Ingham 1959), Argentinian shelf N to 38°S (Cooke & Mills 1972). Distribution in Scotia Sea uncertain. Recorded south to 78°S in Ross Sea (Ainley et al. 1984). In winter, Antarctic waters round S. Georgia (Hunter 1984c), S. Orkney (Conroy 1972) and S. Sandwich Is (Eakin et al. 1986); giant-petrels seen at edge of pack-ice (Sziji 1967) assumed to be giganteus, which occasionally visit Antarctic breeding grounds in May-June and return July (Mougin 1968; Johnstone et al. 1973). Little information on mid-ocean distribution; very rare north of 50°S in s. Indian Ocean (J-C. Stahl). Off w. South America, from Straits of Magellan to 15°S (Sladen et al. 1968; Jehl 1973); off Argentina, N to 36°S (Jehl 1974). Regular South Africa (Brooke & Sinclair 1978). N to c. 24°S off Aust. (Aust. Atlas); may outnumber M. halli in NSW (Milledge 1977) and probably in SA (Cox 1976) and off n. NZ (Sibson 1969).

Immatures range further N than adults in winter and spring, when predominant off Argentina (Jehl 1974; Rumboll & Jehl 1977), Aust. (Milledge 1977) and NZ (Sibson 1969); disperse further N than M. halli, as recoveries from Mauritius and New Guinea (Hunter 1984c), Fiji (Gartshore et al. 1988), Tahiti (Downes et al. 1954), Easter I. (Orton 1963). In summer, immatures predominant (82%) in Ross Sea (Zink 1981a), Argentinian and Chilean waters (Devillers & Terschuren 1980). Only one valid n. hemisphere record: adult off Ushant, France, Nov. 1967 (Meeth 1969).

BREEDING Breed along coast of Antarctica and at islands S of Antarctic Convergence (Johnstone 1977). Sympatric breeding range with M. halli: Macquarie I., Iles Crozet, S. Georgia, Marion and Prince Edward Is (Johnstone 1977; Hunter 1983b); possibly Iles Kerguelen (Hunter 1984b). At Macquarie I., breeding c. 6 weeks later than M. halli, thus acting as reproductive isolating mechanism (Carrick & Ingham 1970; Johnstone 1977). At Signy I., S. Orkney Is, M.



halli breed 5-6 weeks earlier than M. giganteus (Hunter 1984b). Localities and population estimates in Table 1. Extralimitally, breed Gough I. (Williams 1984), Diego Ramirez Is (Schlater 1984), Isla Noir (Chile; Clark *et al.* 1984), Chubut Province, Argentina (Humphrey & Livezey 1983) and Falkland Is (Croxall *et al.* 1984a). Giant-petrels (possibly giganteus) formerly bred Tristan da Cunha, extirpated *c.* 1870 (Hagen 1952). Giant-petrels breeding Isla de los Estados (Staten I., Argentina) probably giganteus, according to breeding schedule (Humphrey & Livezey 1983). Falkland Is population decreased following shooting of adults and destruction of eggs, as giant-petrels considered menace to sheep (Woods 1975). Population on Heard I. decreased from 4000 pairs in early 1950s (Downes *et al.* 1959) to 2350 pairs in 1980 (Johnstone 1982). Colonies near wintering bases have disappeared or decreased at Signy I. (Conroy 1972) and Pointe Géologie (Jouventin *et al.* 1984).

**MOVEMENTS** Partially migratory; some adults resident at most sites (except Antarctica where rare visitor May-June; Mougin 1968) but numbers drop during winter at all sites; immatures and some adults disperse widely, probably

#### Table 1

Locality	Year	Numbers (pairs)	Reference
Bouvetøya	1981	ica 12 10 jo de te man vidente	Aussenessen Alessen
Prince Edward Is	<1984	1747	2
	1984	c. 3000	3
Iles Crozet	1981-82	1017	4
Iles Kerguelen	1984-87	3-5	5
Heard I.	<1984	2350	2
Macquarie I.	1977	4000	6
S. Georgia	<1984	5000	7
S. Sandwich Is	<1984	800	7
S. Orkney Is	<1984	8755	7
S. Shetland Is	<1984	6185	7
Antarctica	persuperangel hour one broke		stored oave angeota
Enderby Ld: Holme Bay, Rookery Is			8
Davis: Hawker I.		30-40	9
Windmill Is: Frazier Grp	1956	2.50	10
Terre Adélie			10
Pte Géologie	1980-82	9-11	4
C. Crozier		1	11
Antarctic Pen.	<1984	1125	7

References: (1) Watkins (1981); (2) Williams (1984); (3) S. Hunter; (4) Jouventin *et al.* (1984); (5) Weimerskirch *et al.* (1989); (6) Rounsevell & Brothers (1984); (7) Croxall *et al.* (1984b); (8) Conroy (1972); (9) Johnstone *et al.* (1973); (10) Ingham (1959); (11) Woehler & Johnstone (1988).



circumnavigating Antarctica. At S. Georgia, birds usually return to natal colony but one recorded breeding Signy I. (Hunter 1984b); at Signy I., young birds first return to natal colony but may finally breed elsewhere on island (Conroy 1972).

DEPARTURE Juveniles leave Davis late Mar. to early May though adults recorded all months (Johnstone *et al.* 1973); S. Georgia, mean departure 8 May (Croxall & Prince 1987); Anvers I., about 3 May (Holdgate 1963; Parmelee & Parmelee 1987); Pointe Géologie, 12 Apr.–10 May (Mougin 1968). Signy I., mean fledging date, 12 May (5.3 days; 27 Apr.– 30 May; 387) (Conroy 1972); Iles Crozet, 5 Mar.–5 May (Voisin 1968, 1976); Heard I., Apr. (Downes *et al.* 1959); Macquarie I., May (Johnstone 1977). Though some birds present Signy I. all year, failed and pre-breeders leave end Apr., breeding adults, early May and fledgelings by early June, leaving only small population of unknown age and status through rest of winter (Conroy 1972) but perhaps all breeding birds (Rootes 1988).

NON-BREEDING Movement in winter extensive and complex; first-year birds apparently travel farther N than adult giganteus or immature M. halli (Sibson 1969); first-year birds apparently undertake circumpolar movements, birds from Signy I. dispersing eastwards: mean interval between fledging and recovery of Signy I. chicks: se. South America, 1.3 months; South Africa, 1.9; WA, Aust., 2.4; NSW, Aust., 3.4; NI, NZ, 4.3; SI, NZ, 5.5; sw. South America, 9.6 (Conroy 1972). Movements of pre-breeding birds after first year uncertain but most not seen at natal colonies until 6–7 years after fledging (Conroy 1972); perhaps largely pelagic during these ages though several recoveries indicate they sometimes visit other breeding colonies, occasionally staying to breed (Hunter 1984a). Waters off se. Aust. may be particularly important wintering grounds (Araya 1973; Jones 1973; Hunter 1984a; Woehler & Johnstone 1988).

RETURN Most adults returning to Signy I. in July were failed breeders from previous season (67.5% of 92 individually identified birds), rest having bred successfully previous season though most of these return in Aug. (Conroy 1972). Numbers at Davis also increase during July (Johnstone *et al.* 1973) and birds arrive Pointe Géologie, 30 June–12 July (Mougin 1968).

BREEDING Foraging range from S. Georgia in summer estimated at 189 km (Croxall & Prince 1987), 469 km from Palmer I., travelling 23.9 h at 39.2 km/h (Obst 1985) and 30 km from Davis (Green 1986). Six of seven birds carrying satellite transmitters from Palmer Stn travelled up and down Antarctic Pen. but one moved over 2000 km into South Pacific Ocean, W of Antarctic Pen. (Parmelee *et al.* 1985; Strikwerda *et al.* 1986; Parmelee & Parmelee 1987) and col-



our-dyed birds at S. Georgia seen 200 km away immediately before laying and during incubation. In South Pacific and se. Indian Oceans in summer, mainly occur S of Antarctic Convergence (Johnstone 1974); but present at C. Crozier most years only between 4 Jan.-14 Feb. (Ainley *et al.* 1978).

BANDING Returns from Casey Stn, Antarctica (ABBBS), S. Shetland Is (CEMAVE, SOPAN, VH), Campbell I. (NZNBS) and Marion I. (SABRU) summarized Figs 1–4. Nearly all recoveries of chicks within year of fledging, most within first winter (Conroy 1972; Johnstone *et al.* 1973; Weimerskirch *et al.* 1985; Parmelee & Parmelee 1987; Woehler & Johnstone 1988). Dates of recovery indicate e. circumpolar movement during first year though there may be some w.

movement from Signy I. to e. coast South America immediately after fledging (Conroy 1972). Breeding adults banded Signy I. recovered coastal South America and NZ (Conroy 1972). Most notable recoveries: one banded near Palmer Stn as chick, recaptured off Fiji at age 6 months and again when 10 years old at nest near Palmer (Parmelee & Parmelee 1987); one banded Bird I., S. Georgia, as nestling, recovered Mauritius (Hunter 1984c); one banded Bird I., S. Georgia, recovered Gulf of Papua, PNG, 10–12 weeks after fledging (Hudson & Conroy 1975); one banded Heard I. as nestling, recovered Tahiti (Downes *et al.* 1954); one banded Frazier Grp, Wilkes Land, as nestling, recovered Easter I. after 7 months (Orton 1963).





FOOD Opportunist scavenger and predator; in summer at least scavenge primarily penguin carcasses. BEHAVIOUR. At sea, food taken largely by surface-seizing; also scavenge on land. Usually approach food by swimming across water after alighting nearby (Murphy) and catch live birds by wing and batter them against water before eating them. Disable birds by battering them with outstretched wings (Harper 1987). Albatrosses approached while asleep; neck seized and head forced beneath surface until bird drowned (Cox 1978); viscera consumed after belly exposed, though group can open back of albatross (Barton 1979). Cephalopods usually taken by surface-seizing, being secured with unguis of bill, shaken vigorously, then swallowed whole or chopped into small pieces (Harper 1987); euphausiids scooped from surface (Obst 1985); also reported to attack humans in water (Murphy). Possibly do not dive from surface, unlike M. halli (Harper 1987). On land, walk strongly, if awkwardly (Prince & Morgan 1987). Attack seal carcasses during first 3-4 days after death via anal orifice, flanks immediately behind fore-flippers and sometimes behind scapulars (Hunter 1983a). Will take portions of penguin from beside feeding Leopard Seal Hydrurga leptonyx (Downes et al. 1959) and most penguins in diet may be dead (Bonner & Hunter 1982) or injured (Johnstone 1977) animals first attacked by seals. Apparently locate food by smell (Murphy) and feed chicks both day and night, though fewer feeds given 24:00-03:00 than in other periods (Hunter 1983a). Follow ships regularly (Hunter 1983b; J-C. Stahl; contra Johnstone 1974).

NON-BREEDING In Drake Passage (3; Linkowski & Rembiszewski 1978) penguin predominated, Euphausia superba present in two stomachs, Themisto gaudichaudii and algae in one each; at King George I., S. Shetland Is, faeces contained euphausiids (Jablonski 1985); thought to take mostly fish off S. Georgia during winter (Hunter 1983a); seen killing then eating Cape Petrel Daption capense (Harper 1987), immature Black-browed Albatross Diomedea melanophrys (Cox 1978) and immature Yellow-nosed Albatross Diomedea chlororhynchos (Barton 1979). At Marion I. in winter, males regularly kill and scavenge chicks of King Penguins Aptenodytes patagonicus (S. Hunter).

BREEDING Summarized Table 2. At Bird I., S. Georgia (Hunter 1983a) food of chicks <20 days old almost entirely liquid, probably with high lipid content, with the little solid matter mostly unidentifiable. Food of chicks >20 days old, 52% liquid (19, 128). Of solid matter (Table 1), penguins were mainly adult Macaroni Penguins Eudyptes chrysolophus, some Gentoo Penguins Pygoscelis papua; no. euphausiid crustaceans in samples: for males 120 (66; 25-250; 11), for females 162 (117; 40-450; 12); mammals were Fur-Seals Arctocephalus gazella 3.3% wt., 5% freq., other birds were Common Diving-Petrel Pelecanoides urinatrix, South Georgian Diving-Petrel P. georgicus, Blue Petrel Halobaena caerulea, Antarctic Prion Pachyptila desolata, Thin-billed Prion P. belcheri, Wilson's Storm-Petrel Oceanites oceanicus, Greater Sheathbill Chionis alba, Great Skua Catharacta skua; cephalopods (nine beaks) incl. Kondakovia longimanna 22.2% no., 505 g, Martialia hyadesi 22.2, 104, Galiteuthis glacialis 55.6, 72.0 g; fish mostly Nototheniidae and other foods incl. jellyfish of 30, 75 and 110 g and crustaceans probably consumed by accident. Diet differed between years and sexes, changes in diet of penguin being inversely related to availability of euphausiids, males taking more penguin and fewer euphausiids than females.

At Macquarie I. (310 samples: adult regurgitations 32%,

chicks 58%, boluses 10%; Johnstone 1977) penguins mostly Eudyptes chrysocome, E. schlegeli, rarely Aptenodytes patagonicus; other birds Grey Petrel Procellaria cinerea 0.7% freq., White-headed Petrel Pterodroma lessonii 1.0, Antarctic Prion 2.2, unident. prions 1.3, Sooty Shearwater Puffinus griseus 0.3, Short-tailed Shearwater P. tenuirostris 1.6, unident. feathers 11; mammals were Southern Elephant Seal Mirounga leonina, rabbit Oryctolagus cuniculus; cephalopods Onychoteuthidae/Gonatidae 3.2, Histioteuthis 0.6, Nototodarus sloani 2.3, Cranchiidae 1.3; crustaceans mysidaceans Gnathophausia 4.2, amphipods 0.6 incl. Hyperiidea 0.3, Gammaridea 0.3, isopods Anurops 0.6, prawns/shrimps 4.2; other foods incl. unident. carrion 60, kelp 4.

At Signy I. (167 samples, 71 adults [66.2% regurgitations, 33.8% from dead birds], 96 chicks [66.2% regurgitations, 33.8% from dead birds]; Conroy 1972) mammals were Weddell Seal Leptonychotes weddelli, Southern Elephant Seal; non-euphausiid crustaceans incl. amphipod Eurythenes magellanicus, other food vegetable matter 3% freq. Also recorded scavenging fin-whale Balaenoptera physalus, and killing jellyfish Desmonema gaudichaudi and Wilson's Storm-Petrel and having remains of Cape Petrel and Southern Fulmar Fulmarus glacialoides near nest-site (Conroy 1972).

At Davis Stn (60 regurgitations; Green 1986) penguins were Adelie Penguin Pygoscelis adeliae; other birds Southern Fulmar 10, Snow Petrel 10, Antarctic Petrel 1.7, Cape Petrel 1.7, Wilson's Storm-Petrel 1.7; mammals Weddell Seal 11.7, Southern Elephant Seal 3.3. Other samples from same site (96 regurgitations; Johnstone *et al.* 1973) contained cephalopods, penguins, Cape Petrel, Antarctic Petrel *Thalassoica ant arctica*, Southern Fulmar and prions. Adults and chicks at Terre Adélie (18 stomachs; Mougin 1968) birds were mostly Adelie Penguin, some petrels; other items, plants 6.

Over continental slope of **Ross Sea** (two stomachs, birds probably incubating; Ainley *et al.* 1984) cephalopods 93.6% wt. (*Psychroteuthis glacialis* 1.5% no., 50% freq.; *Galiteuthis glacialis* 1.5, 50; unident. 3.0, 50), crustaceans 6.4 (*Euphausia superba* 92.3, 50).

At Heard I. commonest item regurgitated small intestines of birds, then cephalopods, also remains of adult and chicks of penguins, seal skin and fish, terns, diving-petrels and remains of many bird species including conspecifics (Downes et al. 1959). At Gough I., commonly fed on carcasses of Amsterdam Island Fur-Seal Arctocephalus tropicalis (Cooper 1983) and in Antarctica will take young Emperor Penguin Aptenodytes forsteri (Prévost 1953).

Table 2. Breeding diet of M. giganteus

	% w	rt.		% freq		
	1	1	2	3	4	5
BIRDS	81.9	71-93	80-87	75-85	82-100	70
PENGUINS	4.7	71	80	75	82	13113
OTHER	7.2	22	7	10	10-25	
CRUSTACEANS	10.7	22	13	49-54	22	
EUPHAUSIIDS	10.7	22	13	49		
FISH	0.8	4	6	3	13	11
CEPHALOPODS	1.7	12	36	49	3	11
MAMMALS	3.3	5	1	15	12-15	28
OTHER	1.8	4	60-64	3-8	6	

(1) Hunter (1983a); (2) Johnstone (1977); (3) Conroy (1972); (4) Green (1986); (5) Mougin (1970).

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INTAKE At Bird I. total food fed to chicks differed between sexes: males received 75.0 kg (n=4), females 54.7 kg (n=9); though both sexes fed meals of similar size, frequency of meal declined more rapidly for females than males: 0-20 days: mean meal wt. 145 g (18), feeding freq. males 1.82 meals/day (0.67; 28), females 3.29 (1.11; 7); 21-40 days: 265 (57), males 2.10 (1.18; 21), females 2.00 (1.12; 28); 41-60 days: 361 (49), males 2.43 (1.01; 14), females 1.75 (0.75; 12); 61-80 days: 427 (47), males 1.88 (0.81; 16), females 1.33 (0.90; 31); 81-100 days: 340 (23), males 1.57 (0.85; 14), females 1.20 (1.30; 5) (Hunter 1983a). At Signy I., size of meal increased from mean 4.2 g/day during first 5 days to 153 g at 60-70 days (Conroy 1972). Food supplies at Bird I. sufficiently abundant during summer to allow breeding and moult to occur simultaneously (Hunter 1984b).

**SOCIAL ORGANIZATION** Gregarious on land. At sea, less gregarious than M. *halli*; often observed solitarily or in small groups (2–4), but will congregate round sources of food (Johnstone 1974), fishing vessels (Jehl 1974), sewage outfalls (Milledge 1977) and outfalls of freezing works. When feeding on land, often associated with M. *halli* (Johnstone 1979).

BONDS Sustained monogamous, although divorces occur in a few pairs (Hunter 1984b). Young birds return to colonies when 5–7 years old (Lacan *et al.* 1969; Conroy 1972). Age at first breeding from 6 years on (Hunter 1987; Woehler & Johnstone 1988). Breeders re-establish pair-bond during pre-egg period (July–Oct.). Pre-breeders present at colonies Dec.–Mar. at Signy I. (Conroy 1972). At Macquarie I., sexual displays throughout year, including nest-building by subadults in Feb. (Warham 1962). Both parents incubate and tend young until c. 22 days after hatching (Mougin 1968; Conroy 1972; Hunter 1984b); male undertakes higher proportion of incubation and guarding of chicks (Hunter 1984b). Juveniles disperse out to sea for 3–4 years after fledging (Hunter 1984a; Woehler & Johnstone 1988).

BREEDING DISPERSION Colonial. Ten to 170 nests in colony; usual distance between nests 3–5 m, with minimum distance of 1.5 m on Macquarie I. (Warham 1962). Radius of 1.5–2.0 m round nest-site defended, particularly by chick, which spits proventricular oil at intruder.

ROOSTING Some breeding colonies partly occupied during winter, but many birds roost on coastal beaches and round lakes on Macquarie I. Groups of resting and preening or washing birds on sea or lakes through day. During breeding season, unoccupied birds spend much time in or round colonies and on adjacent water; no known differences between sexes.

**SOCIAL BEHAVIOUR** Detailed studies by Bretagnolle (1988, 1989), form basis account of agonistic and sexual displays; study by Warham (1962) made before separation of *giganteus* and *halli*. Partial data also in Voisin (1978) and Johnstone (1979). Birds nervous of humans and easily disturbed, but easy to observe because they are large and live in open habitat. Many aspects of social behaviour identical to those of *M. halli* (Voisin 1978); some sexual displays similar to those of Southern *Fulmarus glacialoides* and Northern *F. glacialis* Fulmars (Warham 1962). Minimum distance between individuals in roost 1.5 m. When breeding, parents sit alongside chicks and partners beside each other.

AGONISTIC BEHAVIOUR Alarm Display. Bird sitting on nest stretches neck upwards, bill bent downwards,

feathers of head and neck ruffled; display mostly used by males against conspecific flying 5-20 m overhead; highly communicative; version suggesting shyness observed at approach of human observer 20-50 m away. Low-intensity Attitude (sitting or standing). Bird on nest has neck stretched upwards bill bent forward, head and neck feathers ruffled; performs head-sweeping movement of 120°, head turning a further 90° at end of each sweep, accompanied by whinnying and growling calls; mostly by adult males and well-grown chicks. Mostly response to conspecific moving at close range. When it approaches closer, bird stands up, with neck almost at right angle to body, and performs similarly. Both lowintensity attitudes may be prelude to pecking. THREAT DIS-PLAYS. Stretched Head Threat. Sitting bird ruffles neckfeathers and emits growling calls; aggressive response to moving conspecific and agonistic displays; equivalent to Forward Threat, but bill open and agonistic call given; most aggressive response of brooding adults (mostly males) and chicks on nest, often leading to oil-spitting. Adults feeding in presence of others may indulge in elaborate threat displays: Sealmaster Posture: dominant bird tilts tail upwards vertically with tailfeathers fanned out, wings outspread with tips arched downwards; feathers of head, neck and back ruffled. Display also used when victorious birds return to sources of food, serving to discourage others that have moved in while challenge being settled. Subordinate birds feeding at same carcass keep wings folded and tail feathers closed and lowered. Retreat only means of preventing or stopping attack. Upright Threat. Neck arched, with bill pointed downwards and feathers of nape ruffled, head waved vigorously from side to side, tail tilted vertically and wings outspread with tips arched downwards; response to displays by potential or actual aggressor; individual and territorial proclamation, warning approaching bird that fight may ensue. Challenger may run at dominant bird (Forward Threat) or display in standing or squatting position, facing any direction. Defending bird may retreat or adopt similar posture and attack. FIGHTING. Combat can be lengthy, with bills interlocked and bodies pushed together, straining upwards. Bird usually wins if it grasps back of opponent's head (Warham 1962). Loser moves well away from disputed carcass and squats down or sits out on water. Both Warham (1962) and Johnstone (1979) considered dominance as function of hunger, and that dominant birds are continually replaced by challengers as former become satiated. APPEASE-MENT POSTURE. Like Alarm Display, but bill held upward and feathers not erected; Submissive Display mostly used by females on nest in response to moving congeners or agonistic displays.

SEXUAL BEHAVIOUR AERIAL DISPLAY: seen throughout year. Bird glides, with wings arched downwards, legs lowered and webbed feet spread, tail fanned, neck outstretched, neck feathers ruffled, head raised and may be waved sideways; loud whinnying (or neighing) call emitted. In this posture, bird will rise a few metres losing speed until it stalls, then descend again in short curve picking up speed. COURT-SHIP usually initiated by Head-raising: head and bill lifted 45° above horizontal, bill partly open; a distinct version involves also stretching of neck; serves as temporal marker for beginning of courtship sequence. Courtship sequences include following displays. Sexual Low-intensity Attitude: as Low-intensity Attitude of Alarm Display but sweeping movement of lower amplitude and feathers not ruffled; partial agonistic display appearing when partners bring heads closer to each other; paired with Bill-fencing, when bills fenced 6-

12 times per display. Bill-touching: display looks like a kind of kiss, often seen just after Bill-fencing; little ritualized display, barely modified feeding behaviour. MUTUAL ALLOPREENING: of head, throat and flanks. Four stages of COURTSHIP recognized: (1) partners little synchronized, physically separated (Bill-touching and mutual preening rare), low aggressive intensity; female very shy (numerous appeasement postures) but initiating most sequences; (2) sequences become more complex, partners more synchronized, closer to each other (maximum of Bill-touching and Mutual Preening) resulting in increasing aggression (including Low-intensity Attitudes and Upright Threats); male initiates as many sequences as female; (3) pair at closest physically, minimum of agonistic displays, sequences less complex, partners synchronized (male and female courtships similar); (4) as preceding, but increased aggression (Low-intensity Attitudes, Upright Threats) as copulations occur without warning (copulation usually does not complete courtship) and high rate of incomplete copulations. Courtship of pre-breeders identical to stage (1) but more movement and Low-intensity Attitudes. COPULATION. Just before copulation, male usually initiates Pre-mount Billing. On mounting, male holds bill vertically down and rubs it rapidly across female's bill. Male's wings partly spread and tail sways sideways. Female thrusts bill up into feathers on male's throat, breast or flanks at intervals. Male spreads wings towards climax, then stops movements of bill and swings tail sideways to make cloacal contact. Attempts at copulation can last 5-10 min, but not possible to distinguish effective and ineffective mating. Copulation recorded by Warham (1962) before and after female laid eggs. On Signy I., Conroy (1972) recorded copulation within 12 h of laying, but mating normally took place before pre-laying exodus by females.

**RELATIONS WITHIN FAMILY GROUP** Warham (1962) recorded chicks being shaded for 15-24 days at Macquarie I. but did not distinguish separate guard-stage. At Signy I., Conroy (1972) found average guard-stage 21.9 days (17-26) of which brood-stage averaged 18.9 days. After guardstage, attendance by parents declines until c. seventeenth day, after which parents rarely seen at nests; no proper desertion period and chicks may be fed up to day of fledging (S. Hunter). Chicks beg for food by stroking or pecking at parent's bill and head, usually calling at same time; older chicks aggressively bill-fence with parent to stimulate regurgitation (S. Hunter). Feeding by incomplete regurgitation directly from parent's bill into that of chick; both parents feed young. Call of newly hatched chick is quiet peep changing to deep guttural snorting during non-guard-stage; not known if adults communicate vocally with young. Adults allopreen chicks during brooding.

**VOICE** Reasonably well known. Descriptions by Murphy, and Warham (1962) before separation of species; sonagrams and functions discussed by Bretagnolle (1988). In-

formation supplied by J-C. Stahl. Usually silent at sea, except when squabbling over food; noisy throughout most of year on breeding grounds. Sexual or individual differences not studied so far; no regional variations known. Calls apparently similar to those of *M. halli*, except for display call which, in *M. giganteus*, seems softer and more high-pitched (Voisin 1968). NON-VOCAL SOUNDS. Bill-clicks during Pre-mount Billing, audible some 100 m away (Warham 1962).

ADULT Agonistic Call (Bretagnolle 1988): described as 'nauseated gurgle' by Murphy; uttered both by chicks and adults combined with threat of oil-spitting; usually, but not necessarily preceding oil-spitting; short call lasting c. 0.25 s. Whinnying (Murphy; Bretagnolle 1988) or Neighing Call (Warham 1962): long-drawn expiratory tremulous cry; uttered by adults only, both sexes; agonistic meaning, frequency directly related to level of aggression; emitted during Upright Threat, Low-intensity Attitude and Aerial Display. Growling (Bretagnolle 1988): low guttural rattling note (sonagram A), which may be uttered by adults of both sexes when alone, but more often preceded by Whinnying; uttered during Upright Threat, Low-intensity Attitude and Stretched Head Threat; agonistic meaning. Cat-like Mewing accompanies mutual display of breeders. Braying Call (Warham 1962) emitted during Low-intensity Attitude; soft braving during mutual display. Variety of gulping, rasping and squawking sounds reported in older chicks and adults when handled.

YOUNG Vocalizations confined to chicks include **Piping**, emitted from time to time by brooded, newly hatched chicks (Murphy), and **Food-begging Call** (Bretagnolle 1988): short, c. 0.25 s, emitted every 0.5–0.8 s when chick being fed. Also variety of gulps, rasps and squawks as adult.

**BREEDING** Studied at S. Georgia (Hunter 1984b), Signy I. (Conroy 1972), Iles Crozet (Voisin 1968, 1976) and Pointe Géologie, Terre Adélie (Mougin 1968, 1975); study at Macquarie I. (Warham 1962) made before separation of species. Partial data for Heard I. (Downes *et al.* 1959). Information supplied by J-C. Stahl. Colonial breeder on open flats or hillsides of subantarctic and Antarctic islands, Antarctic continent and South America.

SEASON Arrival at colonies: Pointe Géologie 30 June-12 July; Signy I. begins July, most late Aug.; S. Shetland Is, late July (Jablonski 1986); Iles Crozet, early Sept.; Heard I., 23 Sept. Some birds present throughout year in most localities. Pre-laying period, 105 days (Mougin 1975). Laying. Gough I., late Aug.-mid. Sept. (Johnstone *et al.* 1976); Iles Crozet, 24 Sept.-17 Oct., most before 5 Oct. in one season, first egg, 24 Sept. (3; 20-28 Sept.; 5 years); Macquarie I., 27 Sept.-19 Oct. (Johnstone 1978); Marion I., 18 Sept.-20 Oct. in two seasons (Burger 1978); Heard I., first egg mean 20 Oct. (2; 17-12 Oct.; 5 years); Pointe Géologie, first egg mean 23 Oct. (4; 20-31 Oct.; 7 years), laying period in one season 20



Oct.-15 Nov.; Falkland Is and Argentina, late Oct. (Woods 1975; Humphrey & Livezey 1983); S. Georgia, mean 8-11 Nov. (4.5-4.6; 30 Oct.-24 Nov.; 3 years); Signy I., first egg mean 5 Nov. (3; 30 Oct.-11 Nov.; 29 years) (Rootes 1988), mean 13 Nov., (4; 4-26 Nov.; 24); King George I., begins early Nov., most by 13 Nov. (Jablonski 1986). At Signy I., males usually arrive first. Nests visited for periods of 1-4 days (Mougin 1968). Most copulations before pre-laying exodus of females, which lasts c. 12 days (Conroy 1972). At Signy I., first pre-breeders arrive mid-Dec. (Conroy 1972). Departure of young: Macquarie I., late Mar.-Apr.; Heard I., Apr.; Pointe Géologie, 12 Apr.-10 May; Signy I., 12 May (5 days; 27 Apr.-30 May; 387). At Signy I., last non-breeders and failed breeders leave in Apr., most breeders in early May.



d) Heard I.

SITE At n. localities, nests established on exposed flats, gentle slopes or ridge tops, usually in open vegetation (Deschampsia meadows, Azorella); not common among tussock-grass as in M. halli; in dense vegetation (tussock, tree ferns) at Gough I. (Swales 1965; Johnstone et al. 1976) and among scrub at Isla Noir (Clark et al. 1984). Also on sandy beaches at Falkland Is (Murphy). On Antarctica and surrounding islands, nest on open gravel areas and rocky outcrops. At Signy I., 93% (n=127) of pairs used same nest-site in three seasons; at Iles Crozet, new nests built every year and movements of up to 3 km in consecutive seasons; at Pointe Géologie, only 29% of breeders (n=17) at same nest in three seasons. Some competition for nest-sites with Wandering Albatross at S. Georgia; possibly with penguins at Signy I.; slight association with Wandering Albatross and M. halli at Iles Crozet.

NEST, MATERIALS Nest usually low, cup-shaped, size depending on availability of material. Usual material includes tussock-grass, *Acaena*, moss in Subantarctic, small stones and bones in Antarctic. Some nests simply scratched in grass, *Azorella*, or bare peat or sand, or mere depression in rock. External diameter 50–150 cm, height c. 20 cm; diameter of cup 45 cm, depth of cup 10–25 cm. Nest built by both sexes (Conroy 1972); maintained during incubation and by chick. Material gathered round nest. Building activity during prelaying period; during Mar. by failed breeders and non-breeders (Conroy 1972). EGGS Rounded ovate to elongated ovate (Murphy); finely pitted to extremely rough; white. MEASUREMENTS:

Falkland Is 101.7 (94.5–108.1; 4) x 64.7 (62.6–66.0) (Murphy)

S. Georgia 105.1 (3.7; 96.2–112.6; 49) x 65.8 (1.8; 61.7–69.4) (Hunter 1984b)

Signy I.  $104.9 \pm 4.0 \ge 65.7 \pm 2.2$  (Conroy 1972)

King George I. 105.7 (96.6–115.1; 108) x 66.4 (57.4–70.8) (Jablonski 1986)

Iles Crozet 105 (101–110; 12) x 68 (60–74) (Voisin 1968)

Pointe Géologie 105.7 (97.2–114.3; 8) x 66.5 (64.7–67.8) (Mougin 1968)

WEIGHTS:

S. Georgia 260.6 (10.6; 242-274; 15) (Hunter 1984b)

Signy I. 250.6 ± 17.8 (Conroy 1972)

King George I. 224.5 (170.0–270.0; 108) (Jablonski 1986) Pointe Géologie 268 g (253–283; 2) (Mougin 1968)

CLUTCH-SIZE One. Two eggs result from laying by two females (Conroy 1972).

LAYING Not well synchronized. No replacement laying; at S. Georgia, 26.9% of breeders did not nest again in following season.

INCUBATION By both sexes. At Signy I., average 11 shifts, with males having longer shifts (6.4 days on average) than females (5.4 days); shortest, first by female 2.1 days; longest, first by male 8.3 days (Conroy 1972). At S. Georgia, average of 12.7 shifts, 54.2% of incubation by male; shortest shift, first by female 1.7 days; longest, sixth and eighth by male, 7.1 days. At Pointe Géologie, shifts of 3–4 days during second half of incubation. At Iles Crozet, partner often present at nest during incubation. INCUBATION PERIOD. Iles Crozet, 63 days (62–65; 4); Pointe Géologie, 59.0 days (2.0; 55–61; 10); Signy I., 60.1 days (1.3; 56–63; 37); S. Georgia, 60.6 days (1.5; 57–66; 90).

NESTLING Hatching takes few hours to 4 days; chipping up to 4 days before hatching. Young chick, light grey with crown slightly darker, not patterned as M. halli (Voisin 1968); white-phase chicks have white down. Natal down replaced after 2 weeks; first feather sheaths after 30 days (Conroy 1972). NESTLING PERIOD. S. Georgia, males 123.2 days (5.0; 115-132; 15), females 117.0 days (5.6; 105-126; 18); Signy I., 118.5 days (5.1; 107-128; 21); Pointe Géologie, 116 days (104-128; 23), but year to year variations. Chick attended by both parents. Brood-stage: S. Georgia, 18.4 days (2.2; 14-23; 22); Signy I., 18.9 days (n=37), shifts of 2.4 days (1-6); Pointe Géologie, 17 days (15-19; 3). Guard-stage: S. Georgia 2.4 (2.2; 0-7; 22). Total brood- + guard-stage: Point Géologie, 22 days (14-27; 15); Signy I., 21.9 days (17-26; 37). Brood- and guardstage shared equally by both sexes; parents return in adverse weather at end of guard-stage (Conroy 1972). Chick fed by incomplete regurgitation; chick inserts beak at right angle into that of parent; individual feeds last c. 10 s (Conroy 1972). Chick's usual defence against predators is oil-ejection, recorded from age of 6 days onwards (Conroy 1972).

GROWTH At S. Georgia, weight at hatching 182.7 g(12.4; 105–202; 24); maximum weight, male 6370 g(120% ad. weight), female 4960 g (128%) after 80–90 days; weight at fledging, male 5610 g(106%), female, 4430 g(114%). At Signy I., weight at hatching 161.4 (11.8; 150–170; 7); maximum weight, male 6970 g (141%), female, 5890 g (153%), after 60–100 days; weight at fledging, male 4840 g (98%), female 4020 g (104%). At Iles Crozet, maximum weight 6920 g (151%) after 70–80 days, weight at fledging 5850 g (128% ad. weight). At

Point Géologie, weight at hatching 155 g; maximum weight 5215 g after 78 days; on average, weight at fledging 3865 g.

FLEDGING TO MATURITY Independent of parents at fledging. Age at first return to colonies: Pointe Géologie, earliest 5 years (Lacan *et al.* 1969); Signy I. earliest 2.3 years, mean 6.7 years, males from 5 years onwards, females from 6 years onwards. Age at first breeding: Signy I. minimum females 4 years, males 7 years, average *c*. 10 years (Croxall 1982); S. Georgia, minimum 6 years, peak, males 7 years, females 8 years; Macquarie I., earliest 6 years, peak 9–11 years (Woehler & Johnstone 1988); Pointe Géologie, 8–13 years (Lacan *et al.* 1969).

SUCCESS S. Georgia, eggs 87.7% (6.0; 81.1-93.0; 3 years, 171 eggs), chicks 82.1% (14.6; 65.2-91.1; 3 years, 152 chicks); total success 69.9% (4.5; 65.5-75.6; 4 years, 2048 eggs). Signy I., eggs 60.3%, chicks 68.6%, total 41.4% (174 eggs in one season). Pointe Géologie, eggs 59.4% (10.4%; 50.0-77.3; 5 years, 122 eggs), chicks 88.6% (10.2; 75.0-100.0; 5 years, 73 chicks), total 52.4% (10.4; 40.0-68.2; 122 eggs). Iles Crozet, eggs 42.2% (2.3; 38.9-45.5; 2 years, 51 eggs). Heard I., total c. 80%. Mean annual adult survival: S. Georgia 90%, slightly higher in males than females; Pointe Géologie 36%. Most loss of eggs just after laying and before hatching. Main causes of loss: desertion and subsequent predation by skuas and sheathbills, infertility (8.8% at Signy I.), damage by incubation, severe snow-storms. Maximum loss of chicks first 2-6 weeks after hatching; main causes trampling by parent, starvation, exposure during severe weather, predation by skuas. Human disturbance round wintering bases has led to disappearance or reduction of colonies at Signy I. and Pointe Géologie.

**PLUMAGES** Dimorphic. At Signy I., S. Orkney Is, age of first breeding 4–6 years in males; 7–8 in females, with average c. 10 years (Conroy 1972; Croxall 1984). At Bird I., S. Georgia, males 6–8 years; females 8 years (Hunter 1984b). At Macquarie I., 6 years (Woehler & Johnstone 1988). For diagrammatic representation of morphs see Conroy et al. (1975).

ADULT Dark morph. HEAD AND NECK vary: often has mottled appearance, or entirely white; see figure in Johnstone (1974) illustrating extent of white on head and neck. Crown, dark brown (121), feathers narrowly tipped light greybrown (119D) to brown (119B). Hindneck, dark brown (121) with open pennaceous dark-brown (119A) tips; concealed bases of feathers, white and sometimes exposed. Short white filoplumes on crown and nape. Forehead, white; feathers tipped dark brown (121); with wear, tips lost or narrow. Lores and malar region, white varyingly tipped dark brown (121); tips broader at ear-coverts. Chin to base of foreneck, white to dull-white, varyingly tipped pale dark-brown (121); rachis, light grey-brown (119D) or entirely white. UPPERPARTS. Mantle, dark brown (c121) with broad pale dark-brown (121) open pennaceous tips. Back, rump and scapulars similar, but tips narrower; scapulars have rounded webs; grey-black (82) rachis obvious on mantle and back; when worn, tips of feathers, dark brown (119A) to light grey-brown (119C). Upper tail-coverts similar to mantle-feathers. TAIL, black-brown (119); rachis, dull-white basally, merging to grey-black (82) distally. UPPERWING. Remiges, black-brown (119), paler on inner webs; rachis, cream-yellow basally merging to grey-black (82). All coverts, including alula, dark brown (121) with slightly paler open pennaceous tips. When worn, tips on coverts, including alula, dark brown (119A) to light grey-brown (119D). UNDERPARTS. Breast-feathers, pale dark-brown (121),

with open pennaceous light grey-brown (119C) tips; concealed bases, white merging to dark brown (121); rachis, grey-black (82). Breast to vent, dark brown-grey (80) to pale brown-grey (79) with open pennaceous light grey-brown (119D) tips; rachis, light grey-brown (119D). Flanks, dark brown (121) with broad open pennaceous pale dark-brown (121) tips; rachis, grey-black (82) and obvious. Under tail-coverts, similar to breast-feathers but paler; rachis, light greybrown (119D). When worn, tips on underparts, dark brown (119A) to brown (119B) to dull-white. Axillaries, dark brown (121); rachis, grey-black (82). UNDERWING. All greater coverts, dark brown-grey (80). Rest of coverts, pale dark-brown (121); grey-black (82) rachis obvious.

White morph. Entirely white, apart from scattered darkbrown (119) feathers on body, except on tail; has dark-brown feathers on wing (Cox 1976; *contra* BWP).

DOWNY YOUNG Protoptile, all light grey, almost white with slightly darker cap; white morphs hatch with white down. After c. 2 weeks, mesoptile appears, uniform grey (Voisin 1968). First feather-sheaths appear after 30 days, initially on belly and breast. Underparts completely feathered by 55 days; last down lost on face about 100 days (Conroy 1972). Full details of plumage changes to juvenile in Downes *et al.* (1959), Warham (1962), Mougin (1968) and Conroy (1972). Mesoptile, pale brown-grey (79). On skins at MV, down retained last on head, neck and mantle.

JUVENILE Dark morph. Plumage coloration similar to Sooty Shearwater *Puffinus griseus*; underwing differs: greater coverts, brown-grey (79); rest of coverts, pale darkbrown (121). White morph. Similar to adult white morph (Lowe & Kinnear 1930).

SUBSEQUENT PLUMAGES Dark morph. Gradually like adult, becoming whiter on head, beginning at throat; some birds have pale leading-edges to wing (Johnstone 1974); some birds may still have dark plumage at 8–13 years (Carrick & Ingham 1970; Conroy *et al.* 1975).

ABERRANT PLUMAGES Albinistic and leucistic birds recorded (Conroy 1972; Cox 1976); leucistic birds lack scattered dark-brown (119A) feathers on body (Conroy et al. 1975); and regarded as homozygous white; differ from albinos in having dark-brown irides (Shaughnessy & Conroy 1977). Interbreeding with M. halli reported at Marion I. (Burger 1978) and Macquarie I. (Johnstone 1978), though no eggs hatched successfully. Successful interbreeding has occurred at S. Georgia (Hunter 1982). Incidence of hybridization: at Bird I., S. Georgia, 1.5% of breeding pairs; at Marion I., two pairs in 1490 birds, 0.1% (Burger 1978); at Macquarie I., 1 pair in c. 5000, 0.02% (Johnstone 1978). All known pairings involve male giganteus paired to female halli (Burger 1978; Johnstone 1978; Hunter 1982). Chicks from interspecific pairs hatch at dates intermediate between those of the two species. Suggested that indeterminate birds are hybrids (Hunter 1982); plumages of these birds have not been adequately described; Hunter (1982) states that chicks show characteristics of both species, without further information, and also that bare parts differ. Falla (1937) suggested that grey heads and necks of some adults were accentuated by bleaching from feeding at carcasses of dead seals and that light-headed birds were result of bleaching action of seal-blood. Warham (1962) showed that colour of feathers was not changed after prolonged immersion in blood.

BARE PARTS Based on photos in NZRD, Lindsey (1986) and NZDOC Library, except where stated. For ad-

ditional details see Johnstone (1971, 1974) and Conroy *et al.* (1975).

ADULT Iris, dark brown (219); varies through freckled greyish brown to pale grey (Johnstone 1971, 1974); in white morph, dark brown (219). Some asymmetry in colour of iris: one iris pale grey, other dark brown (Johnstone 1974); unknown at what rate colour of iris changes; for details of frequency of colours at Macquarie I., see Johnstone (1974). Bill and nasal tube, sphincter-pink (6); ungues, light brown (223D) with light green (159), tipped dark olive-brown (129); colour of bill apparently varies: pale yellow-green, pink-ochre or pale horn. Legs and feet, dark grey (83); in white morph, dull bluegrey to pink-grey (Johnstone 1974).

DOWNY YOUNG Iris, dark brown. Bill, dull yellowish brown; ungues, lucent green; colour of ungues apparent when 2–3 weeks old (Johnstone 1974). Legs and feet: in some white morphs, pale greyish flesh; most, pale blue with flesh-coloured webs (Warham 1962). In leucistic morphs: iris, dark brown; feet, pink (Warham 1962; Conroy 1972). At Marion I., newly fledged birds said to have white eyelids; bill, dull-yellow; gape, pink (Rand 1954).

JUVENILE, IMMATURE Apparently like adult (Falla 1937; Voisin 1968; Johnstone 1974).

ABERRANT BARE PARTS Leucistic birds have uniformly horn-coloured bill and pink feet (Conroy *et al.* 1975). Hybrids with *M. halli* at S. Georgia (see Aberrant Plumages and Geographical Variation) have bills weak horncolour throughout, lacking dark-red tip of *M. halli* or palegreen tip of *M. giganteus*. Hybrid chicks have bill rather paler and less yellowish than *M. halli* chicks and lacking both reddish tip that some of these show and green tip of *M. giganteus* chicks (Hunter 1982).

MOULTS Based on Hunter (1984a), except where stated.

ADULT POST-BREEDING Complete; primaries moult outwards. Moult synchronic in both wings; during wing-moult, two or more feathers lost simultaneously. At Bird I., S. Georgia, males start primary moult before females, in late Oct.-early Nov.; females, Dec.; initiation dates vary; 16 weeks separation in females; in males most moult in c. 4 weeks; 5% of population start moult later. Males start primary moult at time of laying; females at time of hatching, c. 60 days later; most do not start until chick hatched. Both sexes moult significantly earlier in relation to nesting cycle of M. halli. Rate of replacement varies with sex and stage of breeding cycle. In males, primary moult starts with two or more, often three, innermost primaries shed simultaneously; then feathers lost singly; number of actively moulting primaries decreases to mean of 0.6 (3 weeks after mean hatching date); some suspended moult; active moult restricted to one or two primaries at a time. In females, two feathers normally dropped at a time, rest singly during chick period. No data available to indicate whether males and females shed feathers at rapid rate at a time when chicks reach 13 weeks after hatching. Failure of nest caused birds to start primary moult; in addition they moulted 3-4 feathers concurrently in active moult. Primary moult not uniform between sexes. In non-breeders, estimated minimum duration 132 days; in breeders, estimated maximum 333 days. Estimate of duration of moult in successful breeders, 228 days in males; 189 days in females; longer in males than females and longer than in M. halli. Secondary moult begins half-way through primary moult; sequence unknown; not all secondaries moulted annually. Tail-moult requires further study;

possibly not all rectrices moulted annually. Small amount of body-moult throughout season; may be continuous (Hunter 1984a). Body-moult starts on abdomen about time of laying and continues with breast, head, neck and back. Primary moult begins after hatching of chick. In n. colonies (e.g. Macquarie I.; Warham 1962), breeding 1 month earlier than in s. colonies (Signy I.; Conroy 1972), but primary moult 2 months earlier (Dec. compared to Feb.). Moult may not be complete when adults leave colony, last stages possibly slow as in Northern Fulmar. Some records of moult during winter; May and Aug. (Lowe & Kinnear 1930), June (Falla 1937). Finished at colony on return (Conroy 1972). Tail-moult starts when p6 or p7 growing, probably ending at same time as wing (Stresemann & Stresemann 1966). Failed breeders start earlier than successful breeders; immatures earlier than adults.

POST-JUVENILE Immatures probably start moult during Nov.; 2–5 feathers lost initially; primary moult complete by Mar. or Apr. (Hunter 1984a).

MEASUREMENTS All from Voisin & Bester (1981); methods unknown. (1) Antarctic Pen. and adjacent islands, skins. (2) Frazier Is. (3) Iles Crozet, skins. (4) Macquarie I. (5) Signy I., S. Orkney Is. (6) Terre Adélie, skins. (7) Falkland Is, skins. (8) Gough I., skins.

		MALES	FEMALES	
WING	(1)	510.0 (25.17; 465-552; 8)	499.8 (13.44; 477-515; 8)	
	(2)	542.0 (8.54; 530-550; 7)	512.0 (7.18; 500-518; 5)	*
	(3)	533.2 (14.1; 492-555; 15)	494.9 (23.85; 460-522; 7)	*
	(4)	552.0 (10.66; 534-577; 20)	526.8 (8.52; 513-540; 21)	*
	(5)	553.5 (10.86; 534-571; 13)	518.9 (15.21; 498-541; 13)	*
	(6)	534.2 (15.45; 517-549; 5)	506.3 (493-514; 3)	
	(7)	507.3 (6.18; 500-515; 4)	484.0 (9.45; 470-500; 10)	*
	(8)	507.5 (485-535; 4)	478, 491	
BILL	(1)	98.5 (2.02; 96-102; 9)	89.1 (3.97; 85.5-95; 8)	*
	(2)	98.9 (2.29; 96-103.1; 7)	88.0 (2.09; 85.8-90.4; 5)	*
	(3)	104.7 (3.97; 97-111; 16)	89.1 (3.28; 84-94; 8)	*
	(4)	101.9 (2.15; 95.8-106; 20)	89.7 (2.41; 84.6-93.5; 21)	*
	(5)	101.4 (2.45; 97.4-108.2; 66)	87.4 (3.00; 82-97; 73)	*
	(6)	98.2 (4.39; 92-104; 6)	85.2 (83-89; 3)	
	(7)	98.9 (2.98; 95-102; 4)	84.1 (3.05; 80-89; 9)	*
	(8)	95.2 (2.36; 91.5-98.5; 17)	83.3 (2.90; 79.5-88.0; 12)	*
BILL D	(1)	34.3 (3.31; 30.5-39; 8)	31.7 (3.95; 26.5-35; 8)	
	(3)	33.0 (1.89; 30-36; 12)	28.6 (0.99; 27.5-30.0; 7)	*
	(6)	30.1 (1.80; 27-32; 5)	27.5 (27-28; 3)	
	(7)	30.5 (1.68; 28.5-32.5; 4)	25.9 (1.06; 27.5-24.5; 8)	*
	(8)	30.0 (1.08; 28.5-32; 17)	27.3 (0.69; 27-28.5; 12)	*
TARSUS	(1)	94.7 (5.12; 85-101; 9)	89.0 (3.29; 84-93; 6)	*
	(2)	99.3 (2.34; 95.8-102; 7)	90.4 (2.19; 87.8-93.8; 5)	*
	(3)	102.4 (2.64; 97-107; 14)	95.1 (6.83; 88-111; 8)	*
	(4)	102.7 (1.71; 99.5-105.3; 20)	94.2 (1.88; 90.1-98.0; 21)	*
	(5)	96.3 (1.69; 94-99; 13)	87.1 (5.45; 82-95; 13)	*
	(6)	96.0 (3.29; 91-99; 6)	92.0 (89-94; 3)	
	(7)	93.4 (1.38; 92-95; 4)	83.1 (2.99; 77-86; 10)	*
	(8)	95.3 (2.02; 92-99; 17)	88.3 (3.11; 85-95; 12)	*

Nelly and Dewart Is, Antarctica, adults, live; methods unknown (ABBBS).

Human Bo	UNSEXED	hill and the second second second
WING	529.7 (16.03; 500-550; 13)	Shitubhi hawata (DA
BILL	93.6 (5.99; 85.3-103.1; 13)	
TARSUS	95.2 (4.83; 87.8-102; 13)	

Only one species of giant-petrel recognized before Bourne & Warham (1966) separated M. halli. Carrick & Ingham (1970) and others confirmed separation. Measurements before 1966 (e.g. Murphy; Glauert 1937–38; and others) of little use, unless from allopatric breeding colonies or of white birds. Additional measurements in Bourne & Warham (1966), Voisin (1968, 1976, 1982), Conroy (1972), BWP, Johnstone (1977), Williams & Imber (1982) and Hunter (1984b). Details of growth rates of chicks in Mougin (1968, 1975), Conroy (1972) and Hunter (1984b).

WEIGHTS All from Voisin & Bester (1981). (1) Iles Crozet, skins. (2) Macquarie I. (3) Signy I., S. Orkney Is. (4) Terre Adélie, skins. (5) Gough I., skins. All in kg.

	MALES	FEMALES	
(1)	4.93 (0.34; 4.2-5.5; 15)	3.95 (0.17: 4.7-5.3: 8)	*
(2)	5.14 (0.42; 4.3-5.6; 20)	4.22 (0.44; 3.3–5.15; 21)	*
(3)	4.94 (0.41; 4.1-5.8; 37)	3.85 (0.37; 3.0-4.8; 37)	*
(4)	4.86 (0.72; 4.1–5.9; 5)		
(5)	3.77 (0.36; 2.3-4.55;11)	3.17 (0.11; 2.7-3.9; 11)	*

At Signy I., S. Orkney Is, maximum weights of returning birds in Aug.; weight of males declines from Aug. to Nov. with lowest weight recorded late Oct. Weight of females almost constant throughout this period. During incubation, both sexes gain weight till hatching. Loss of weight occurs in both sexes during Feb.

	MALES	FEMALES	
RETURN (AUG.) (SEPT.) (OCT.) LAYING (NOV.) AFTER LAYING HATCHING (JAN.)	5.16 (0.32; 5) 	4.06 (0.33; 5) 3.92 (0.24; 5) 4.0 (0.28; 12) 3.76 (0.31; 12) 3.84 (0.28; 9)	

Weight of breeding and non-breeding birds also differs: breeding birds  $4.71 \pm 0.62$ , non-breeders  $4.34 \pm 0.78$ . Weights for male and female breeders and non-breeders:

	BREEDING	NON-BREEDING	
MALES	4.41 (0.48)	4.85 (0.42)	
FEMALES	3.74 (0.25)	3.57 (0.28)	

By Mar. weights of non-breeders (failed and suspected pre-breeders) increase (Conroy 1972). Full details of seasonal changes in Conroy (1972).

At Macquarie I., adult birds guarding chicks: males 4.64 kg (0.44; 3.8–5.4; 35); females 3.69 (0.34; 2.6–4.7; 41) (Johnstone 1977). Additional weights in Falla (1937), Voisin (1968, 1976), BWP and Hunter (1984b). Details of changes of weight of chicks in Voisin (1968), Mougin (1968, 1975), Conroy (1972) and Hunter (1984b).

STRUCTURE Wing, long and narrow. Eleven primaries: p10 longest, p9 12-13 mm shorter, p8 30-32, p7 62–64, p6 92–99, p5 127–139, p4 167–178, p3-p1 shorter in steps of 30–40 mm. No emarginations. Twenty-six to 29 secondaries (Hunter 1984a). Tail, strongly rounded; 16 rectrices; t8 *c*. 40 mm shorter than t1. Bill, long and massive; nostril tubes 50% of bill length; nostrils, shallow, rather wide and directed forwards; septum, subterminal arched opening. Maxillary unguis, large and strongly hooked. In juveniles, ridge on nostril tubes with fine parallel striae extending short distance forwards. In adults, striae numerous; also arcuate growth rings at base of culmen and base of latericorn. In juveniles, bill smooth; flaky in adults; limy encrustation at base of bill, found in both sexes (Conroy 1972), *contra* Condon (1939) who suggested in females only. Tarsus, rounded, with slight lateral compression. Outer and middle toes about equal, inner *c*. 82% of middle, hind (claw only) *c*. 10%.

**SEXING** Adults sexed on bill length (though division between sexes varies between populations): males >97 mm, females <95 (Voison 1968; Conroy 1972; Johnstone 1977; Hunter 1984a,b); birds in range 95–97, sexed with reference to partner, if available (Hunter 1984a,b). Measurements by Hunter (1984a,b) apply to S. Georgia and are similar to Iles Crozet and Signy I.; overlap zones differ for smaller Gough I. and Terre Adélie populations. Adults also sexed on cloaca at time of laying and behaviour of birds during copulation (Conroy 1972).

**RECOGNITION** Plumage characteristics and identification characters discussed fully in Warham (1962), Bourne & Warham (1966), Voisin (1968, 1976), Johnstone (1971, 1974), Conroy (1972), Conroy *et al.* (1975) and Hunter (1983b).

**GEOGRAPHICAL VARIATION** Larger size of body but smaller extremities towards S; difference not conspicuous (Voisin 1968; BWP). Populations on Gough I. and Falkland Is shorter in wing than others (Voisin & Bester 1981). See Voisin & Bester (1981) for discussion of geographical variation of mensural characters. Peters regards *M. giganteus* as monotypic, noting that breeding birds at Gough and Falkland Is are of uncertain systematic status.

Following review of Falkland and Gough populations by Johnstone *et al.* (1976), Voisin & Bester (1981) concluded that breeding birds at Gough may warrant subspecific status, but more study needed; found that these birds become light less quickly with age than birds from s. Indian Ocean, most corresponding to Fig. 1.2 in Conroy *et al.* (1975), and, in addition, had a more vivid-green coloration on bill. Although birds on Gough I. are morphologically like M. giganteus, their breeding schedule much earlier than all other populations of giganteus and similar to many populations of *halli*. Bourne & Warham (1966) regarded these birds as M. *halli*.

The Falkland Is population shares similar intermediate characters with Gough I. birds, and sometimes regarded as being subspecifically distinct *M.g. solanderi* (e.g. Mathews 1910–27; Voisin 1982). Breeding population recognized since in Argentina (Humphrey & Livezey 1983). Both Argentinian and Falkland birds have breeding schedules similar to those of other populations of giganteus.

Proportion of white morph varies, fewer than 10% in entire population; absent or scarce in Antarctic colonies; proportion on Antarctic and subantarctic islands, 0–15.1%, without relation to climatic conditions or latitude (Shaughnessy 1971). At Signy I., S. Orkney Is, white morph, 2.85% (Conroy 1972). No differential migration of white and dark morphs, at least in juveniles (nestling to 3 years old) (Conroy 1971). Proportions of white morphs at various breeding localities summarized in Conroy (1972). Summary of plumage inheritance in Shaughnessy & Conroy (1977). RMO

#### REFERENCES

- Ainley, D.G., et al. 1978. Wilson Bull. 90: 492-510.
- Ainley, D.G., et al. 1984. AOU orn. Monogr. 32: 1-97.
- Araya, B. 1973. Revta Biol. Mar. 15: 111-14.
- Barton, D. 1979. A'sian Seabird Grp Newsl. 12: 29-30.
- Bonner, W.N., & S. Hunter. 1982. Br. Antarct. Surv. Bull. 56: 75-9.
- Bourne, W.R.P., & J. Warham. 1966. Ardea 54: 45-67.
- Bretagnolle, V. 1988. Ostrich 59: 116-25.
- Bretagnolle, V. 1989. Ethology 80: 245-54.
- Brooke, R.K. & J.C. Sinclair. 1978. Cormorant 4: 10-17.
- Burger, A.E. 1978. Emu 78: 234-5.
- Carrick, R., & S.E. Ingham. 1970. Pp. 505–25. In: Holdgate 1970. Clark, G.S., et al. 1984. Notornis 31: 320–4.
- Clark, O.S., et al. 1964. Notothis 51: 520-4.
- Condon, H.T. 1939. Trans. R. Soc. S. Aust. 63: 311-30.
- Conroy, J.W.H. 1971. Br. Antarct. Surv. Bull 24: 113-15.
- Conroy, J.W.H. 1972. Br. Antarct. Surv. Sci. Rep. 75: 1-74.
- Conroy, J.W.H., et al. 1975. Ardea 63: 87-92.
- Cooke, F., & E.L. Mills. 1972. Ibis 114: 245-51.
- Cooper, J. 1983. S. Afr. J. Antarct. Res. 13: 47-8.
- Cowan, A.N. 1979. Aust. Bird Watcher 8: 66-7.
- Cox, J.B. 1976. S. Aust. Orn. 27: 28-82.
- Cox, J.B. 1978. Emu 78: 94-5.
- Croxall, J.P. 1982. J. Anim. Ecol. 51: 177-94.
- Croxall, J.P. 1984. Pp. 533-616. In: Laws 1984.
- Croxall, J.P. (Ed.) 1987. Seabirds: Feeding Ecology and Role in Marine Ecosystems.
- Croxall, J.P. & P.A. Prince. 1987. Pp. 347-68. In: Croxall 1987.
- Croxall, J.P., et al. 1984a. ICBP Tech. Publ. 2: 271-91.
- Croxall, J.P., et al. 1984b. ICBP Tech. Publ. 2: 637-66.
- Devillers, P., & J.A. Terschuren. 1980. Gerfaut 70: 447-54.
- Downes, M.C., et al. 1954. Emu 54: 257-62.
- Downes, M.C., et al. 1959. ANARE Rep. Ser. B, 1.
- Eakin, R.R., et al. 1986. Ant. Res. Ser. 44: 69-86.
- Falla, R.A. 1937. Rep. B.A.N.Z. Antarct. Res. Exped. 1929–1931. Ser. B., II.
- Gartshore, N.A., et al. 1988. S. Afr. J. Ant. Res. 18: 23-9.
- Glauert, L. 1937-38. J. R. Soc. West. Aust. 24: 59-61.
- Green, K. 1986. Notornis 33: 90-2.
- Hagen. Y. 1952. Res. Norw. Scient. Exped. to Tristan da Cunha 1937– 1938 20: 1–248.
- Harper, P.C. 1987. Notornis 34: 169-92.
- Holdgate, M.W. (Ed.). 1970. Antarctic Ecology.
- Holdgate, M.W. 1963. Br. Antarct. Surv. Bull. 2: 45-51.
- Hudson, R., & J.W.H. Conroy. 1975. Emu 75: 43-4.
- Humphrey, P.S., & B.C. Livezey. 1983. Gerfaut 73: 3-8.
- Hunter, S. 1982. Emu 82: 312-14.
- Hunter, S. 1983a. J. Zool., Lond. 200: 521-38.
- Hunter, S. 1983b. Sea Swallow 32: 72-7.
- Hunter, S. 1984a. Ibis 126: 119-32.
- Hunter, S. 1984b. J. Zool., Lond. 203: 441-60.
- Hunter, S. 1984c. Ringing Migration 5: 105-12.
- Hunter, S. 1987. Polar Biol. 7: 295-301.
- Ingham, S.E. 1959. Emu 59: 198-200.
- Jablonski, B. 1985. Acta. zool. Cracov. 29: 117-86.
- Jablonski, B. 1986. Polish Polar Res. 7: 217-60.
- Jehl, J.R. Jr. 1973. Auk 90: 114-35.
- Jehl, J.R. Jr. 1974. Trans. San Diego Soc. nat. Hist. 17: 217-34.
- Johnstone, G.W. 1971. Aust. Bird Bander 10: 52-6.
- Johnstone, G.W. 1974. Emu 74: 209-18.
- Johnstone, G.W. 1977. Pp. 647-68. In: Llano 1977.
- Johnstone, G.W. 1978. Emu 78: 235.
- Johnstone, G.W. 1979. Emu 79: 129-32.
- Johnstone, G.W. 1982. Pp. 33-7. In: Exped. Aust. Terr. Heard and McDonald Is, 1980. Div. Natn Mapping Tech. Rep. 31.
- Johnstone, G.W., et al. 1973. ANARE Sci. Rep. Ser. B, I, 123.

- Johnstone, G.W., et al. 1976. S. Afr. J. Ant. Res. 6: 19-22.
- Jones, B. 1973. Aust. Bird Bander 11: 47-50.
- Jouventin, P., et al. 1982. Com. natn. fr. Rech. Antarct. 51: 457-67.
- Jouventin, P., et al. 1984. ICBP Tech. Publ. 2: 609-25.
- Lacan, F., et al. 1969. Oiseau Revue fr. Orn. 39: 11-32.
- Laws, R.M. (Ed.). 1984. Antarctic Ecology. Lindsey, T.R. 1986. The Seabirds of Australia.
- Linkowski, T.B., & J.M. Rembiszewski. 1978. Pol. Arch. Hydrobiol. 25: 717–27.
- Llano, G.A. (Ed.). 1977. Adaptations Within Antarctic Ecosystems.
- Lowe, P.R., & N.B. Kinnear. 1930. Nat. Hist. Rep. Br. Antarct. Terra Nova Exped 1910 4: 103–193.
- Marchant, S. 1977. Emu 77: 7-18.
- Mathews, G.M. 1910-27. Birds of Australia.
- McQuaid, C.D., & L.H. Ricketts. 1984. Cormorant 12: 14-28.
- Meeth, P. 1969. Ardea 27: 92.
- Milledge, D. 1977. Corella 1: 1-12.
- Mochizuki, H., & I. Kasuga. 1985. Trans. Tokyo Univ. Fish 6: 155-65.
- Mougin, J-L. 1968. Oiseau Revue fr. Orn. 38 (Spec. No.): 1-52.
- Mougin, J-L. 1970. Oiseau Revue fr. Orn. 40 (Spec. No.): 62-96.
- Mougin, J-L. 1975. Com. natn. fr. Rech. Antarct. 36: 1-195.
- Obst, B.S. 1985. Auk 102: 540-9.
- Orton, N.M. 1963. Emu 63: 260.
- Parmelee, D.F., & J.M. Parmelee. 1987. Ringing Migration 8: 115-18.
- Parmelee, D.F., et al. 1985. Antarct. J. US 19: 162-3.



#### Plate 25

- Southern Giant-Petrel Macronectes giganteus
- 1. Adult, dark morph, dorsal
- 2. Adult, dark morph, ventral
- 3. Adult, white morph, ventral
- 4. Adult head, white morph
- 5. Immature, ventral
- 6. Juvenile, ventral

Prévost, J. 1953. Alauda 21: 157-61. Prince, P.A., & R.A. Morgan. 1987. Pp 135-71. In: Croxall 1987. Rand, R.W. 1954. Ibis 96: 173-206. Rootes, D.M. 1988. Br. Antarct. Surv. Bull. 80: 87-119. Rounsevell, D.E., & N.P. Brothers. 1984. ICBP Tech. Publ. 2: 587-92 Rumboll, M.A.E., & J.R. Jehl Jr. 1977. Trans. San Diego Soc. nat. Hist. 19: 1-16. Schlatter, R.P. 1984. ICBP Tech. Publ. 2: 261-9. Shaughnessy, P.D. 1971. Aust. J. Zool. 19: 77-83. Shaughnessy, P.D., & J.W.H. Conroy. 1977. Br. Antarct. Surv. Bull. 45: 25-8. Sibson, R.B. 1969. Notornis 16: 45-50. Sladen, W.J.L., et al. 1968. Ant. Res. Ser. 12: 213-62. Stahl, J.C. 1987. TAAF MR Rap Campagnes mer 84-01: 175-90. Stresemann, E., & V. Stresemann. 1966. J. Orn. Lpz., 107, Sonderheft Strikwerda, T.E., et al. 1986. John Hopkins APL Technical Digest 7: 203-208 Swales, M.K. 1965. Ibis 107: 17-42. Szijj, L.J. 1967. Auk 84: 366-78.

Voisin, J-F. 1968. Oiseau Revue fr. Orn. 38 (spec. no.): 95-122. Voisin, J.F. 1976. Alauda 44: 411-29. Voisin, J.F. 1978. Alauda 46: 209-34. Voisin, J.F. 1980. Cormorant 8: 53-8. Voisin, J.F. 1982. Gerfaut 72: 367-80. Voisin, J-F., & M.N. Bester. 1981. Proc. Symp. Birds Sea Shore: 215-22. Wanless, S., & M.P. Harris. 1988. Br. Antarct. Surv. Bull. 81: 87-92. Warham, J. 1962. Auk 79: 139-60. Watkins, B.P. 1981. S. Afr. J. Ant. Res. 10/11: 38-40. Weimerskirch, H., et al. 1985. Emu 85: 22-33. Weimerskirch, H., et al. 1989. Emu 89: 15-29. Williams, A.I. 1984. ICBP Tech. Publ. 2: 627-35. Williams, A.J., & M.J. Imber. 1982. S. Afr. J. Antarct. Res. 12: 40-45. Woehler, E.J., & G.W. Johnstone. 1988. Pap. Proc. R. Soc. Tas. 122: 143-52. Woods, R.W. 1975. The Birds of the Falkland Islands. Zink, R.M. 1981a. Wilson Bull. 93: 1-20. Zink, R.M. 1981b. Gerfaut 71: 59-74.





## Volume 1 (Part A), Plate 25

- Southern Giant Petrel *Macronectes giganteus* 1. Adult, dark morph, dorsal 2. Adult, dark morph, ventral 3. Adult, white morph, ventral 4. Adult head, white morph 5. Immature, ventral 6. Juvenile, ventral

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