

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 DIOMEDEIDAE albatrosses

The albatrosses are a small group of some 13-16 large petrels with long wings adapted for gliding flight and with long powerful beaks adapted for seizing prey at the surface; nine species breed in our region and one other has been recorded as a vagrant. Because they are so large, they must breed in the open, where they walk well for petrels. Most s. species build substantial conical nests but n. ones, breeding in warm climates, make only scrapes. Young birds in some species have a drab plumage but adults of many species develop bolder markings with brightly coloured stripes on the bill, used in social displays when breeding. Three distinct groups occur in the Southern Ocean but the distinction between two is blurred by intermediate forms that occur in North Pacific:

(1) The great albatrosses are huge, long-winged, long- and pale-billed, short-tailed birds that glide round the world in Southern Ocean. Until recently, there were thought to be two species: the more pelagic Wandering Albatross *D. exulans* breeding on most of the subantarctic islands, which is dark with a white underwing when young, becoming more or less white with dark wing-tips when adult; and the more coastal Royal Albatross *D. epomophora*, breeding round NZ, which resembles the extreme white adult Wanderer throughout its life but has a dark cutting-edge to the upper mandible. A few birds breeding in extreme immature *exulans*-type of plumage on Ile Amsterdam in the Indian Ocean have recently been described as a third species *D. amsterdamensis* but there is continuing debate whether this is justified owing to the occurrence of similar populations in South Atlantic and round NZ (Bourne 1989).

(2) The medium-sized albatrosses *Diomedea* (*Thalassarche*), often called mollymawks, are a compact group of white-bodied, dark-backed species with brightly marked bills in adults, all five species being found in our region. They consist of two comparatively coastal species, the Black-browed Albatross *melanophrys* with main breeding colonies round South America, and the Shy *cauta* with 3-4 rather well-defined subspecies, sometimes treated as separate species, breeding in A'asia. There are also three pelagic species: Grey-headed *chrysostoma* to the south, Yellow-nosed *chlororhynchus* in subtropical South Atlantic and Indian Oceans, and Buller's *bulleri* in equivalent parts of South Pacific.

The differences between Groups (1) and (2) are rather marked and they would doubtless be treated as distinct genera if it were not that four other albatrosses with intermediate characters breed in North Pacific: Black-footed *nigripes* with plumage resembling that of sooty albatrosses, though shape differs; Laysan *immutabilis* with plumage like that of the medium-sized albatrosses (Group 2); Short-tailed *albatrus* with a sequence of plumages rather like those of Wanderer, though smaller; and the Waved *irrorata* with dark plumage except for pale head, neck and underwing. Because it is hard to make any clear distinction between these birds they are normally all included in an unusually wide genus *Diomedea*.

(3) The sooty albatrosses *Phoebastria*. Two extremely aerial, highly pelagic and rather aggressive or predatory species with fairly small bills with a groove along the lower mandible; long wings; long pointed tails; and dark plumage; nest on steep places and have vocal aerial displays.

General characters are: body, short and broad; head, large; neck, short. Wing, long and narrow, folded in three almost equal parts, 11 primaries, p10 longest, p11 minute; up to about 40 secondaries, diastataxic. Tail, short and square in *Diomedea*, longer and wedge-shaped in *Phoebetria*, 12 feathers. Bill, heavy and composed of several horny plates; hooked; nostrils in tubes on either side. Legs, strong; three front toes joined by web; hind toe absent or vestigial. Oil gland, feathered. Sexes similar; male larger on average. Plumage mainly white except in *Phoebetria*, in which it is dark grey. Juveniles and immatures generally separable but mostly not very different from adults except in *D. exulans* and *D. albatrus*; fully adult plumage attained only after several years. Stance upright and able to walk much better than most other Procellariiformes. Swim and rest on sea buoyantly with head held high. Feed mostly on fish and squid by surface-seizing or shallow diving, but sooty albatrosses also take birds. Follow ships for scavenging.

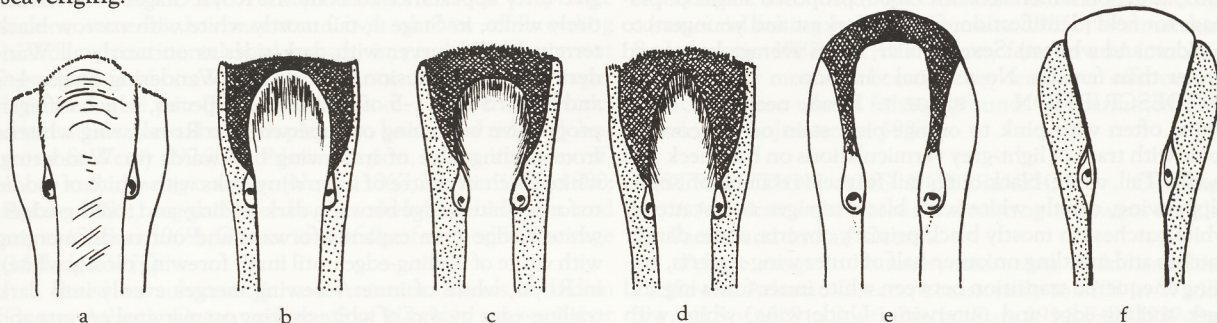


Fig. 1 Dorsal view of base of bill of small *Diomedea*

Fig. 1a Black-browed Albatross *D. melanoprys*

Fig. 1b Grey-headed Albatross *D. chrysostoma*

Fig. 1c Yellow-nosed Albatross, *D. chlorohynchos*, subspecies *chlorohynchos*

Fig. 1d Yellow-nosed Albatross, *D. chlorohynchos*, subspecies *bassi*

Fig. 1e Shy Albatross *D. cauta*

Fig. 1f Buller's Albatross *D. bulleri*

Long-lasting monogamous pair-bond. Breed colonially, pairs often returning to same site. Defend small nest-territories. Perform spectacular agonistic and sexual displays at nest in *Diomedea*; vocal aerial displays in *Phoebetria*. Eggs, white, minutely spotted reddish. Clutch-size; one; no replacement laying. Incubation by both sexes in long alternate spells. Incubation period, 2 or more months. Nestling, semi-altricial, nidicolous; hatched in down. Brooded for a short time after hatching; then left alone in nest, parents returning only to feed chick by incomplete regurgitation. Nestling period long, up to 12 months, and so in some species successful adults cannot breed annually. Young independent on fledging. Maturity reached only after several years. Some populations were reduced in the past, notably by egg-collecting, but there appear to be few threats now except that some great albatrosses are caught by long-line fishing.

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Diomedea chrysostoma **Grey-headed Albatross**

COLOUR PLATE FACING PAGE 305

Diomedea chrysostoma J.R. Forster, 1785, *Mem. Math. Phys. Acad. Sci., Paris* 10: 571, Pl. 14 — vicinity of Antarctic Circle and in Pacific Ocean = South Georgia (Murphy 1936) or 'off Staten Island, South America' (Mathews 1943).

The specific name (χρυσός gold + στόμα mouth) alludes to the chrome-yellow markings on bill of adults.

OTHER ENGLISH NAMES Flat-billed, Gould's, Grey-mantled or Yellow-nosed Albatross (Mollymawk).

MONOTYPIC

FIELD IDENTIFICATION Length 70–85 cm; wingspan 180–205 cm; weight: males 3.4–3.7 kg, females 3.0–3.6. Medium-sized albatross with size and proportions as Black-browed Albatross *D. melanophrys*. Adult has distinctive combination of wholly grey head, black bill with narrow yellow stripes along culmen and bottom of lower mandible, mostly white underwing with broad black leading-edge. Sexes alike. No seasonal changes in plumages. Juveniles and immatures recognizable.

DESCRIPTION ADULT. Head, neck and mantle, wholly light grey, forming distinct grey hood with slightly paler forecrown, short black brow and prominent white crescent behind and below eye; hood sharply demarcated from white underparts. Throat and hindneck slightly paler than rest of head when worn, giving appearance of pearly-grey collar between head and mantle, but merges evenly into greyish-black mantle. Back, scapulars and upperwing, uniform blackish; white bases to primary shafts visible in outer primaries. Rump and upper tail-coverts, white. Tail, grey, becoming darker when worn. Underwing, white, with black wing-tip (formed by black primaries), narrow black trailing-edge, and broad black leading-edge about one-third of width of wing for most of length; narrowest at carpal joint, thicker towards body and broadening abruptly to form dark wedge at elbow, where a few short black streaks jut backwards, giving margin of wedge fuzzy appearance; margin broadens outside carpal joint, with black streaks radiating across white ground of median primary coverts. Bill, mostly glossy black with bright-yellow stripe on culmen, becoming peach-red on ridge of maxillary unguis; side-plates, glossy black except for narrow yellow stripe on basal two-thirds of ramicorn, tapering to gonys; narrow strip of black skin over rounded base of culminicorn broadens between culminicorn and latericorn and extends forward in thick strip to nostrils; nostrils, black; cheek-stripe (exposed only during display) and narrow vertical strip of skin jutting up at base of lower mandible, bright orange. Iris, brown. Legs and feet, whitish with varying grey or pink suffusion. **JUVENILE.** Head and neck, entirely dark grey, though typically ear-coverts and posterior cheeks paler grey to whitish, showing as pale cheek-patch; black brow before and narrowly over eye; narrow white crescent bordering rear and bottom of eye duller and less conspicuous than in adult. Grey on head and neck reduced by wear; progressive exposure of white bases of feathers, on cheeks, chin, throat, forehead and crown till head and neck appear mostly white, with hindneck collar of varying extent; grey smudging on sides of head and round dark brow usually gives grubby-faced appearance and increases apparent size and prominence of brow. Dark grey of hindneck merges into grey of mantle; entire upperparts appear uniformly dark except for white rump and upper tail-coverts. Underbody, from upper breast to under tail-coverts, white, except for grey axillaries and tips to lateral upper-breast feathers; undersurface of tail, blackish. Underwing mostly blackish, with slightly paler greyish to grey-white stripe down centre. Bill, dark grey on sides, with blackish unguis; culminicorn and narrow tapering stripe along bottom edge of ramicorn, dirty brown, slightly paler than side-plates; bare skin round base of culminicorn and between culminicorn and latericorn, as adult; cheek-stripe and vertical strip of bare skin bordering base of lower mandible, black. Side-plates darken to blackish, and brownish bill-stripes become paler. **IMMATURE.** Changes in plumage and colour of bill with age not understood. Plumage gradually becomes more like adult but differs by (1) grey hood slightly paler; much affected by wear;

soon develops patchy appearance until head and neck mostly white except for pronounced grey hindneck; (2) underwing adult-like, broad black margins enclose white central stripe; leading-edge along innerwing appears broader and less sharply demarcated from white stripe; dark streaks across white of median coverts heavier, and form bolder 'finger-patch'; series of bold dark streaks run off elbow-wedge across white central stripe to join dark trailing-edge; generally messier wing-pit. Full adult plumage attained before colour of bill definitive; thus older immatures often recognizable from adult only by slightly duller yellow stripes and duller orange tip on bill.

SIMILAR SPECIES Buller's *D. bulleri* and Yellow-nosed *D.c. chlororhynchos* Albatrosses (q.v.) distinguished by underwing pattern, having narrower dark leading-edge without dark wedge midway along innerwing. **Black-browed Albatross** distinguished by white head and bright yellow-orange bill. Juvenile and immature Black-browed have similar underwing patterns and overlap in head patterns. Juvenile Black-browed differs (1) head and neck mostly white except for pronounced grey hindneck, giving characteristic collared appearance; and can appear hooded though never matching solid dark hood of Grey-headed. Black-browed shows clean white head with neat black brow. (2) Bill, dark olive-brown with contrasting black tip. Immature Black-browed has white

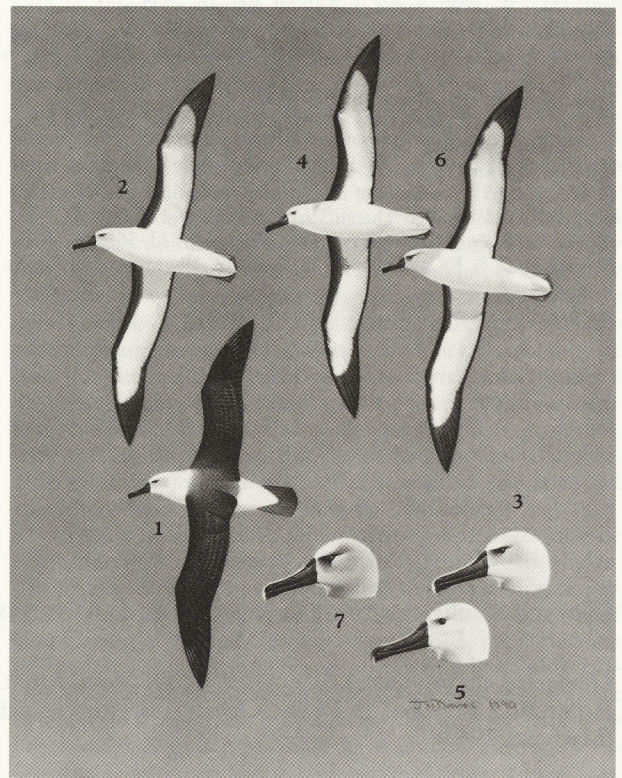


Plate 21

Yellow-nosed Albatross *Diomedea chlororhynchos*

1. Adult, subspecies *bassi*, dorsal
2. Adult, subspecies *bassi*, ventral
3. Adult, subspecies *bassi*, head
4. Juvenile, subspecies *bassi*, ventral
5. Juvenile, subspecies *bassi*, head
6. Adult, subspecies *chlororhynchos*, ventral
7. Adult, subspecies *chlororhynchos*, head

head with neat black brow; bill of Black-browed brownish-yellow with contrasting black tip; at all ages no black skin round base of culmen extending forward to nostrils.

Pelagic, in shelf-break and deeper offshore waters; only occurring inshore in rough weather. Mix freely with conspecifics and other albatrosses and petrels. Breed colonially on well-vegetated Antarctic and subantarctic islands. Flight effortless and graceful, in strong winds wheeling in broad arcs well above horizon and soaring on stiff almost motionless wings; flap more in light winds but in calms tends to sit on water. Patter on sea-surface when taking flight, flapping vigorously till well clear of waves. Feed by surface-sieving, occasionally surface-diving and shallow-plunging. Solitary or gregarious at sea. Sometimes follow ships but much less regularly and for shorter periods than Black-browed Albatross; attend trawlers for offal. Silent at sea; at colony, loud croaks and wails, quiet groans and several percussive clicks caused by contact of bills.

HABITAT Marine, in three major oceans. In summer, in subantarctic and Antarctic seas, feeding mainly in cold waters on either side of Antarctic Convergence (Hicks 1973; Brown *et al.* 1975; Thomas 1982; Ainley *et al.* 1984; Weimerskirch *et al.* 1986); in winter, most leave Antarctic Zone and range extends into s. Subtropics (Amiet 1958;

Secker 1969; Brown *et al.* 1975). Avoid pack-ice (Zink 1981a). Generally pelagic, feeding far from shelf waters round breeding islands and continental land masses (Rand 1963; Jehl *et al.* 1979; Weimerskirch *et al.* 1986; Weimerskirch *et al.* 1988); but occur occasionally in inshore and offshore waters in A'asian region (Secker 1969; Barton 1979), and off South America occur 4–30 km offshore in cool Humboldt Current (Jehl 1973). In Cook Strait, NZ, concentrate over tidal rips (Secker 1969).

Breed on subantarctic and Antarctic islands of Indian Ocean, Atlantic Ocean and seas S of NZ. Nest on tussock-covered cliffs, steep slopes and hillsides, which overlook sea or run inland from coast (Rand 1954; Bailey & Sorensen 1962; Tickell & Pinder 1975; Grindley 1981; Weimerskirch *et al.* 1988); often among Black-browed Albatrosses.

Fly low to fairly high, using updraft off wave-fronts for lift.

On Campbell I., feral sheep attracted to lush vegetation round colony disturb chicks and cause breeding failure (Bailey & Sorensen 1962).

DISTRIBUTION AND POPULATION Circumpolar. During summer, subantarctic and Antarctic waters between 46–64°S; during winter, between 39–51° S. Breed subantarctic islands between 46–56°S. Regular visitor to Aust. and NZ.

During summer, generally subantarctic waters between 46 and 52°S. Extend into Antarctic waters S of breeding islands: to 64°S in sw. Indian Ocean (30–90°E); to 68°S in A'asian sector of Southern Ocean (140–180°E); to 68°S in se. Pacific; and to 62°S in Scotia and Weddell Seas (Gain 1914; Falla 1937; Bierman & Voous 1950; van Oordt & Kruijt 1954; Holgersen 1957; Dell 1960; Ozawa *et al.* 1964, 1968; Ozawa 1967; Tickell & Woods 1972; Zink 1981a,b; Thurston 1982; Starck & Wyrzykowski 1982; Harris 1982; McQuaid & Ricketts 1984; Mochizuki & Kasuga 1985; Clark 1986; Weimerskirch *et al.* 1986; Stahl 1987). From late autumn to early spring, range shifts N, generally between 39 and 51°S, occasionally to 31°S. At this time, most have left Antarctic waters but stragglers recorded S to 58°S (Falla 1937; Rand 1963; Szijj 1967; Shuntov 1968; Tickell & Woods 1972; Rumboll & Jehl 1977; Hansen 1978; Duhamel 1981; Grindley 1981; Jouventin *et al.* 1982; Bourne & Curtis 1985; Clark 1987). In sw. Indian Ocean, most immatures spend summer in Subantarctic, but in winter range may extend further N into Subtropics than adults (Stahl 1987; J-C. Stahl).

Extension of range along Humboldt Current uncertain: most appear to remain S of 41°S throughout year, a few occurring N to 31°S (Jehl 1973; Brown *et al.* 1975). Past reports as far N as 11°S but most of these records probably result from confusion with Buller's Albatross *D. bulleri* (Murphy). Accidental off Brazil, N to 23°S in Sept. (Teixeria *et al.* 1985); occasional Tristan da Cunha and Gough I., June–Nov. (Williams & Imber 1982; Enticott 1984; Richardson 1984); rare visitor to South Africa (Brooke & Sinclair 1978). All records in n. hemisphere doubtful (Bourne 1967).

AUST. Regular winter visitor to s. Aust., from se. NSW to sw. WA and waters round Tas. Occasional summer records (Aust. Atlas). Records to 25°45'S off WA doubtful (see below). Said to occur exceptionally to 24°45'S off e. coast Qld but details not given (Storr 1973). NT. No records. Qld. One beachcast, 27 Sept. 1959, Stradbroke I. (Hines 1962); RAOU Historical Atlas also lists records between s. end Bribe I. and Southport Spit, beachcast some time between

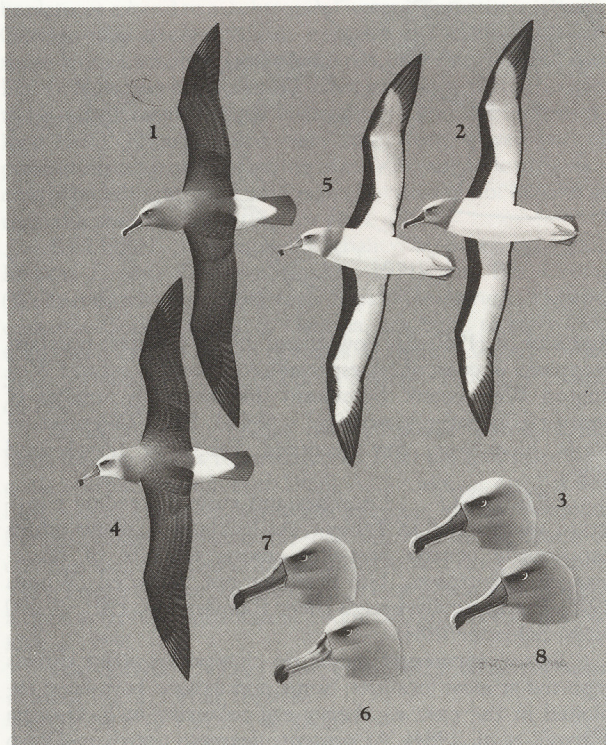
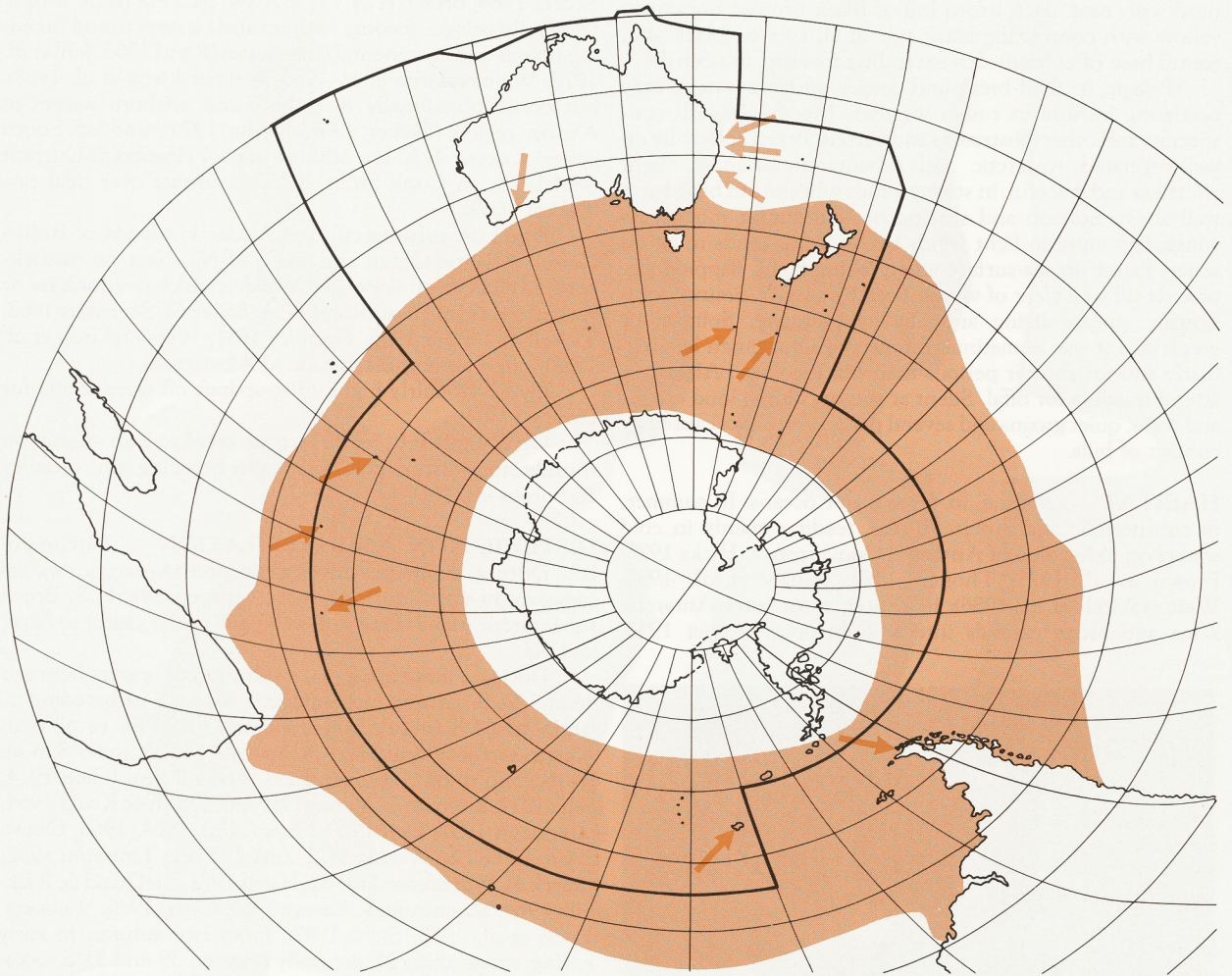


Plate 22

- Buller's Albatross *Diomedea bulleri*
 1. Adult, subspecies *bulleri*, dorsal
 2. Adult, subspecies *bulleri*, ventral
 3. Adult, subspecies *bulleri* head
 4. Juvenile, subspecies *bulleri*, dorsal
 5. Juvenile, subspecies *bulleri*, ventral
 6. Juvenile, subspecies *bulleri* head
 7. Immature, subspecies *bulleri* head
 8. Adult, subspecies *platei* head



1971-76 and also at Raby Bay, early Sept. 1968 (Aust. Atlas); Storr (1973) states three records, Apr. and Sept. without further details; two, beachcast, N. Stradbroke I., 22 July 1973; three more beachcast to 1979 (Roberts 1973, 1979). NSW. Regular in small numbers, mostly in SE from Green Cape to Sydney; several records in NE, from Yamba-Iluka to Tweed Heads (Hindwood & McGill 1958; Morris *et al.* 1981; Aust. Atlas). Vic., SA. Regular in small numbers, to inshore and offshore waters of coast; at least 25 records, 1975-84 (Aust. Atlas; Vic Atlas); few records Great Australian Bight (Aust. Atlas; Condon 1969; Parker *et al.* 1979). Tas. Regular in Tas. waters and beachcast; however, during Aust. Field Atlas, only two records: single, 30 miles off Pt Hibbs, 30 Jan. 1981; one, beachcast, Five-mile Bluff, 21 Oct. 1978 (Aust. Atlas). WA. Few published records; most records round SW (Aust. Atlas) to about 31°S (Aust. Atlas). Said to occur Great Australian Bight and round coast to Perth; reports off Dirk Hartog I., Shark Bay (25°45'S) (one sighted, Gregory 1941; Davies & Chapman 1975; unknown sources, possibly Gregory also, Serventy & Whittell 1976) of doubtful validity, certainly not confirmed by Gregory (1941); 1975-81, one record, beachcast, Hopetoun, 29 Dec. 1978 (Aust. Atlas).

NZ Regular round coasts (592 recovered 1960-83, one bird/100 km coast covered); not recorded beachcast on coasts of Cook Str. in NI and SI nor on Westland and Otago

coasts of SI (1960-83; Powlesland 1985). Greatest numbers recovered w. coast of NI, especially Auckland West and Wellington West coasts. Significant differences in number of recoveries between seasons ($\chi^2 = 684.21$, $P < 0.001$); most records June-Nov.; few recorded Feb.-May (Powlesland 1985).

BREEDING Localities and annual breeding population summarized in Table 1. At Falkland Is, single adults occasionally occupy nest-sites among colonies of Black-browed Albatrosses, but breeding not recorded (Woods 1975). Extraliminally, breeds Diego Ramirez Is (<1981: 20 000 birds; Schlatter 1984).

Status, apparently stable; no changes or major threats reported at most localities. Some populations have been exploited in the past, e.g. heavy egg collecting at S. Georgia (Croxall *et al.* 1984). At present, decrease noted on Diego Ramirez I. (Schlatter 1984); no changes or major threats reported at other localities.

POPULATION Total estimated 60 000 pairs (Croxall *et al.* 1984).

MOVEMENTS Migratory though pattern of movement away from breeding islands poorly understood.

DEPARTURE Macquarie I., late Apr.-mid May, rarely early June (Copson 1988); Campbell I., early-mid-May

Table 1.

Locality	Year of Estimate	Estimate (pairs)	Ref.
Prince Edward Is	<1984	4870	1
Iles Crozet	1981-82	5940	2
Iles Kerguelen	1984-87	7900	3
Macquarie I.	1980	58	4
	1977-85	80-100	5
Campbell I.	1975	11 530	6
S. Georgia	1971-76	38 000+	7

References. (1) Williams (1984); (2) Jouventin *et al.* (1984); (3) Weimerskirch *et al.* (1989); (4) Rounsevell & Brothers (1984); (5) Copson (1988); (6) Robertson (1980); (7) Prince & Payne (1979).

(Bailey & Sorensen 1962); S. Georgia, late May-early June with median fledging date 19 May (24 Apr.-17 June; 19; Tickell & Pinder 1975).

NON-BREEDING Some dispersal N in winter, when few remain in Antarctic waters and many cross Subtropical Convergence (Jouventin *et al.* 1982). Recoveries so far suggest adults remain Subantarctic Zone, while juveniles and immatures extend to s. subtropical waters. Immatures from S. Georgia may circumnavigate Antarctica (Tickell 1964) but those from Campbell I. all recovered near Aust. or NZ (see Fig. 1). Numbers beachcast NZ coast peak July-Oct., thought to be mostly newly fledged young from Campbell I. (Powlesland 1985). Though breed every other year, at least part of population returns to breeding islands in year following successful breeding attempt with males but usually not females in reproductive condition (Hector *et al.* 1986).

RETURN Campbell I. (Bailey & Sorensen 1962), Marion I. (van Zinderen Bakker 1971) and Iles Crozet (Weimerskirch *et al.* 1986), early Sept.; Macquarie I., 13 Sept. onwards (Copson 1988); S. Georgia, late Sept. to early Oct. with mean date of return of males 22 Sept. (4.0 days; 16-27 Sept.; 7), females 30 Sept. (4.2 days; 24 Sept.-7 Oct.; 7) (Tickell & Pinder 1975).

BREEDING Forage over s. pelagic waters. Dyed birds feeding chicks reported up to 1850 km from Iles Kerguelen (Weimerskirch *et al.* 1988). At S. Georgia, one banded bird feeding chick recovered 844 km from colony; potential foraging range estimated 437-888 km, diet and location of colonies suggesting main foraging area to W (Prince & Francis 1984; Prince & Morgan 1987). At Prince Edward Is, thought to feed as far N as Subantarctic Front, 330 km to N (Hunter & Klages 1989).

BANDING Data from Campbell I. (NZNBS) summarized Fig. 1. Other records:

46S37E 04 P U 3 9737 146 SABRU

46S37E 01 P U 7 4724 103 SABRU

Recoveries of banded chicks from S. Georgia suggest circumpolar navigation E but no distant recoveries of adults outside breeding season (Tickell 1967a,b).

FOOD Cephalopods and fish, proportion varying with locality, with lampreys, krill and carrion important near S. Georgia. **BEHAVIOUR.** Food usually obtained by surface-seizing; occasionally surface-diving or shallow-plunging (Harper *et al.* 1985). When aerial foraging within 7 m of sea-surface,



Fig. 1. 52S 169E 10X10 NZNBS

mean height of flight 3.5 m (Pennycuik 1982), spending on average 16.5 h/day in flight, 1.6 h on water in daytime, 5.9 h on water at night. Feeding thus assumed to be largely nocturnal (Prince & Morgan 1987). Feed alone or in company with other petrels and albatrosses; Grey-headed usually dominates all species except Wandering Albatross *D. exulans*, Black-browed Albatross and giant-petrels *Macronectes* (Weimerskirch *et al.* 1986). Have been seen feeding in association with Minke Whales *Balaenoptera acutorostrata*, Pilot Whales *Globiocephala* and Killer Whales *Orcinus orca* (Voisin 1969; Hunt & Veit 1983; Enticott 1986), sometimes in flocks of hundreds (Jehl *et al.* 1979). Do not usually follow fishing boats (Robertson & Jenkins 1981) except at Falkland Is where large numbers gather round fishing boats in winter (Bourne & Curtis 1985).

NON-BREEDING One beachcast NZ contained remains of Common Diving-Petrel *Pelecanoides urinatrix* and cephalopod beaks (Tarburton 1980); another, remains of Salvini's Prion *Pachyptila salvini* (Skegg *et al.* 1960).

BREEDING Summarized Table 1. At **Bird I., S. Georgia** (132 adult regurgitations; Prince 1980) liquid matter 51.7% vol., unidentifiable solids 0.8%. Of identifiable solids, lampreys *Geotria australis* 45.9 cm (0.9, 41, 54.9 g), other fish incl. Myctophidae 12.1% freq.; crustaceans *Euphausia superba* 16.3% wt., 57.0% freq., 5.3.0 cm (3.8; 12), *E. frigida* 2.51 cm (3.6; 11), amphipods *Themisto gaudichaudii* 12.8% freq., 1.30 cm (1.0; 10), shrimps *Acanthephyra* 7.5% freq. Of cephalopod beaks (322; Clarke & Prince 1981) most were *Todarodes* 91.4% wt., 88.2% no. with rest *Kondakovia longimana* 3.9, 0.6, 940 g, *Histioteuthis* 0.2, 0.6, 54 g, *Chiroteuthis veranyi* 0.2, 0.3, *Mastigoteuthis* 0.4, 0.6, Cranchiidae 3.9, 7.5, unident. 2.2% no.

Regurgitations by chicks at **Bird I.** (170, Prince 1980; 111, Tickell 1964) also contained mostly cephalopods (74.7% freq., Prince, 90.1%, Tickell) similar to those of adults: fish lamprey *G. australis* 32.9, 21.6, other fish 37.6, 71.2; crustaceans *E. superba* 69.4, 50.5, amphipods 11.7, 27.1, decapods 23.5, 73.9; salps, incl. *Salpa thompsoni*, 0, 46.8. Of the cephalopods, 94% were *Todarodes*, 114 ± 58.4 g in Jan., 183 ± 77 g in Feb.-Mar. (Prince 1980).

At **Prince Edward Is** (88 regurgitations; Hunter & Klages 1989) liquid matter 55.4% vol. (26.4; 0-96.1; 88). Of

solids, fish incl. *Channichthys rhinoceros* 245 g, 350 mm, *Dysalotus alcockii* 24, 164, crustaceans incl. amphipods *Themisto gaudichaudii*, penguin 2.7% wt., 3.4% freq., other 2.2, 5.7 incl. barnacles *Lepas*, ctenophores, seal carrion, non-cephalopod mollusc. Of the cephalopod beaks (n=105) *Taningia danae* 1% no., 403.6 g, *Moroteuthis knipovitchi* 2, 982.0 g (1814.6; 2), *M. sp. 1*, 1029 g, *Kondakovia longimana* 46, 186.8 g (253.6; 45), unident. Onychoteuthidae 1, *Gonatus antarcticus* 1, 151.7 g, *Histioteuthis eltaninae* 37, 78.3 g (20.7; 39), *Chiroteuthis* 2, 48.4 g (123.1; 2), *Galiteuthis glacialis* 6, 89.7 g (31.4; 6), *G. sp. 1*, 85.4 g, unident squid 3.

In earlier study at **Marion I.** (796 cephalopod beaks; Brooke & Klages 1986) *Moroteuthis knipovitchi* 2.6% wt., 13.7% no., mean wt. 244 g, *M. robsoni* 0.9, 1.5, 792 g, *Kondakovia longimana* 95.8, 75.8, 1659 g, *Discoteuthis* 0.1, 0.3, 578 g, *Gonatus antarcticus* 0.3, 1.4, 251 g, *Histioteuthis eltaninae* <0.1, 1.0, 64 g, *Chiroteuthis* 0.1, 1.1, 61 g, *Mastigoteuthis* <0.1, 0.1, 430 g, *Teuthowenia antarctica* 0.1, 1.4, 59 g, *Galiteuthis glacialis* 0.2, 3.8, 81g.

At **Campbell I.** (seven samples; Bailey & Sorensen 1962) cephalopods 100% freq., fish 29, penguin remains 14. At **Iles Crozet** (Despin *et al.* 1972; Weimerskirch *et al.* 1986) 50% of 51 samples dominated by fish (actual freq. 56.8%) with cephalopods predominating in 41% (58.8, largely Ommastrephidae), crustaceans 2 (25.5) and carrion 7 (13.7, penguins).

INTAKE At Iles Crozet, chicks received 0.44 meals/day gaining 60 g/day (Weimerskirch *et al.* 1986). At S. Georgia each chick given 0.9 meals/day (Croxall & Prince 1987) receiving 600 g/meal and gaining mean of 63 g/day (Croxall & Prince 1980); 16 meals at same site averaged 778 g (312–1278; Tickell & Pinder 1975). At Prince Edward Is, adults about to feed chicks regurgitated 343 g (165; 35–850; 88) (Hunter & Klages 1989). Mean efficiency of food conversion 36% (7–55; 7; Ricketts & Prince 1984).

Table 1.

Percentages	wt.		freq.	
	1	2	1	2
CEPHALOPODS	49.0	34.2	62.1	63.6
LAMPREYS	10.4	-	34.1	-
OTHER FISH	24.1	58.0	36.4	59.1
CRUSTACEANS	16.5	3.0	59.1	14.8

(1) S. Georgia (Croxall & Prince 1980); (2) Prince Edward Is (Hunter & Klages 1989).

SOCIAL ORGANIZATION At sea, generally solitary or in small groups throughout year (Weimerskirch *et al.* 1986), but up to several hundreds reported following fishing vessels or whales (Jehl *et al.* 1979; Bourne & Curtis 1985); highly gregarious on breeding grounds. Remain at sea outside breeding season; juveniles spend several years before returning to natal island. Breeding colonies contain birds of different ages and breeding experience; older more experienced birds return first and younger birds arrive later. Occasionally associate with other species of albatross, giant-petrels, smaller procellariiforms and cetaceans.

BONDS Monogamous; pair-bond probably lifelong, but no data on fidelity and divorce rate between successive breeding cycles. Sex ratio apparently balanced. When juvenile finally returns to colony, may take several more years to acquire mate, nest-site and breed successfully; most establish

pair-bonds when between 4–11 years old. Pair-formation begins when birds return to colonies (Tickell 1969; Robertson 1980; Copson 1988). Both sexes incubate eggs and attend young; young dependent until fledging.

BREEDING DISPERSION Nest colonially. At S. Georgia, average density 5980 nests/ha, nests 1.3 m (0.3; 0.6–2.3; 203) apart (Tickell & Pinder 1975). Territorial only when breeding, defending nest and surrounds.

ROOSTING No information.

SOCIAL BEHAVIOUR Based on detailed study at S. Georgia (Tickell 1984). Information supplied by J-C. Stahl. Displays easy to observe but difficult to separate in the field. Social behaviour similar to that of other small mollymawks except for apparent absence of ritualized **Scooping** during courtship although similar action seen before take-off. **AUTOPREENING.** Frequent while standing or sitting. Involves all parts of body that can be reached; when preening over back, wings slightly parted; much rolling of back of head over preen-gland followed by similar movements on wings; folded wings lifted slightly while preening flanks and legs; settles head-feathers by fluffing, then vigorously shaking head from side to side, which also causes bill to rattle; occasionally head scratched with one foot.

AGONISTIC BEHAVIOUR **THREAT.** Aggression usually relates to territorial defence including times when neighbours try to steal nest-material. Three main levels of territorial display: (a) **Gawky Look**, which may incorporate (b) exposure of gape-stripe and may develop into (c) **Croaking**. **Gawky Look:** neck stretched forward fully, with head and bill making obtuse angle at throat; stare with concentrated attention, accentuated by white eye-flashes. May intensify to expose orange gape-stripe by parting minute contour feathers behind mouth; if this develops into **Croaking**, may provoke **Rapier Action** by partner (see below). Commonly signal to occupants of adjacent nests or passing birds by **Croaking:** while sitting-up or standing with spread raised tail, and bill pointing anywhere between horizontal or downwards up to 90° from horizontal, birds bend or rock forward while lifting and slightly parting folded wings and lifting tail farther to angle of 20–30° to body axis; open bill slightly, exposing orange gape-stripe, and vibrate mandibles slowly, uttering bursts of 3–4 croaking calls separated by pauses. When **Croaking** most intense, rock forward at same time as calls and bill may almost touch rim of nest or ground. Infectious, often stimulates **Croaking** chorus among neighbours. Most widespread during pre-egg period when a bird may display at more than one site; from incubation onwards more likely to display at nest-site only; when pair together at nest, jointly perform at intruder nearby; common among subadults, except youngest (4–5 years old). May precede or follow fighting; also seen between pairs (see below). Other threat displays have also been recorded. **Charge.** Run to threaten or attack another bird; common because some male owners of nests leave and stand elsewhere; when male hunting for nest investigates owner's nest, he charges back. When defending nest-site, chases intruder through colony, may emit loud **Wail:** bill open at widest while single strident call emitted. Given by both sexes. Also uttered by birds on landing, stepping onto or off nest or taking off. Often accompanied by **Flagging:** sharp turning of head from side to side as if keeping several birds in view. Most frequent when bird among others and not at nest. Most common aggressive display, **Gulping:** bird, usually sitting on nest, stretches and twists head and neck at intruder

(conspecific or predator) or occupant of adjacent nest with mandibles half open; with increased aggression, gulping actions or sounds made (no ejection of oil observed) and snapping of mandibles; seen in both sexes. Most frequent at start of season. Often fighting follows but if opponent out of reach, aggression redirected into **Ground Stabbing**, including pulling or shaking tussock grass. Sitting bird may pull overhanging wing or tail of occupant of adjacent nest but appears to be non-aggressive and result of long periods of inactivity; disturbed bird will Wail or Croak. **FIGHTING**. Rare, because escape almost always possible. Bills interlock and birds wrestle by twisting heads from side to side. Interspecific aggression seen when parents feeding young harassed by skuas and sheathbills; threaten with fierce lunges and snaps.

SEXUAL BEHAVIOUR **Aerial Activity** common early in season where birds fly repeated circuits over nests, landing and taking off every few minutes. Displays at or near nest-site as follows. Copulations begin within a few days of birds' return and before nests properly constructed. **COURTSHIP**. No obvious preliminary behaviour before copulation that could be called courtship. **GREETING AND MAINTENANCE OF PAIR-BOND**. Behaviour at nest-relief varies, involving short bouts of Croaking, mutual Rapier Action and mutual allopreening. **Croaking** (see above): appears also to function in individual recognition; pair at nest may give prolonged performances in unison; often indicative of subadults or pairs that have not yet established strong pair-bond; also seen between pairs, known to have bred before, towards returning partner, which sometimes responds in same manner. **Rapier Action**: lunges head and neck in straight line forwards and upwards with throat conspicuously swollen and bill open or occasionally closed, usually pointing to head of partner, while emitting throbbing call; tail fanned; held for 1-2 s, head then quickly withdrawn and action repeated. The higher the intensity, the lower the thrust. Response by other bird, often mirror-image of display. When performed in synchrony, one bird points as other withdraws. Seen in all age-classes, sometimes with occasional bill-snappings; may be associated with Scapular Action and Bowing, and evolve into Bill-clashing, Jabbing or, if partner quiescent, into allopreening. Acceptance of Rapier Action appears to signify recognition of close relationship. Reduced aggression between partners may be achieved by Scapular Action and Bowing. **Scapular Action**: stand with tail slightly fanned, quickly turn head and place bill on midline of back above folded wings, which are often slightly raised and opened, and remain motionless for 1-2 s; as head turned, spread tail widely. When bill enters feathers, preen-snaps may be heard. Variations: **Wing Action**, bill held on one side just above folded wing; **Leg Action**, bill held below folded wing or on top of thigh. Performed by male to reduce tension, independently or associated with Rapier action. **Bowing**: bend forward, bill pointing towards or touching feet, or between legs (**Sub-belly Bow**); sometimes slight sideways twist of neck to right or left often pushing bill into feathers at side of breast where two to three audible preening snaps made; variation is shallow quick bow, **Nod**. By both sexes, most often as part of duets including Croaking or Rapier Action. Bird may respond to another performing Rapier Action in manner that leads to **Bill-clashing**: bird hits bill of partner that is attempting Rapier Action with its bill, by lateral action, causing the two bills to clash together; both birds nearly always standing. May revert to Rapier Action itself. In more aggressive response **Jabbing**: bill-clashing more vigorous, with thrusting downwards towards partner. **ALLO-**

PREENING. Commonly seen throughout breeding; mostly round head and neck. If pair facing each other, one may preen crown, sides of face, chin or neck of partner; recipient presents untreated areas by moving its head; mutual allopreening also seen. Sometimes preening bird lays bill across nape of partner. Likely function to reduce aggression and strengthen bond between partners. **COPULATION**. Male steps onto female; sometimes shaken off; co-operation of female essential if male to stay on back. Once mounted, male stretches over and round female's head and preens female's breast; female's bill normally horizontal; male's bill taps female's so that it is rapidly pushed or knocked slightly to one side. Similar contact of bill in Buller's Albatross, described by Richdale (1949) as **Tattoo**, but did not appear to be associated with allopreening. Male dismounts immediately cloacae disengage. Usually pair remain sitting, with female on nest and male close beside. Afterwards, female sometimes preens her back where male had trampled and ruffles her plumage while male preens her head. After a while, male may force female off nest and take over. Copulation may be repeated several times; once six times in half an hour.

RELATIONS WITHIN FAMILY GROUP Sitting bird will repair nest by stretching out, scraping in new material with bill and then patting into nest with flat side of bill; also often appears to scrape nest-bowl with one foot, often accompanied by wing-stretching on same side; Tickell (1984) noted this commonly among chicks and fledgelings of all ages and considered it as muscle-stretching rather than nest-building. Both sexes share incubation and attend young. Nest-relief usually accompanied by short bouts of Croaking, mutual Rapier Action and allopreening. Waiting partner immediately takes over, usually within 15 min of arrival. Material sometimes collected by relieved partner before leaving colony. **FEEDING OF YOUNG**. Adult often Croaks during brief visit to feed young. Feeding may start within 3 min of landing and finish, with parent gone, in 10 min. **Begging**. Arrival of adult leads to widespread gruff calling from chicks in area; when parent approaches own chick, call intensifies and chick adopts submissive posture: **Head Away**, similar to Bowing or Scapular Action. Allopreening by parent intensifies chicks' response and leads to begging. Chick trembles bill on side of adult's bill (**Bill-rattling**). Parent responds to begging, by pivoting forward, contracting abdomen and regurgitating partially digested food. Chick inserts open bill within parent's mandibles. Usually several feedings follow at short intervals. **COMMUNICATIONS**. Response of chick to predator or intruder gradually develops by sitting up, emitting hollow snappings of mandibles and, at last resort, vomiting oil. Usually other chicks in area will chorus. First Croaking heard at 80 days old. That parents do not recognize own chicks shown by cross-fostering experiments, very likely because chicks do not leave nest (Tickell 1972). **DEPENDENCE OF YOUNG ON ADULTS**. Remain on nest until shortly before departing to sea, when independent.

VOICE Reasonably well known; comparative analysis with Buller's Albatross by Warham & Fitzsimons (1987) but sample small; descriptions in Tickell (1984). Information supplied by J.C. Stahl. Usually silent at sea; rather quiet (C.J.R. Robertson) or rather noisy (Tickell 1984; Warham & Fitzsimons 1987) at colonies; call mostly during pre-laying period; occasionally call in flight near nest-site. Three types of vocalizations recorded in adults: staccato braying Croak; loud strident, monosyllabic Wail; and barely audible Throbbing.

Sexual differences suggested in structure of Wail call but characteristics not analysed (Warham & Fitzsimons 1987). Vocabulary and structure of calls similar to other small albatrosses; compared to Buller's Albatross, Croak consists of shorter notes with less well-defined harmonic structure; Wail shows harmonic bands with finer frequency modulation (Warham & Fitzsimons 1987). **NON-VOCAL SOUNDS:** range of sounds produced by clashing of bills or mandibles. No pattern of individual differences or regional variations described.

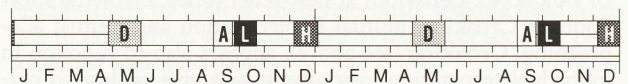
ADULT **Croak:** rapid bleating or braying *aaahaa-haahaaha* (Warham & Fitzsimons 1987) accompanied by bill vibration, emitted during Croaking display; uttered in bursts of 3–4 notes separated by regular or irregular pauses (Tickell 1984). Duration of calls 2.0 s; individual notes, 0.05 s long and repeated at 0.09 s intervals; frequency range c. 0–6 kHz (n=1; Warham & Fitzsimons 1987). Functions as indicating possession of territory and possibly in individual recognition. Noticeably different from Croaks of Buller's and Black-browed Albatrosses. **Wail:** drawn-out monosyllabic strident *mbaaaa* (Tickell 1984; C.J.R. Robertson). Duration 2.5 s; harmonics at c. 250 Hz intervals reaching 6 kHz (n=1); when stressed, maximum frequency (to 6.5 kHz) and frequency interval between harmonics (to 500 Hz) increase (Warham & Fitzsimons 1987). Functions as warning signal directed at surrounding birds when landing or taking off; also stress-call when charging or being charged by another bird; sometimes given in flight, either after take-off or before landing. **Throbbing Vocalization:** low-frequency, low-amplitude call emitted by male during Rapier Action; equivalent to Groan of Buller's Albatross. **NON-VOCAL SOUNDS.** Several sharp percussive sounds reported, but not well described; produced by contact of upper and lower mandibles or by contact of bills of two birds, and used in particular circumstances: (A) **Tattoo** (= Bill Rattle of Tickell) produced by actions of male during Copulation; (B) **Mandible Spar:** produced during Rapier Action. (C) **Bill-clashing.** (D) **Bill-Clop:** produced by rapidly closing bill during Gulping Display. **Bill-rattle.** Castanet-like sound produced by contact of upper and lower mandibles as bird shakes head. Muted clicks or clocks made during Scapular-action.

YOUNG Chicks beg with gruff continuously repeated *wa wa wa* (Tickell 1984) before and during feeding; begging chicks bill-tap at base of parent's bill. Chicks first gave Croaks at about 80 days old (Tickell 1984).

BREEDING Fairly well known. Detailed studies: S. Georgia (Tickell & Pinder 1975; Ricketts & Prince 1981; Astheimer *et al.* 1985). Also data from Marion I. (van Zinderen Bakker 1971); Iles Crozet (Despin *et al.* 1972; Weimerskirch *et al.* 1986); Macquarie I. (Copson 1988); Campbell I. (Bailey & Sorensen 1962; Robertson 1980). Information supplied by J.C. Stahl. Breed in small (15 pairs) to huge (10 000 pairs) colonies on coastal cliffs or nearby hill-slopes, often associated with other species of albatross.

SEASON Broadly Sept.–May. Arrival in first half Sept. at Marion, Crozet, Macquarie and Campbell Is. At S. Georgia, males (22) arrived 16 Sept.–5 Oct. and females (22) 21 Sept.–7 Oct.; pre-breeding period, 26 days (5.6; 14–45; 41) when males ashore on 53% of days and females on 9%; pre-laying exodus of females of 15 prs, 16.4 days (5.2; 11–25), returning about 16 Oct. (12–19); copulations occurred 23 Sept.–5 Oct. and last seen 1 day before laying, fertilization probably about 14 days before laying. Laying, end Sept. to end Oct. (details below). Hatching at most localities, mid-Dec. to

early Jan. Successful breeders leave when chicks fledge: Macquarie I., end Apr.–end May or early June; Campbell I., early to mid-May; S. Georgia, about 19 May (5 May–17 June; 180). Unsuccessful breeders leave S. Georgia soon after failure; non-breeders, by 1 Mar. Essentially breed once every two years (Tickell & Pinder 1967; Copson 1988) but important variations from year to year. At S. Georgia, 58% of unsuccessful breeders nested again one year later but during 7 years proportion varied from 34 to 83%, few birds coming into condition in season after food shortage and about 1% not breeding at all in the 7 years. Of successful breeders, up to 1.9% bred again one year later; during 6 years, 61% bred 2 years later but proportion varied from 30 to 78% and about 1% did not breed at all in the 6 years (Prince 1985). Monogamous habits lead to breeding by males only once in every two years because development of testes occurs only after nesting cycle is finished; in females, development of ovary blocked by progesterone secretion, probably induced by nutritional factors during season following successful nesting. Of successful breeders, 39% return to colony next season, perhaps to defend nest-site or to maintain pair-bond or both (Hector *et al.* 1986).



SITE On cliff ledges, often muddy, or on steeply sloping shelves among tussock.

NEST, MATERIALS Column of packed soil and grass with bowl-shaped depression at top. Material gathered from round nest, sometimes from nearby nests, which can lead to fierce fights (Rand 1954; Bailey & Sorensen 1962; Tickell & Pinder 1975; Tickell 1984). Nest probably often used by same pair in different seasons but biennial breeding probably leads to some changes (Tickell & Pinder 1975). **MEASUREMENTS:** height, 10–45 cm; outside diameter at base, 30–40 cm, at top, 25–28 cm; depth of cup, 5–9 cm (Bailey & Sorensen 1962; Despin *et al.* 1972; Tickell & Pinder 1975). Nests renovated at start of breeding season. Some new nests built on remains of older ones. Incubating birds continue improvements with material collected by relieving partner before it leaves (Despin *et al.* 1972; Tickell 1984).

EGGS Oblong, elongate; somewhat rough shell, like egg of hen (Emerson 1886); dull white with varying ring of fine red-brown spots at broad end (Tickell & Pinder 1975).

MEASUREMENTS:

Marion I.: 107.9 (101.5–114.4; 11) x 68.5 (65.9–71.7) (Rand 1954);

Iles Crozet: 103 (98.9–108; 3) x 69 (68.9–69.1) (Despin *et al.* 1972);

Campbell I.: 106.8 (4.3; 98–116; 124) x 67.3 (2.0; 61–72) (Robertson 1980);

S. Georgia: 106 (3.9; 93–114; 63) x 68 (2.5; 60–72) (Tickell & Pinder 1975).

WEIGHTS:

Campbell I.: 213–269 (n=12; Bailey & Sorensen 1962);

S. Georgia: 276 (14; 180–330; 63) (Tickell & Pinder 1975).

CLUTCH-SIZE One. At S. Georgia, two eggs found in 1–2% of nests, always laid by two females (Tickell & Pinder 1966). No replacement laying.

LAYING Well synchronized within colonies and between breeding localities: Iles Crozet, 10 Oct. (3 days; 30 Sept.–21 Oct.; 93) (Weimerskirch *et al.* 1986); Macquarie I., start mid-Oct., peak third week Oct. (Copson 1988); Camp-

bell I., 28 Sept.–9 Oct. (Robertson 1980); Diego Ramirez I., before 20 Oct. (Johnson 1965); S. Georgia, 19 Oct. (3 days; 12–31 Oct.; 278) (Tickell & Pinder 1975), 17 Oct. (3 days; 13–21 Oct.; 15) (Astheimer *et al.* 1985). Laying dates vary little from year to year.

INCUBATION Shared equally by both sexes. At Iles Crozet, first shift shortest, by female, 3.1 days (2.1; 0–8; 18); sixth shift longest, by male, 10.4 days (2.5; 6–15; 16) (Weimerskirch *et al.* 1986). At Iles Kerguelen, average length of shifts 10.5 days during second half of incubation (Weimerskirch *et al.* 1986). At S. Georgia, 5–10 shifts, eighth shortest, by male, 3.6 days (3.5; 1–11; 6); fourth longest, by male 14.5 days (3.5; 1–22; 34) (Tickell & Pinder 1975). Number and length of shifts vary from year to year, possibly because environmental factors differ (Astheimer *et al.* 1985). Mean loss of weight during shifts 45 g/day in males, 43 g/day in females (Prince *et al.* 1981); mean increase in mass during days at sea, 118 g/day (Costa & Prince 1987). **INCUBATION PERIOD:** Iles Crozet, 73.2 days (1.3; 71–75; 18) (Weimerskirch *et al.* 1986); at S. Georgia, 72.4 days (1.6; 69–78; 103) (Tickell & Pinder 1975).

NESTLING Semi-altricial, nidicolous. Chipping to emergence takes about 4 days. Hatched covered in pale-grey down (Tickell & Pinder 1975). At Iles Crozet, brooded for 23.1 days (3.8; 18–32; 15) by both parents in alternate shifts of 2.4 days (1.1; 1–6; 135). At S. Georgia, brood-stage lasts 22.6 days (2.8; 18–27; 27); mean length of shifts 2.9 days (1–7; 196). Chick fed by both parents until fledging. Feeding by incomplete regurgitation, chick inserting its open beak crosswise between mandibles of parent (Bailey & Sorensen 1962; Tickell 1984). Nestling period: S. Georgia, 141 days.

GROWTH At S. Georgia, weight at hatching, 197 g (33; 150–260; 25). Growth from 10 to 90% of asymptotic weight takes 60 days with mean daily gain of 63 g. Maximum weight, 4655 g (613; 3294–6049; 116) or 126% adult mass after 92–95 days. Weight at fledging, 3355 g (395; 2471–4061; 33) or 91% adult mass (Tickell & Pinder 1975; Ricketts & Prince 1981). Growth faster and higher asymptotic mass reached when experimentally fostered by *D. melanophrys* because feeds are more often and food contains more energy (Ricketts & Prince 1981). At Iles Crozet, mean daily gain of weight, 60 g or 1.7% adult mass at age 8–58 days (Weimerskirch *et al.* 1986).

FLEDGING TO MATURITY Independent of parents on fledging. At S. Georgia, of 34 birds banded as chicks, one (3%) returned when 2 years old, eight (23%) when 4 years old, and 25 (74%) when 5 years old (Tickell 1969). At Macquarie I., immatures return after 6–11 years (Copson 1988); at Campbell I., when at least 6 years old (Robertson 1980). Age of first breeding, at least 7 years old at Macquarie I. (Copson 1988); at least 9 years old at S. Georgia, mean 13 years old (Croxall 1982).

SUCCESS Hatching success: S. Georgia, 54.3% (127 eggs); Macquarie I., 83.3% (58.1–94.1 over 7 years: 28–51 eggs). Fledging success: S. Georgia, 87.3% (606 chicks); Macquarie I., 86.9% (66.7–100 over 7 years; 17–40 chicks). Important year-to-year variations in total breeding success: S. Georgia, 46.4% (12.9; 21.6–64.0 over 8 years; 250–444 eggs laid) (Prince 1985). Macquarie I., 72.3% (11.5; 58.0–85.7 over 7 years; 28–51 eggs laid). At S. Georgia, mean annual survival of adults 95% (Croxall 1982). Unattended eggs and young chicks taken by skuas and sheathbills (Bailey & Sorensen 1962; Tickell & Pinder 1975). At Iles Crozet, some loss of eggs, chicks and adults caused by landslides on wet slopes (Despin *et*

al. 1972). Wild sheep may cause heavy local desertions (Bailey & Sorensen 1962). At S. Georgia, success less affected by annual variations in availability of food than in Black-browed Albatross (Prince 1985).

PLUMAGES

ADULT Definitive basic; unknown if attained long before age of first breeding. **HEAD AND NECK**, slightly bluish grey (c87) with lighter (bluish 85) forehead and forecrown, merging to pale-grey (c86) chin, throat and interramal region. Foreneck, and sometimes lower throat, white. Feathers of lower eyelid short, white, forming curved lined just below eye. Small dark-grey (83) supercilium, narrowest above eye, extends about half eye-width in front of and behind eye. All feathers have white bases, most extensive in hindneck and throat; these areas tend to look paler, especially when worn, through exposure of bases. **UPPERPARTS**. Mantle as hindneck. Back and scapulars, black-brown (c119), fading to dark brown (119A) with wear. Feathers have narrow open pennaceous tips; dark brown (121) when fresh, pale brown when worn. Rump and upper tail-coverts, white. **TAIL**, black-brown with strong grey (84) gloss when fresh, fading to dark brown (119A) with wear; all feathers have white shafts. **UPPERWING**. Tertiaries and all coverts black-brown (c119) with dark-brown (121) open pennaceous tips when fresh; dark brown (119A) with paler brown tips when worn. Remiges, black-brown (c119) when fresh, dark brown (119A) when worn; grey (84) basal half of inner edges merges to concealed white bases. White base of primary shafts usually concealed; those of outer primaries exposed in flight. **UNDERPARTS**, white. **UNDERWING**, white, with broad dark leading-edge, tips and narrow trailing-edge. Leading-edge c. 30% of width of wing at base, c. 50% at elbow (where widest), about one-quarter of width at carpal joint (where narrowest), about one-third width between carpal joint and p10. Dark leading-edge formed by black-brown (119) marginal coverts, first two rows of lesser coverts, outermost median and greater primary coverts; these feathers fade to dark brown (119A) with wear. Third row of lesser coverts, black-brown (119) between axilla and point, one-third of distance between elbow and carpal joint; those outside, white with light grey-brown patches in centre, sometimes making border of dark leading-edge look slightly blurred. Fourth row of lesser coverts, brownish grey (brownish 84) at elbow, whitish elsewhere. Other under wing-coverts, white; long subhumeral have grey (brownish 84) basal halves, and many greater coverts have light grey (brownish 85) smudges near end. Remiges, grey-black (c82) in diffuse light; can appear light grey (85) when reflecting direct light. Remiges more reflective near base; bases of outer primaries usually exposed in flight.

DOWNY YOUNG Mostly covered by long grey-white down, with pure-white facial mask of very short down.

JUVENILE **HEAD AND NECK**. When very fresh, crown, nape, throat and hindneck grey (84), slightly lighter on forehead; darker and less blue than adult. All feathers have white bases and grey (84) tips; tips broadest on hindneck and hindcrown, narrowest in facial area, central throat and sides of uppermost throat. With wear, some grey tips lost, leaving grey (84) hindcrown, hindneck and half-collar at sides of lower throat. Cheeks are first areas to appear white with wear. Foreneck white, meeting darker throat perhaps sharply when plumage fresh but junction becomes indistinct with wear. Dark grey eye-patch larger than in adult, extending half dis-

tance to bill. UPPERPARTS. Mantle grey (84), rest as adult. TAIL, UPPERWING, as adult. UNDERPARTS, white, with grey (84) axillaries. At sides of upper breast, feathers have grey (84) tips. UNDERWING. Remiges, as adult but humerals grey (84), reflecting light grey (85) at bases in some direct light. Greater coverts, grey (84). Median coverts, grey-black (82) near elbow, grey (84) elsewhere. Other coverts, grey-black (82).

IMMATURES HEAD AND NECK, and mantle: for about first 4 years, similar to worn juveniles, described above; vary somewhat. In darkest, neck and crown, grey (84), contrasting with pale-grey to white face and forehead. In palest, grey restricted to hindneck and narrow half-collar at sides of mid-neck. Head and neck probably become paler with wear; tendency for paler-headed birds to have more white on underwings, and more yellow on bill, but many exceptions show that paleness of head is not directly related to age, and that there must be distinct generations of immature feathers on head and neck. Final colour of head and neck attained in most at 5 years (Tickell 1969). UNDERPARTS. Axillaries white, with light-grey wash at base becoming less extensive with age. UNDERWING, usually assumes adult pattern more slowly; 8-year-old birds at Campbell I. had small white central patch surrounded by wide grey-brown before black outer margins (C.J.R. Robertson). Time taken for underwing to change probably varies; some birds at sea with immature head-pattern have paler underwing than 8-year-old birds from Campbell I. Fourth, and perhaps third row of lesser coverts grey (brownish 84) except near elbow, where blackish; they make boundaries of dark leading-edge poorly defined. Greater coverts, and median coverts between elbow and carpal joint, white with grey (brownish 84) tips; tips become narrower with age and these are first underwing feathers to appear predominantly white. Subhumeral, longer coverts near elbow, and median primary coverts, white with grey (c84) wash at tip of inner webs, and blackish outer webs. Outer webs give these areas streaked appearance; they are last areas to develop adult coloration.

BARE PARTS Based on photographs (Harrison 1987; Lindsey 1986; Aust. RD; NZRD) and labels at NMNZ, except where stated.

ADULT Iris, dark brown (c21); dark olive-green (Murphy). Bill, grey-black (82) to black (89), with buff-yellow (53) culminicorn, and underhalf of proximal two-thirds of ramicorn. Strip of skin at base of ramicorn buff-yellow (53) to buff-orange (118). Rigid skin of gape, yellow (Falla 1937) to orange (NMNZ). Most of maxillary unguis, light peach-red to orange; tip, pale horn (92). Legs and feet, whitish, with blue-grey (c88) to grey-mauve suffusion, strongest on toes, and pinkish (c7-4) suffusion, strongest on webs and tarsus. Claws, buff-yellow (53).

DOWNY YOUNG Iris, as adult. Bill and rictus, grey-black (82). Edges of bill plates, and yellowish trace at base of mandibular rami visible before fledging (Tickell & Pinder 1975; van Zinderen Bakker 1971). No information on colour of feet.

JUVENILE Iris and feet, as adult. Bill, mostly medium to dark brown-grey, contrasting with grey-black (82) unguis. Naricorn, grey-black (82); emergent buff-yellow gives brownish tinge to mandibular rami and later to culminicorn.

IMMATURE Bill, adult colour assumed slowly; in 2-year-old bird, culminicorn just beginning to turn yellow. In 5-year-old birds, bill similar to adult, but yellow usually paler,

variably streaked black or brown; maxillary unguis turning to orange in most, but obscured by black in some (Tickell 1969). Unknown when full adult colour attained.

MOULTS

ADULT POST-BREEDING Primaries probably replaced in staffelmauser, interrupted during breeding season. Breeding usually biennial; of seven fully adult skins examined (MV) only one had no old primaries, which suggests primary moult seldom completed in a year, and presumably interrupted in summers when no breeding occurs. Visitors to breeding grounds that bred successfully in preceding season have very worn plumage, active breeders have fresher plumage (Tickell & Pinder 1975).

POST-JUVENILE, SUBSEQUENT MOULTS Black-billed immature with pale horn appearing on culminicorn and mandibular rami, beachcast Vic., 26 May, had primary moult $N^13^1O^13^1N^2O^3$. An immature beachcast in NZ on 12 May was in complete moult (Falla 1937). No moult recorded in 5-year-old birds at S. Georgia between late Oct. and early Jan. (Tickell 1969).

MEASUREMENTS (1) Campbell I., live birds; methods unknown (Westerskov 1960). (2) S. Georgia, includes adults and 5-year-old non-breeders; methods unknown (Tickell & Pinder 1975).

	MALES	FEMALES	
WING	(1) 516 (12.21; 499-535; 10) (2) 531 (9.61; 512-550; 14)	517 (11.06; 500-540; 33)	**
TAIL	(1) 203 (3.67; 197-210; 10) (2) 220 (4.14; 219-230; 14)	211 (6.31; 202-223; 15)	**
BILL	(1) 111.2 (3.14; 108.0-116.6; 10) (2) 115.8 (2.24; 113-121; 14)	113.8 (2.64; 109-118; 15)	*
TARSUS	(1) 88.6 (2.65; 83-92; 10) (2) 83.6 (2.29; 78-88; 14)	82.8 (2.17; 80-87; 15)	
TOE	(1) 145.1 (4.47; 138.8-154.3; 10) (2) 135.3 (3.24; 128-140; 14)	132.1 (3.00; 126-137; 15)	**

(3) Vic. beachcasts and Macquarie I., definitive skins (MV). (4) Iles Crozet, live birds; methods unknown (Weimerskirch *et al.* 1986). (5) Iles Kerguelen, live birds; methods unknown (Weimerskirch *et al.* 1989). (6) Macquarie I.; wing methods unknown (C.J.R. Robertson).

	UNSEXED	
WING	(3) 510 (21.57; 470-529; 7) (4) 519.6 (15.9; 485-541; 33) (5) 515.5 (10.7; 496-540; 33) (6) 517 (489-552; 28)	
8TH P	(3) 291.3 (11.03; 277-304; 7)	
TAIL	(3) 197.1 (10.92; 181-208; 7) (6) 211 (195-223; 28)	
BILL	(3) 113.3 (3.50; 106.2-118.4; 7) (4) 112.4 (3.6; 102-120; 41) (5) 111.3 (3.6; 103.5-117.5; 40) (6) 115.1 (108-125; 28)	
TARSUS	(3) 86.1 (3.30; 80.3-89.4; 6) (4) 86.5 (4.0; 83-94; 32) (5) 81.1 (3.9; 75-92; 33) (6) 88 (82-93; 28)	
TOE	(3) 123.7 (5.14; 114.1-129.7; 7) (6) 127 (114-133; 28)	

WEIGHTS (All in kg). At Campbell I.: males 3.38 (3.1–3.7; 13), females 2.98 (2.8–3.2; 10; C.J.R. Robertson). At Macquarie I., 3.24 (2.6–3.8; 28; C.J.R. Robertson). At Iles Kerguelen, 3.38 (0.35; 2.80–4.15; 43; Weimerskirch *et al.* 1989). At Iles Crozet, 3.48 (0.3; 2.80–4.15; 31; Weimerskirch *et al.* 1986). At S. Georgia, males 3.68 (0.428; 3.10–4.35; 12), females 3.61 (0.481; 2.84–4.18; 8; Tickell & Pinder 1975); on average both sexes lose 1.2% of body weight per day during incubation shifts (Prince *et al.* 1981). NZ and Vic. beachcasts, with little or no fat, 2.50 (0.319; 2.10–3.24; 11; MV, NMNZ).

STRUCTURE Wing, long and narrow. Eleven primaries, p10 longest, p9 8–19, p8 33–48, p7 68–91, p6 114–137, p5 154–183, p4 194–228, p3 220–267, p2 254–297, p1 275–326; p11 minute. Twenty-five secondaries and about seven tertials; nine humerals. Tail, strongly rounded, 12 feathers (13 recorded once); t1–t6 34–52. Bill, rather long and narrow; maxillary unguis, hooked; mandibular unguis, downcurved. Nostrils, small, in groove between culminicorn and latericorn; naricorn broad. Culminicorn, rounded at base, sides parallel. Tibia, feathered. Tarsus, scaled, slightly compressed; feet webbed; no hind toe. Middle toe longest, outer c. 97%, inner c. 83%.

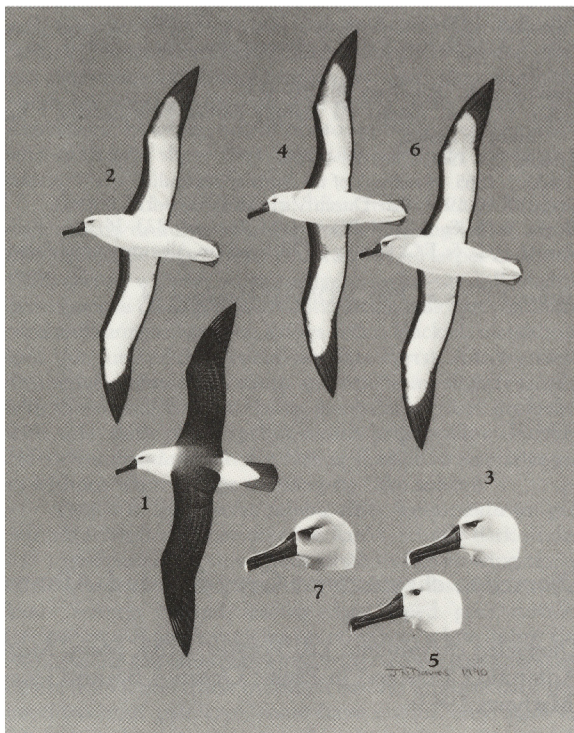
GEOGRAPHICAL VARIATION No subspecies recognized (Peters). Birds from S. Georgia may be larger than those from NZ islands.

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Volume 1 (Part A), Plate 20

Grey-headed Albatross *Diomedea chrysostoma*

- 1. Adult, dorsal
- 2. Adult, ventral
- 3. Immature, ventral
- 4. Juvenile, ventral
- 5. Adult, head

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