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## Order PELECANIFORMES

Medium-sized to very large aquatic birds of marine and inland waters. Worldwide distribution. Six families all breeding in our region. Feed mainly on aquatic animals including fish, arthropods and molluscs. Take-off from water aided by hopping or kicking with both feet together, in synchrony with wing-beat. Totipalmate (four toes connected by three webs). Hind toe rather long and turned inwards. Claws of feet curved and strong to aid in clambering up cliffs and trees. Body-down evenly distributed on both pteryiae and apteria. Contour-feathers without after shaft, except slightly developed in Fregatidae. Pair of oil glands rather large and external opening tufted. Upper mandible has complex rhamphotheca of three or four plates. Pair of salt-glands or nasal glands recessed into underside of frontal bone (not upper side as in other saltwater birds) (Schmidt-Nielson 1959; Siegel-Causey 1990). Salt-glands drain via ducts under rhamphotheca at tip of upper mandible. Moist throat-lining used for evaporative cooling aided by rapid gular-flutter of hyoid bones. Tongue rudimentary, but somewhat larger in Phaethontidae. Throat, oesophagus and stomach united in a distensible gullet. Undigested food remains are regurgitated. Only fluids pass pyloric sphincter.

Sexually dimorphic plumage only in Anhingidae and Fregatidae. Selection of nest-site and initiation of pair-formation by male, but in Pelecanidae female first leads several males in a male-selection (or persistence) chase as in ducks. Nest built by female with material brought to nest-site mainly by male. Copulation normally on nest-site. Both sexes take turns guarding nest-site, incubating eggs, and brooding and feeding chicks. Eggs unicoloured with chalky finish except for Phaethontidae. Webbed feet used to warm eggs. Chicks hatch naked (except in Phaethontidae) and blind. Later fully covered with down for several weeks. Newly hatched chicks take fluid food from tip of parental bill. Older chicks take partly digested food from parental gullet, except in Phaethontidae, in which parent inserts bill into gullet of chick. Chicks become independent usually within a few weeks after fledging and at fledging in gannets *Sula* spp. At nesting colonies severe loss of eggs and chicks may result from human disturbance, parents being forced off nests, so that eggs and chicks become cold or overheat or are taken by predators.

Anatomical and behavioural similarities suggest close phylogenetic affinities between Pelecaniformes and Ciconiiformes, which could perhaps be united. Cottam (1957) found skeletal characters that suggest that the Shoe-billed Stork *Balaeniceps rex*, only member of the African family Balaenicipitidae, ought to be in Pelecaniformes rather than Ciconiiformes. Linnaeus (1758) included all pelecaniform birds known to him, except those in *Phaethon*, in the genus *Pelecanus*, from which Brisson (1760) removed the genera *Sula*, *Anhinga*, *Phalacrocorax* and *Fregata*. Subsequently these genera became the bases of six families in the order Pelecaniformes, formerly known as the Steganopodes. Over the last 200 years there has been debate about whether *Phaethon* and even *Fregata* ought to be included, and whether *Anhinga* ought to be in the same family as *Phalacrocorax*. There is ample behavioural (van Tets 1965), osteological and palaeontological (Olson 1985) evidence to demonstrate that there are six distinct extant families in the Pelecaniformes.

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## Family SULIDAE gannets and boobies

Large to fairly large seabirds, occurring in all oceans except n. North Pacific and s. Southern Oceans. Nine species in two groups: six boobies and three gannets. Though treated here, after Peters, in one genus, for a long time many authorities have proposed two genera: *Sula* (s.s.) for boobies and *Morus* for gannets. Recently a third genus *P. pasula* has been recognized for the forest-booby *S. abbotti*. All are separated on behavioural and osteological characters such as distinctive hypotarsus and number of ossicles per sclerotic ring (Nelson 1978; Olson & Warheit 1988; van Tets et al. 1988). The family appears close to the ancestral stock that gave rise also to the Anhingidae, Phalacrocoracidae, Fregatidae and to the extinct Pelegornithidae (bony-toothed seabirds), Protoplotidae (slender volant divers) and Plotopteridae (robust flightless divers) (Olson 1977, 1985; van Tets 1965; van Tets et al. 1989).

Short thick neck; elongate body; long pointed wings, 11 primaries (p9 or p10 longest) and about 28 secondaries, diastataxic; wedge-shaped, medium-long tail with 12–16 rectrices. Sturdy cone-shaped bill, slightly decurved at tip; cutting edges serrated. Naked skin on gular and facial areas, more extensive in boobies so that eyes set well within bare areas and with thick fleshy eye-ring. Secondary external nares (Ewart 1881; Macdonald 1960). Ventral skin strongly pneumatic with large subcutaneous air-sacs, built for plunge-diving. Plumage, mostly white with black on wings. Some species with white, grey or brown morphs. Bare parts, often brightly coloured. Oil gland, feathered. Sexes similar except in colours of bare parts in some species. Juveniles differ from adults, reaching full adult plumage in 2–4 years. Stance upright, tilted slightly backwards; gait waddling. Diving almost vertical in gannets; at fairly low angle in boobies. Flight, alternate periods of flapping and gliding, often quite high above water. Swim well with head high and tail above water.

Distributed in all temperate and tropical oceans. Gannets are typical of temperate-zone seas and may reach tropics on migration; the three species, of which one breeds and one is a rare vagrant in our region, are allopatric. These are sometimes treated as subspecies of the Northern Gannet *S. bassana* but differ enough in size, distribution of black in wings and tail, length of throat-stripe and pattern on tarsus to be treated as separate species, composing a superspecies. Boobies (excluding Abbott's) are tropical and subtropical; five species, of which three breed in our region, in sympatry. The one species of forest-booby is now confined to Christmas I. (Ind.) but formerly was more widespread (Bourne 1976; Nelson 1974; Olson & Warheit 1988). Strictly marine, inshore and offshore rather than pelagic, except for some boobies, with rather aerial habits, tending to fly quite high. Plunge-dive for food, often spectacularly so when in feeding flocks. White plumage of most species conspicuous, even at considerable distance. Feed chiefly on fish, especially on shoaling species (gannets) or on flying fish (boobies). Migratory and dispersive; juvenile and immature birds may be more so than adults.

Monogamous pair-bond, often long-lasting and probably maintained only at nest-site. Defend nest-site territories. Pairs use same site year after year. Breed mainly in large dense colonies on islands and sometimes on mainland; on cliffs and stacks or on flat sandy cays. Usually nest on ground but *S. abbotti* is entirely arboreal. The Red-footed Booby *S. sula* also nests and roosts in bushes and trees and the Brown Booby *S. leucogaster* perches in trees and bushes but nests on ground. All other species roost and nest on ground. Various displays at breeding grounds for greeting, male-advertising and flight-intention such as sky-pointing, a precursor of various displays in other Pelecaniformes and related to the stretch-display of ardeids (van Tets 1965). Breeding annual and strictly seasonal in gannets; more protracted in boobies, in which it may be non-seasonal and less than annual in some species; in *S. abbotti*, if successful, only once every 2 years. Nests vary from mere shallow depressions on ground without material to substantial heaps of vegetation and debris cemented with guano or to simple stick-nests in trees. Both sexes build but male typically brings material. Density of nests in colonies closest in gannets; often quite dispersed or even solitary in boobies. Eggs, ovate, pale green, blue or white staining brown, with chalky coating. Clutch-size, 1–4, laid at intervals of about 5 days. Replacement laying after loss. Incubation starts with first egg; by both sexes in roughly equal shares; eggs incubated in feet; no brood-patch. Incubation period, 40–55 days. Egg-shells left in nest or discarded. Hatching asynchronous. Young, altricial, nidicolous, downy. Cared for and fed by both parents, usually by incomplete regurgitation. Brooded continuously for 2–3 weeks, then guarded for as long as possible (boobies) or to fledging (gannets). If two chicks hatch from clutches of two, typically only one survives. Nestling period, 85–175 days, with great variation in boobies, depending on food supply. Age at maturity, 4–6 years.

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*Pelecanus Leucogaster* Boddaert, 1783, *Tabl. Planches enlum.*: 57; based on 'Le Fou de Cayenne' of Daubenton, 1765–81, *Planches enlum.*: Pl. 973 — Cayenne.

Leucogaster from the Greek λευκός (white) and γαστήρ (belly) clearly refers to the outstanding plumage character.

OTHER ENGLISH NAMES Brown or Black Gannet, Common Booby, White-bellied Booby or Gannet.

Brown is the obvious choice for this species, which is the brownest of the boobies, at least when adult.

POLYTYPIC Nominate *leucogaster* Red Sea, Atlantic and Caribbean; *plotus* (J.R. Forster, 1844), in e. Pacific from Pitcairn and Bonin Is (Japan), W through Indonesia and Aust. to e. African coast; *brewsteri* Goss, 1888, and *etesiaca* Thayer & Bangs, 1905, in far e. Pacific. All doubtfully distinct.

**FIELD IDENTIFICATION** Length 65–75 cm; wing-span 130–150 cm; weight 900–1500 g. Medium-sized sleek-looking dark-coloured booby with sharply demarcated brown-and-white underparts. Typical sulid shape, but rather small with longish bill and neck, slender body, pointed tail and narrow wings; about 20% smaller than Australasian Gannet *S. serrator*. Sexes similar, distinguishable by colours of bare parts; females average slightly larger. No seasonal differences in plumage. Juveniles and immatures separable by mottled belly.

**DESCRIPTION** ADULT MALE. Upperparts, neck, throat and upperbreast, uniform dark-brown, sharply demarcated from brilliant white lower breast, belly, flanks and vent; undertail, dark brown. Underwing margin dark-brown with broad white centre to innerwing; all remiges, brown, forming dark trailing-edge, broadening towards outerwing where primaries and primary coverts form dark wing-tip; narrow dark-brown leading-edge extends from carpal joint, broadest at carpal. Rest of underwing, white, continuous with white underparts. Bill, long, slender and pointed, bluish grey with deep-blue base. Bare skin of face, eye-ring and gular area, deep blue (like base of bill). Iris, cream, grey, yellow or dark brown. Legs and feet, greenish yellow. ADULT FEMALE. Plumage as for male. Bare skin of face, eye-ring and base of bill, yellow; rest of bill, greenish, yellowish or greyish. JUVENILE. Upperparts, neck, throat and upperbreast, similar to adult but paler brown. Lower breast, belly, flanks and vent, greyish brown flecked with darker brown, still with obvious demarcation between upper and lower breast but less regular and

not sharply defined as in adult. Underwing, like adult but white of innerwing is mottled, duller and not sharply defined from darker borders. Bill and facial skin, dark greyish blue. Iris, light grey-brown to light grey or light blue-grey. Legs and feet, dull orange-grey. IMMATURE. Similar to juvenile, with underparts and underwing gradually whitening and bill becoming paler and developing adult colour.

**SIMILAR SPECIES** Adults distinctive; juveniles and immatures only likely to be confused with other boobies. **Juvenile Masked Booby** *S. dactylatra* differs by white collar, dark-grey bill, more white on underwing, less clean-cut and paler brown appearance, pale underparts with brown mottling, and indistinct demarcation between breast and belly. **Juvenile Red-footed Booby** *S. sula* entirely brown with uniform mottled brown underparts with no demarcation between upper and lower breast, darker bill and darker underwings with no white patches. Older **brown-morph Red-footed Booby**: white tail, uniform pale-brown underparts with no demarcation between upper and lower breast, dark underwings and blue and pink bill.

At sea, fly and feed individually or in flocks, sometimes large mixed-species flocks; often travel in extended skeins. Fly more lightly than other boobies (except Red-footed) and gannets, low over water with glides and bursts of smooth wingbeats. In high winds also glide albatross-like over waves. Pelagic; occur close to shore more often than other boobies. Feed by plunge-diving, less often by aerial-pursuit or pursuit-plunging. Flocks rest by day and roost at night on sandbars, islands, rocks, beacons etc, often in company with terns, nod-

dies and gulls. Sometimes rest on sea with body horizontal and buoyant, head held high. On land, walk with duck-like waddle. Rarely call in flight but do so when fishing or squabbling over food. Noisy at breeding colonies, males giving high-pitched whistles and females harsh quacking or honking.

**HABITAT** Marine, occurring in, but not restricted to, tropical waters of all major oceans. Sight records off coast of Java, where upwelling of cold, nutrient-rich water attracts small fish (Becking 1976). In Tropical Zone may depend on cool waters for feeding, especially when breeding; breeding failure on Christmas I. (Pac.) during El Niño Southern Oscillation, when sea surface-temperature high and food supply poor (Schreiber & Schreiber 1984). Feed in shallow and deep water; in South America, and probably elsewhere, feed beyond breakers, flying parallel to shore, and in areas of rough water where water masses converge (Duffy 1985). In central Pacific, mainly near breeding islands, though some birds 300–1500 km from nearest breeding site (King 1970). Approach mainland coastline more than other boobies; in coastal waters, harbours and estuaries and near offshore islands (Nelson 1978). Off nw. WA, most abundant 18–36 km from land, but also occur inside and outside these limits; within 18 km limit, concentrated where wavelets about 2 m high (just high enough to break), and sea surface-temperature  $<25.5^{\circ}\text{C}$  (Abbott 1979). Seldom fly over land; take most direct route from sea to nest-site (Christmas I. [Ind.]; Gibson-Hill 1947).

Breed on tropical islands remote from continental coastline; on continental islands or sand cays and atolls. Some cays used for nesting as low as 1 m above high water (Limpus & Lyon 1981; King & Limpus 1983); submerged by highest tides and storm-waves and physically unstable under action of winds, currents and waves (e.g. King & Limpus 1983; Walker & Jones 1986). Variety of habitats accepted for nesting; from rugged rocky terrain (cliffs, steep slopes) on larger islands, to beaches, coral rubble and guano flats on cays (Gibson-Hill 1947; Serventy 1959; Stoddart et al. 1981; King et al. 1983; King 1986); do not need sheltering vegetation but may use it where present (Gibson-Hill 1948).

Plunge-dive to unknown depths in shallow waters (BWP). Fly low, seldom  $>30$  m above sea surface. Roost on ground on breeding and other islands, on beaches, sand bars, rocks (Serventy 1959; Warham 1961).

Guano mining on some islands may have depleted colonies (Ellis 1933), but have recovered on most islands no longer mined. Some areas of Christmas I. (Ind.) where there is no breeding probably affected by settlement and associated disturbance and predation, and settling of dust from phosphate drying plant (Woehler 1984). Readily roost on artificial structures (navigation beacons, buoys, piles, railings, shipwrecks) (Serventy 1959; Abbott 1979).

**DISTRIBUTION AND POPULATION** Most common booby, occurring through all tropical oceans approximately bounded by latitudes  $30^{\circ}\text{N}$  and  $30^{\circ}\text{S}$  except for possible gap offshore in e. Pacific Ocean; not common in Indian Ocean E of Seychelles or in broad band NW to SE through e. central Pacific Ocean.

**AUST.** From Bedout I., WA, round coast of NT to Bunker Grp, Qld with occasional reports further S: Bowen I., NSW, Jan. 1978 (Aust. Atlas); Montagu I., NSW, Apr. 1976 (NSW Bird Rep. 1976); adult, Altona, Vic., May 1965 (Anon 1965); Pt Lonsdale, Vic., July 1973 (Smith et al. 1974). More recent reports suggest fairly common S to Tweed Heads,

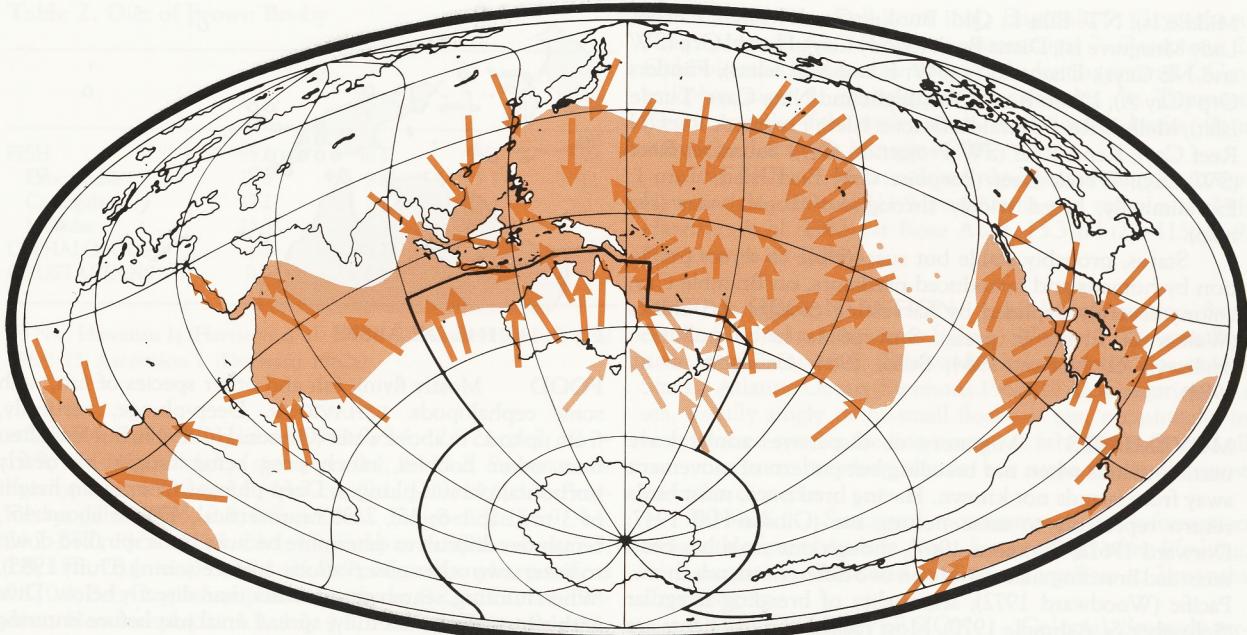
NSW, in E, and to near Onslow, WA, in W (Aust. Atlas).

**NZ** Vagrant; scattered sight and beachcast records, mostly singles: Otaki, 18 May 1957; S of Motiti, Bay of Plenty, 7 Feb. 1960; Mt Manganui, 27 Apr. 1968; Raglan, May 1968; St Andrews coast, Canterbury, 29 Mar. 1969; between C.

**Table 1.** Breeding locations of Brown Booby.

LOCALITY	YEAR	NUMBERS (pairs)	REF
CHRISTMAS I. (IND.)	1984	5000	1
COCOS-KEELING IS	1983	75–100	2
AUST.			
WA			
Bedout I.	1984	9576 ± 1150	3
	1982	5470 ± 550	3
	1978	1300 birds	4
	1975	1000	5
	1972	5000	6
Lacepede I.			
West I.	1982	7370	3
Middle I.	1982	10 300	3
Adele I.	1982	7500 ± 940	3
	1978	185 nests	4
	1972	1000–1500	7
White Is,		4000–5000 birds	8
Qld			
Rocky I.	1965	20 000–30 000 birds	9
Bramble Cay	10		
Moulter (Pandora) Cay	1980	535	11
	1976	22	11
MacLennan Cay	1978	919	12
	1980–82	104–270 nests	11
Raine I.		>6000 annually	13
Ashmore Banks	1981	c. 200 nests	14
Sandbank No 8	1983	56–1080 nests	11
Sandbank No 7	1983	20–49 nests	14
Davie Cay	1981–82	36 nests	15
Tydeman Cay	1982	738 nests	15
Stapleton I.	1984	>1000	16
Sandbank No 1	1984	500	16
Swain Reefs			
Bell Cay	1986	40	17
Bylund Cay	1986	39	17
Frigate Cay	1986	350	17
Gannet Cay	1985–86	248–542	17
Price Cay	1986	316	17
Other cays (6)	1976	524	18
Willis Grp, Mid Islet	1954	141 nests	19
Magdelaine Is, SE Cay	1984	263 nests	19
Coringa Grp, SW Islet	1984	24 nests	19
Chilcott I.	1984	208 nests	19
Lihou Reef			
Georgina I.	1984	32 nests	19
Anne I.	1984	100 nests	19
Brodie I.	1984	124 nests	19
Marion Reef			
Paget		50	8
Carola Cay		7	8

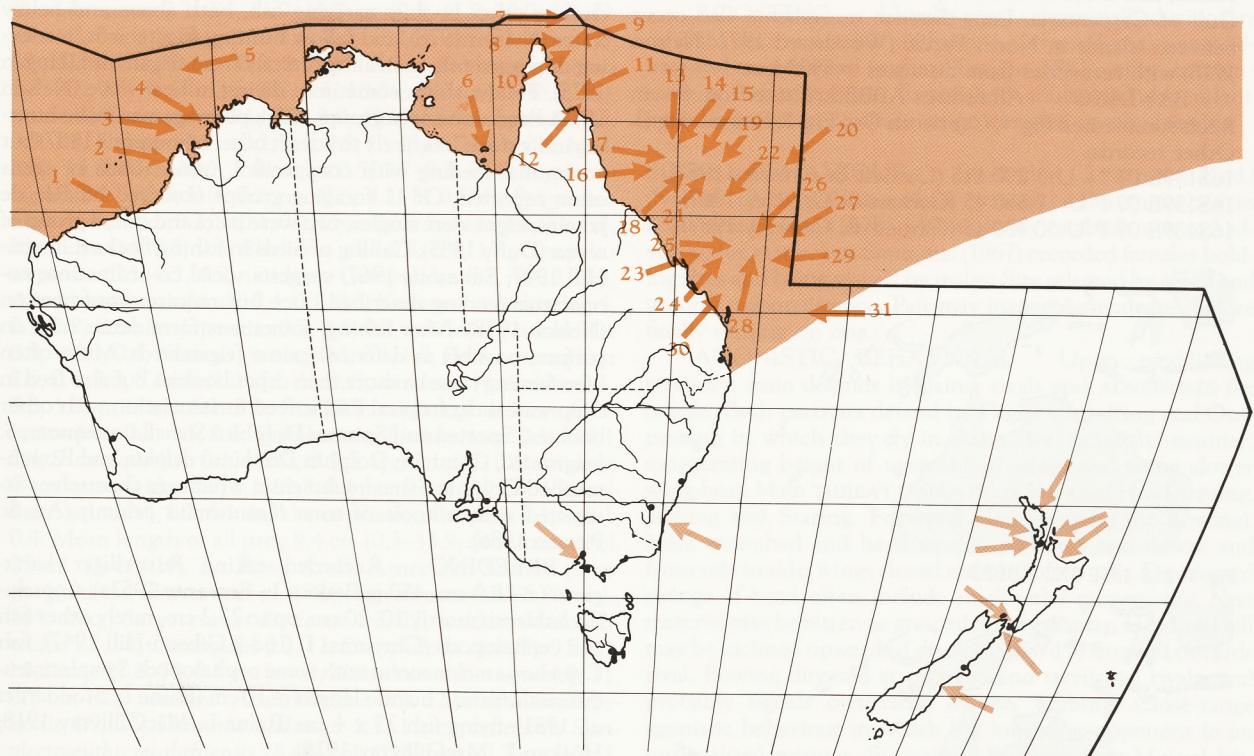
**References:** (1) Stokes (1988); (2) Stokes et al. (1984); (3) Burbidge et al. (1987); (4) Abbott (1979); (5) Kolichis (1977); (6) Bush & Lodge (1977); (7) Smith et al. (1978); (8) Nelson (1978); (9) Aust. NRS; (10) Walker & Elvish in press; (11) King et al. (1983); (12) Limpus (1980); (13) King (1986); (14) King & Limpus (1983); (15) King & Buckley (1985); (16) King (1985); (17) Walker & Jones (1986); (18) Limpus & Lyon (1981); (19) ANPWS.



Karikari and Cavalli I., Apr. 1969; Redhead, Bay of Islands, Aug. 1969; Coromandel I., Gannet Rock, 19 Mar. 1971; Bay of Islands, 23 Oct. 1972; Lower Hutt, NI, June 1975; Petone Beach, 2 Mar. 1976; Picton, 22 Feb. 1980; Muriwai, 6 Apr. 1980; Manukau Harbour, two in Oct. 1985, and one, 18 May

1986 (CSN 8-34; NZ Atlas).

**BREEDING** Within our area, in Aust. seas and Christmas and Cocos-Keeling Is in e. Indian Ocean. Summarized Table 1. Other breeding locations listed in HASB without size of colonies: WA: Ashmore Reef (East, West,



- (1) Bedout I.; (2) Lacepede I.; (3) Adele I.; (4) White Is.; (5) Ashmore Reef; (6) Rocky I.; (7) Bramble Cay; (8) Ashmore Banks; (9) Moulter Cay, MacLennan Cay; (10) Raine I.; (11) Sandbanks No 8, No 7; (12) Davie Cay, Tydeman Cay, Sandbank No 1, Stapleton I.; (13) Diana Bank; (14) Willis Is.; (15) Magdelaine Cay; (16) Flinders Reefs; (17) Herald Grp; (18) Coringa Grp; (19) Lihou Reefs; (20) Mellish Reef; (21) Diamond Is.; (22) Marion Reef; (23) Bell Cay; (24, 25) Swain Reefs; (26) Frederic Reef; (27) Kenn Reef; (28) Saumarez Reef; (29) Wreck Reef; (30) Bunker Grp; (31) Cato I.

Middle Is); NT: Ellis I.; Qld: Bunker Grp (Hoskyn, Fairfax, Lady Musgrave Is); Diana Bank (Sandy Cay); Herald Grp (SW and NE Cays); Diamond Is (SW, E and Mid Islets); Flinders Grp (Cay A); Lihou Reef (One, Eight and Nine Cays, Turtle Islet); Mellish Reef (Herald's Beacon Islet); Frederick Reef (N Reef Cay); Kenn Reef (SW Projection Cay); Saumarez Reef (SW Cay); Wreck Reef (Porpoise Cay, Bird Islet); Cato I. Extralimitally, breed widely throughout tropical seas (see map).

Status, probably stable but susceptible to direct predation by humans and introduced predators; on Bramble Cay, colony severely depleted by harvesting of eggs and chicks (Walker & Elvish in press). Susceptible to oil pollution (Halewyn & Norton 1984; Stiles 1984; Gallagher et al. 1984).

**MOVEMENTS** Migratory or dispersive: adults leave nesting islands when not breeding but pattern of movement away from islands not known. Having bred once, most birds return repeatedly to same nesting site (Gibson-Hill 1947; Dorward 1962a; Simmons 1967), though one male has been recorded breeding successively on two different islands in nw. Pacific (Woodward 1972); seasonality of breeding irregular (Schreiber & Ashmole 1970). Most recorded movements are of young birds (see Banding) with most movement N to distinct but overlapping areas of Coral Sea and Pacific; birds from Swain Reefs recovered round Solomon Is and e. PNG; those from Capricorn Grp along e. coast Qld and e. PNG; those from Raine I. round se. PNG, E of Torres Str. and out into Pacific; and those from Rocky and Manowar Is from within Gulf of Carpentaria. Long-distance movements also occur between islands in North Pacific (Woodward 1972; Nelson 1978) with recoveries from distances  $>5500$  km.

**BANDING** All returns ABBBS. Those from Swain Reefs summarized Fig. 1, Capricorn Grp Fig. 2, Raine I. Fig. 3. Other records:

16S139E 07 2+ U 3 200 115 (Garnett & Crowley 1987)

16S139E 07 P U 17 380 45 (Garnett & Crowley 1987)

16S139E 07 P U 30 400 45 (Garnett & Crowley 1987).



Fig. 1. 21S 152E 2X2 ABBBS



Fig. 2. 23S 152E 2X2 ABBBS

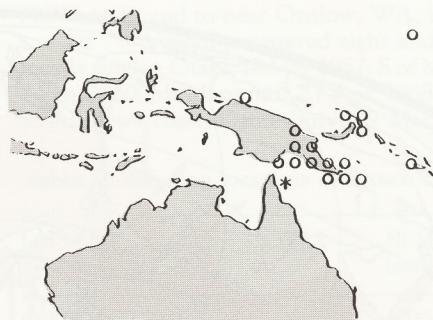


Fig. 3. 11S 144E 2X2 ABBBS

**FOOD** Mostly flying fish and other species of fish, with some cephalopods. **BEHAVIOUR**. Deep-plunge, vertically, from up to 15 m above water (Gibson-Hill 1947), but less often than other boobies, much prey being caught by nearly horizontal pursuit-plunges. Deep-plunges from mean height of 3 m (1.5; 1-8; 35), 23% near vertical, 40% at about 45°, remainder difficult to determine because birds spiralled down to water; two other observations, surface-seizing (Duffy 1985). When hunting, search ahead rather than directly below. Dive with wings partly, tail fully, spread until just before entering water. Swim with feet and flapping of partly-closed wings; can twist and turn in pursuit of prey (Nelson 1978), sometimes staying submerged for up to 40 s (Gibson-Hill 1947) though, in turbid water, mean length of dive 2.2 s (1.1; 0.5-5.6; 35; Duffy 1985). Catch flying fish by flight-feeding but more often just as they re-enter water. Also obtain food by aerial piracy, chasing other boobies carrying fish, both above and below water (Nelson 1978), and follow hunting frigatebirds, retrieving disgorged fish or stealing directly from frigatebird (Hogan 1925). Follow ships, sometimes diving in bow-wave (Nelson 1978). Feed alone or in groups. Dark plumage may make hunting individuals less likely to attract others (Simmons 1967) but communal feeding with conspecifics, other sulids or terns often reported. Of 11 foraging groups observed off Rio de Janeiro, eight were singles, two were pairs and one, a group of seven (Duffy 1985). Calling of birds in fishing flocks (Gibson-Hill 1947; Simmons 1967) suggests social co-ordination; cooperative feeding described once but requires confirmation (Nelson 1978). After fishing, sometimes form dense rafts on surface, possibly as defence against frigatebirds. More often seen feeding close to shore than other boobies but also feed in deep waters. In tropical Pacific feed in association with other boobies, Spotted and Spinner Dolphins *Stenella attenuata*, *S. longirostris*, Common Dolphin *Delphinus delphis*, and Rough-toothed Dolphin *Steno bredanensis*, which are themselves associated with schools of tuna *Katsuwonus pelamis* (Au & Pitman 1986).

**BREEDING** Recorded taking *Rastrelliger kanagurta* ( $\leq 28.0$  cm, 450 g; Bedout I.; Serventy 1952a); *Cypselurus bahiensis* mostly 10-20 cm, up to 27.2 cm, rarely other fish and cephalopods (Christmas I. [Ind.]; Gibson-Hill 1947), fish *Cypselurus melanocerus* with some cephalopods *Symplectoteuthis ovalaniensis*, mantle length  $\leq 10$  cm (Raine I.; Stoddart et al. 1981); flying fish 25 x 4 cm (Raine I., MacGillivray 1918; Hoskyn I., MacGillivray 1928).

Detailed analysis extralimital: summarized Table 2. In nw. Hawaiian Is (244 regurgitations, adults 22%, juveniles 8, chicks 69; 2908 food items; Harrison et al. 1983) fish consisted of Myctophidae  $<0.1\%$  vol.,  $<0.1\%$  no., 0.3% freq., Cheilopogon atrisignis 0.4, 0.2, 0.8, *Cypselurus spilonotopterus* 0.4,

Table 2. Diet of Brown Booby

	% vol.		% no.	
	1	2	1	3
FISH	95.1	48.2	96.5	99
Exocoetidae	25.8	5.8	7.7	11
Carangidae	27.2	2.2	12.4	
Mullidae	15.3	27.3	63.7	
CEPHALOPODS	4.8	43.1	3.5	<1
CRUSTACEANS	0.1	<0.1		

(1) Nw. Hawaiian Is (Harrison et al. 1983). (2) Samoa (Harrison et al. 1984). (3) Ascension I. (Dorward 1962a).

<0.1, 0.4, *Exocoetus volitans* 4.9, 1.9, 9.4, 12.8 cm (1.7; 10.7–17.9; 32), *Hirundichthys speculiger* 0.4, 0.1, 1.2, *Parexocoetus brachypterus* 1.9, 0.8, 2.9, 13.7 cm (0.1; 12.9–14.6; 15), *Prognathus gilbertii* 0.5, 0.3, 0.8, unident. *Exocoetidae* 16.9, 4.4, 24.2–37.0, 12.5 cm (3.1–23.4; 43), *Euleptorhamphus viridis* 7.5, 1.8, 13.1, 28.1 cm (1.3; 19.1–31.9; 9), *Hyporhamphus pacificus* 0.1, 0.1, 0.4, *Oxyporhamphus micropterus* 0.2, <0.1, 0.4, unident. *Hemiramphidae* 1.9, 1.2, 4.5, *Ablennes hians* 0.1, 0.1, 1.6, *Platybelone argalus platyura* 4.4, 1.7, 8.2, 23.1 cm (0.8; 20.5–24.8; 5), *Cololabis saire* 0.3, 0.1, 0.4, 2.3 cm (0.5; 21.8–23.3; 3), *Pranesus insularum* 0.3, 0.3, 0.4, *Priacanthus* 0.1, <0.1, 0.4, unident. *Priacanthidae* 0.1, 0.1, 0.4, *Remora brachyptera* 0.1, 0.1, 0.8, unident. *Echeneidae* <0.1, <0.1, 0.4, *Caranx* 0.1, 0.3, 0.8, *Decapterus macarellus* 0.5, 0.3, 1.6, *D. macrosoma* 7.2, 3.4, 11.9, 15.8 cm (0.7; 11.0–20.0; 12), *D. tabl* 1.3, 0.6, 4.5, *D. spp* 13.8, 5.0, 23.8, 14.6 cm (1.2; 6.3–21.5; 19), *Naucrates ductor* 0.5, 0.2, 0.8, *Selar crumenophthalmus* 0.5, 0.2, 0.8, *Seriola* 3.5, 1.8, 8.2, 10.0 cm (0.6; 4.9–16.5; 27), unident. *Carangidae* 0.1, 0.4, 2.0, *Coryphaena equiselis* 0.5, 0.3, 1.6, *C. hippurus* <0.1, 0.1, 0.8, *C. spp* 0.2, 0.1, 0.4, *Mullidae* 15.3, 63.7, 30.0, 5.4 cm (<0.5; 3.7–8.3; 164), *Kyphosus bigibbus* 3.6, 2.3, 9.0, 7.2 cm (0.6; 4.1–17.0; 24), *Sphyraena novaehollandiae* 0.2, <0.1, 0.4, *Cymolutes leclusei* 0.4, 0.1, 0.4, *Bleniidae* 0.4, 0.2, 0.4, *Bleekeria gillii* 0.3, 0.7, 1.2, *Gempylus serpens* <0.1, 0.1, 1.2, unident. *Gempylidae* 0.1, <0.1, 0.4, *Acanthocybium solandri* 0.4, 0.1, 0.8, *Katsuwonus pelamis* 1.4, 0.3, 2.9, *Scomber japonicus* 0.7, 0.1, 0.8, unident. *Scombridae* 0.1, <0.1, 0.4, *Nameus gronovii* 0.1, 0.1, 1.2, *Psenes cyanophrys* 0.6, 0.4, 2.0, 8.1 cm (1.0; 5.1–12.8; 8), unident. *Nameidae* 0.1, 0.3, 1.6, unident. fish 2.3, 1.6, 17.6; cephalopods were *Ommastrephes* 0.3, 0.1, 0.8, *Symplectoteuthis luminosa* 0.1, <0.1, 0.4, *S. ovalaniensis* 0.1, <0.1, 0.4, *S. spp* 0.1, 0.1, 0.8, unident. *Ommastrephidae* 3.7, 2.1, 12.7, 8.1 cm (0.4; 4.1–12.9; 48), unident. squid 0.5, 1.2, 6.1 and the crustaceans isopods 0.1, <0.1, 0.4. Mean length of all prey 9.4 cm (0.3–33.9; 463), mean vol. 25 ml. (2–68; 19). At Rose Atoll, American Samoa (9 regurgitations; Harrison et al. 1984), fish Exocoetidae 5.8% vol., 56% freq., *Sargocentron diadema* 1.2, 22, unident. Holocentridae 1.1, 56, Carangidae 2.2, 11, *Coryphaena equiselis* 0.8, 11, Mullidae 27.3, 78, 6.1 cm (n=6), *Acanthurus triostegus* 4.9, 11, 3.7 cm (10), unident. Acanthuridae 0.7, 22, *Katsuwonus pelamis* 4.9, 22, *Thunnus alalunga* 1.3, 11; cephalopods *Symplectoteuthis ovalaniensis* 18.4% vol., 33% freq., 7.7 cm (10), *S. spp* 5.6, 22, unident. Ommastrephidae 18.9, 6.7, unident. squid 0.2, 11; 6.7% vol. unident; overall prey length 6.4 cm (29–103; 35). At Ascension I. (56 regurgitations; Dorward 1962a), all large items fish incl. *Exocoetus volitans* 9% no., *Scomberesox saurus* <1, *Selar crumenophthalmus* 1, *Benthodes-*

*mus simonyi* <1; small items incl.: *Engraulis* 7, *Oxyporhamphus micropterus* 2, *Holocentrus ascensionis* 7, *Decapterus* 2, *Ophioblennius steindachneri* 50, *Benthodesmus simonyi* 7, *Centrolophus niger* 4, cephalopods *Hyaloteuthis*. In Tuamotu Arch. mostly fish with some cephalopod beaks (four stomachs; Lacan & Mougin 1974).

INTAKE Mean volume regurgitated samples in nw. Hawaiian Is, 100 ml (11.9 prey items per sample, n=244; Harrison et al. 1983); at Rose Atoll, 73.3 ml (25–115; n=9; Harrison et al. 1984).

**SOCIAL ORGANIZATION** Little information from A'asia. Studied at Christmas I. (Ind.) (Nelson 1978); extrazonally, at Ascension I. (Dorward 1962a,b) and Georgetown Stacks, Atlantic Ocean (Simmons 1967, 1970). Gregarious. At sea, usually singly or in small flocks at sea; occasionally in larger mixed-species feeding parties at fish shoals. Found all year at or near breeding islands, but some adults and most juveniles disperse.

**BONDS** Sustained monogamous. No information on length of pair-bonds in Aust., but probably often life-long. Both parents incubate and tend young until up to 2 months after fledging.

**BREEDING DISPERSION** Colonial. Strongly territorial round nest-site. Interspecific territorial fighting with Masked Booby in mixed colonies. Size of territory varies, but tendency to nest more densely than Masked Booby (see Breeding for densities and size of colonies). No information from Aust. on age of birds at establishment of first territory; believed to be 2–3 years elsewhere.

**ROOSTING** Usually roost communally during day or night on any suitable platform, e.g. ground, rocks or sandbars and on trees and bushes (Traylor 1962); often in company of other species. Established adults and dependent juveniles roost in territory or on elevated perch close by.

**SOCIAL BEHAVIOUR** Studied at Christmas I. (Ind.) (Nelson 1978); well described overseas and summarized in BWP and Nelson (1978). Males usually establish site and advertise for mates, but Simmons (1967) recorded females holding sites and being visited by males. Site selected by aerial and ground reconnaissance. Pair may inspect several sites before finally settling on one.

**AGONISTIC BEHAVIOUR** Upon establishing territory, male defends it against rivals and ADVERTISES for female. Both partners defend by Flight Circuiting and Out-posting in which they fly in distinctive 'butterfly' manner, exaggerating height of upstroke of wings and using slower wing-beat. Main THREAT DISPLAYS are Forward Head-waving, Jabbing and Staring. Forward Head-waving (or Bowing). Neck stretched and head swayed forwards and down, and from side to side; wings closed and bird often calls. Downward swings of head often include small jerky movements. Nest material may be bitten or grasped during display. Head and bill may be inclined upwards if displaying bird orientated towards rival. Bowing directed at partners and territorial rivals, and probably signals ownership of site. Jabbing. Close-range agonistic behaviour in which bill lunged at opponent in an unritualized manner. Sometimes develops into Mutual Jabbing. Wing-flailing: in which partly open wings thrust downwards, sometimes interspersed with Jabbing. Staring: occurs before Forward Head-waving, presumably has signal function. FIGHTING may occur if intruder refuses to retreat; rival seized by bill or neck and pushed over edge of cliff or

down slope; sometimes prolonged with bodies in contact and wings flailing. Fights usually started on land, but owners of site may attack by diving from air, giving intense Landing Calls (see Whistle in Voice). ESCAPE. Defeated rivals take flight and leave territory; may be pursued in air by victorious opponent.

**SEXUAL BEHAVIOUR PAIR-FORMATION.** Pair-bonds started and maintained by Sky-pointing, Staring, Pair Flighting, Mutual Jabbing and Bill-touching, Mutual Preening, Parading, Bill-tucking, Bill-up-face-away Displaying, Wing Rattling and Upward Headshaking. **Sky-pointing** (Fig. 4, 5) used by male holding territory to attract female; displaying bird stretches neck upwards with bill pointed vertically; tail raised to some extent and wings closed; wheezy disyllabic whistle uttered during display. Presence of female, whether in flight or on ground, enough to elicit Sky-pointing, and display may be performed in succession. Functions to attract female to site, to bring her back to it, or to discourage her from leaving. May also help strengthen pair-bond. **Pair Flighting**, in which the two birds circle area, incorporates Sky-pointing into flight; probably helps strengthen bond and attachment to site. **Mutual Jabbing** (Sparring) and **Bill-touching** (Fig. 6) form GREETING CEREMONY when mate joined at site from flight; returning bird lands near other or jumps in close; both Bill-touch, opposing each other's bill frontally, and calling. Mutual Jabbing often occurs after Bill-touching, birds poking and fencing with each other in more hostile manner (but distinct from Jabbing of rivals). These two displays occur often when pair close together at site. Occasionally, Bill-touching may lead to symbolic feeding in which mate places bill inside other's bill without transferring food; recorded often in new pairs. **MUTUAL PREENING**: one bird preens the other, or each preens the other simultaneously; rare. **Parading**: one partner (usually male) leaves other with exaggerated walk, tail cocked and neck outstretched, occurs after close-range interactions, e.g. Mutual Jabbing. **Bill-up-face-away Display**, with bill turned away so that side or back of head towards mate, usually part of Parading. Typically, male Parades away to collect some nesting material; functions to enhance visual impact of movements involved in intimate pair interactions and to help ensure clear communication of intent. **APPEASEMENT**. **Bill-tucking**: neck arched and bill pressed to throat; often precedes Bill-up-face-away Display or vice versa. **Wing-rattling** performed often from Bill-up-face-away positions, often leading to Flight Circuiting or trip for nesting material; involves brisk shake of wings, partly loosened and slightly raised at tips; movement sometimes so quick that wings become a blur. **Upward Headshaking**: brisk exaggerated headshake while head tilted upwards, occurs commonly after Bill-up-face-away Display. Wing-rattling, after hopping up onto vantage point at site and after touching nesting material; function unknown. Partners also engage in symbolic nest-building during which pair lift and present material to each other and give persistent nest calls, often crossing necks in reaching to peck material. Nest-building may lead to **COPULATION**; female solicits by holding head down, with arched neck, and nibbling nesting material (which may continue through copulation). Male moves beside female and may make incipient movements before mounting; positions himself on female's back, making bill movements beside female's head, but does not grip her head during mounting; may nibble her neck-feathers or reach over and touch material that she is nibbling; then moves backwards and lowers his tarsi and tail to achieve cloacal contact. Afterwards, male may Parade away with upheld bill, or may

Fig. 4 Sky pointing

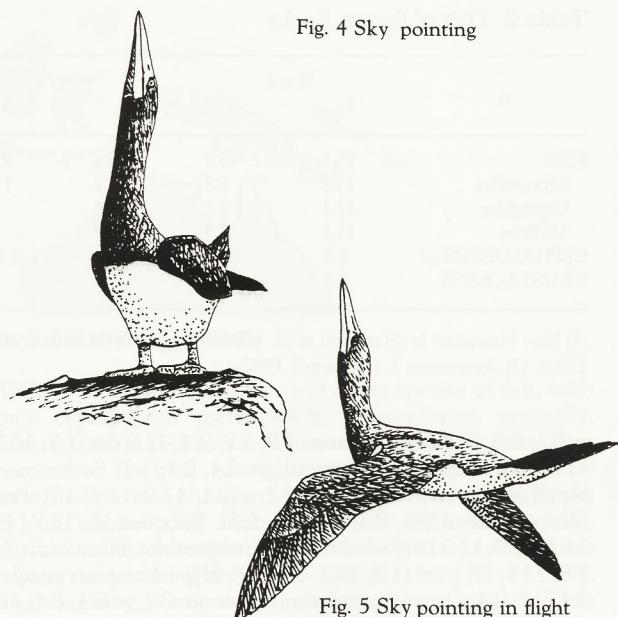


Fig. 5 Sky pointing in flight



Fig. 6 Bill-touching

touch or build nest.

**RELATIONS WITHIN FAMILY GROUP** Parents take turns to brood, shield or guard young for first 5–6 weeks; guarding occurs during entire nestling period only if food situation favourable. Eggs may be incubated by placing webbed feet beside them and standing above. Young chicks not brooded on top of webs, unlike Masked Booby. Off-duty bird usually absent for much of day, but can be beside mate at night. At change-over, incoming bird lands, Forward Head-waves, then pair may Bill-touch or exhibit Mutual Jabbing with Bill-up-face-away Display and Bill-tucking. Relieved bird then moves off nest. Sometimes, nest-relief associated with one bird bringing nesting material. First chick to hatch from two-egg clutch attacks and bullies smaller sibling when it hatches. After 3–5 days, second chick is dead or has been ejected from nest-site and dies. Adults take no active part in this process, and will accept ejected chick if placed back in nest, but will not retrieve it. Rarely, two chicks survive. Young chicks show weak uncoordinated head-movements and emit faint chipping calls. Older chicks crouch and turn head up, moving it sideways and up and down, calling continuously; wings also flailed, at times vigorously. Bill-hiding not shown by chicks when attacked by adults. Temperature regulation achieved by fluttering skin of gular pouch once

chicks reach 4–5 days-old. No special sleeping posture. In first weeks after fledging, juveniles usually wait at site, leaving only to feed and bathe. Parents tend to avoid fledgeling, meeting only briefly for feeding.

**VOICE** Reasonably well known; observations at Christmas I. (Ind.) (Gibson-Hill 1947; Nelson 1978) and general summary in Nelson (1978); extralimitally, studied at Ascension I. (Dorward 1962a,b; Simmons 1967) and summary in BWP. Do not call often in flight (Gibson-Hill 1947) but reported to call at sea when fishing (Gibson-Hill 1947; Simmons 1967) and when squabbling over food (BWP); moderately noisy at breeding colonies (though less so than Masked Booby, possibly because nests more widely spaced). Distinct sexual differences in voice: males utter quiet sibilant whistles; females, harsh loud goose-like honks or quacks (which are dominant sound at colonies); given in various agonistic and sexual circumstances, though fundamentally always aggressive (Nelson 1978). Calls vary with circumstances: louder, longer and repeated more during intense interactions though differences less obvious in males (BWP) and probably continuum of variation within each sex. Both male and female subadults reported to utter loud honking calls. No information on individual differences or geographical variation. Non-vocal sounds: adults and juveniles rattle mandibles (Dorward 1962b).

**ADULT MALE** **Whistle.** Main call; high-pitched sibilant two-syllable whistle *swee-oo*, much quieter than calls of females; whistle has wheezy quality and sometimes almost hiss; call varies with intensity of interaction: at high intensities, utter violent whistling *chuff chuff* ('Steam-engine whistle'; Nelson 1978). Used in various circumstances: when Outposting, supplanting other rivals or intruders, when returning to site after Flight Circuiting (Landing Call of BWP), during Sky-pointing (but see below), Wing-flailing, Jabbing, Forward Head-waving (Bowing) and as greeting. Functions in advertising and as greeting. Gibson-Hill (1947) reports that call when Sky-pointing, soft *iruk-iruk-iruk...* **Alarm Call.** Loud agonized *karrk*. Birds rattle mandibles, rattling often louder than call (Gibson-Hill 1947).

**ADULT FEMALE** **Honk.** Main call, harsh quacking or honking *kaak-kaak-kaak...* or *ar-k, ar-k, ar-k...* Used in same circumstances as male Whistle. **Alarm Call.** As male. Females rattle mandibles (Gibson-Hill 1947).

**YOUNG** Small chicks beg with faint *yip*. When older, give short grunting *agk agk agk* calls with much rattling of mandibles. Juveniles and subadults utter female-type calls as Threat Call; suggested that subadult males retain call for at least 2 years (Nelson 1978).

**BREEDING** Well known. In Aust., partly studied at Raine I. (B.R. King) and fuller study at Christmas I. (Ind.) (Nelson 1978). Extralimitally, detailed study at Ascension I. (Dorward 1962b; Simmons 1967); Christmas I. (Pac.) (Schreiber & Ashmole 1970). Information supplied by B.R. King. Breed in simple pairs, colonially, on islands, oceanic or well offshore preferably. Sometimes associated with Masked Boobies (Raine I.; King 1986; B.R. King). Size of colonies varies: at Raine I., c. 6600 all over island (King 1986; B.R. King); Christmas I. (Ind.), groups of 2–3 to 100–200, particularly round edge of island (Nelson 1978).

**SEASON** Laying recorded throughout year in different parts of range. Cocos-Keeling Is: no well-defined season, eggs in all months (Gibson-Hill 1950); Christmas I. (Ind.),

laying all months, peak Apr.–May, little from Jan. to July (Gibson-Hill 1947; Nelson 1978); at Bedout I., WA: in Oct. 1949, most with eggs and a few newly hatched chicks (Serventy 1952a); in May 1972, eggs and small and large young observed (Bush & Lodge 1977); in May 1975, eggs and one large young seen (Kolichis 1977) indicating two periods of laying; in Coral Sea, laying all months, peaks Mar.–Apr., June–Oct. (HASB); Raine I., most laying Sept.–Nov. (B.R. King). Generally inadequate Aust. information.

**SITE** On ground, in various terrains from beaches and central flats of sandy cays to rocky areas and cliffs above sea or inland; on bare and vegetated areas. Probably able to use greater variety of sites than other boobies because better able to perch and manoeuvre in precarious places (Nelson 1978). On Christmas I. (Ind.), nest on edges and high ledges of sea-cliffs, flat places between boulders and rock-pinnacles, under trees, shrubs, and other vegetation well inside forest (Gibson-Hill 1947; Nelson 1978). Also nest on low sandy cays with vegetational cover of low shrubs, herbs, grasses, varying from 0 to 75% (Limpus & Lyon 1981); nests may be little more than 1 m above sea-level and in danger of flooding by high tides and storm-waves. On different islands apparent preferences for vegetated over bare areas or vice versa (Stoddart et al. 1981; King & Limpus 1983; King et al. 1983; Serventy 1959). On Raine I., most open areas avoided and left to Masked Booby (B.R. King). At Bedout I., on beaches, above high-water mark (Kolichis 1977). On Tydeman Cay, sites varied seasonally: in winter, on central grassy flats; in summer, also on strand among *Salsola*, *Tribulus* and *Portulaca* (King & Buckley 1985). Nesting density greater than for Masked Boobies: Raine I., av. 7.7 nests (0–17) per 100 m<sup>2</sup> in 28x100-m<sup>2</sup> quadrats (B.R. King) and 6.8 nests per 100 m<sup>2</sup> in five x 100-m<sup>2</sup> central quadrats (Stoddart et al. 1981); Bramble Cay 'so dense that it was hard to walk between nests' (North); Christmas I., av. 3.7 m (0.6–27; 52) (Nelson 1978) between nests; Rocky I., Gulf of Carpentaria, 257 nests in 17 800 m<sup>2</sup> (1/69.3 m<sup>2</sup>) (S.T. Garritt).

**NEST, MATERIALS** Varies from nil on unvegetated cays to substantial (plant remains, twigs, seaweed, bones, feathers, turtle egg-shells, debris), loosely assembled; scattered by adults and young until all lost. At Bedout I., laid directly on ground or in nests made of *Spinifex longifolius* (Kolichis 1977). Dimensions c. 15 cm high x 60 cm across (HASB); at Willis and Coral Sea islands, 45 cm across (Serventy 1952b; Hindwood et al. 1963); at Bedout I., WA, c. 45 cm across and 4 cm deep (Kolichis 1977). Most material brought by male before and during incubation and placed on nest or presented to female; adjustment and rearrangement during incubation. Material stolen from neighbouring nests, especially on sandy cays with only beach debris.

**EGGS** Elliptical, ovate or elongate ovate; smooth, unpolished; pale blue to pale turquoise when newly laid; chalky white surface develops over blue undersurface and by scratching, chipping exposes blue layer; becomes dirty, stained with age.

#### MEASUREMENTS:

Christmas I. (Ind.): first egg: 63.4 (58–69; 44) x 42.7 (36–45.3); second egg: 60.2 (56.2–65; 18) x 41.1. (38–43)

Coral Sea: two first eggs: 59.5–60.5 x 41.4–42.5; two second eggs: 56.4–59.5 x 40.6–44.7

Bedout I., WA: 61 (56–66; 10) x 40 (36–43) (Bush & Lodge 1977)

Bedout I., WA: 59.5 (3.56; 53.3–65.1; 12 eggs ex 6 clutches) x 41.2 (1.70; 38.3–44.5) (Kolichis 1977)

**WEIGHTS:**

First egg: 57.3 (40–60; 27); second egg: 53.2 (45–67; 20) (Nelson 1978)

Coral Sea: three first eggs, av. 62.5; three second, 59.1 (Sentry 1959). Weight of C/2, 8.1% of female weight.

**CLUTCH-SIZE** Not fully established; proportions of 1- and 2-egg clutches differ at different times of year at Christmas I. (Ind.) (Nelson 1978) but clearly C/2 most common, C/1, C/3 rare or less usual. At Bedout I., WA, in May 1975, 2-egg clutches most common with rest being C/1 (Kolichis 1977); in May 1972, most C/2 with only one C/3 observed (Bush & Lodge 1977). Counts of nests at Raine I.: 40xC/1, 73xC/2, 30 x 1 egg, one chick, 6 x 2 chicks (B.R. King). At Christmas I. (Ind.): clutches, 34xC/1, 16xC/2; and 41 x 1 egg, 30 x 2 eggs, 1 x 3 eggs (Nelson 1978). Best data from Kure for four seasons (n=93 clutches): 83.9% C/2, 8.6% C/3, 7.5% C/1; average annual clutch-size ranged from 1.9–2.1, total average 2.01 (Woodward 1972).

**LAYING** Apparently not well or always synchronized but probably better in subcolonies (Nelson 1978). Interval between eggs: Kure, av. 5.2 days (3–9) (Woodward 1972). Replacement of lost clutches in less than half nests (Kure); after 20–34 days (Christmas I. [Ind.]). One annual attempt but on Ascension breeding occurs at less than annual intervals (Nelson 1978).

**INCUBATION** By both parents alternately, under webs of feet covered by body or simply by shading. Starts with first egg. Change-overs mostly at dawn. Lengths of shifts av. 12 h (1–37) at Ascension (Dorward 1962a); apparently longer at Christmas I. (Ind.) (Nelson 1978). **INCUBATION PERIOD:** Christmas I. (Ind.) (Nelson 1978): av. 42.8 days (42–43; 5); no other Aust. data. Hatching asynchronous at av. interval 4.6 days (1–9) (Kure; Woodward 1972). Eggshells stay in nest till displaced or blown away (B.R. King).

**YOUNG** Altricial, nidicolous. Brooded and guarded by both parents for ≥21 and even for 61 days, average 41 days (Christmas I. [Ind.]; Nelson 1978); in spells average 9.3 h (n=27) at Ascension (Dorward 1962a,b). Chicks do not climb onto webs of parents' feet when being brooded. One parent usually in attendance by day; both at nest by night. When older, sometimes left alone by day. Fed by both parents by incomplete regurgitation; perhaps about twice a day. No nest sanitation; adults and older chicks eject away from nest or on legs and feet, for thermoregulation. Dropped food removed and carried away by Silver Gulls *Larus novaehollandiae*, Buff-banded Rails *Gallirallus philippensis*, land crabs (B.R. King). Vigorous defence of nests by adults and large young. **BROOD REDUCTION:** almost invariably only one chick reared; second chick nearly always succumbs in <4 days (B.R. King) to persecution by sibling, unless first chick dies young. Survival of both birds known twice at Raine I. (B.R. King), once at Bird I., Coral Sea (Hindwood et al. 1963). **NESTLING PERIOD:** 14–15 weeks. Many chicks can fly at 99 days, most by 105 and all but weaklings by 119 (Nelson 1978). At Christmas, departure av. at 96 days (87–100; 11) (Nelson 1978).

**GROWTH** Hatched naked, slaty-grey or pinkish-mauve skin; eyes closed but may open on first day; bill, grey with pink tip; egg-tooth, white or yellow (Nelson 1978), which retained for up to 27 days (B.R. King). Maximum weight of c. 1400 g reached when about 70–80 days old and declines to fledging, when still above mean adult weight. Well able to withstand spells of malnutrition and loss of condition (Dorward 1962a,b). Summary of other development: Week 1, becomes covered with sparse white down; Week 3–4, down

thick; Week 4–5, primaries begin to erupt; Week 7, almost as large as adult, covered with fluffy white down, primaries, rectrices, scapulars may be conspicuous; Week 8–9, longest primary up to 89 mm, rectrices to 97 mm, feathers on forehead; Week 9, secondaries well grown, scapulars meet across back; Week 10, down thinning; Week 11, down usually thick only on flanks, thighs; Week 12, well feathered all over, little down left; end Week 14, most young without down (Nelson 1978). At Christmas I. (Ind.), depend on parents for 1–2 months after departure, returning to nest to be fed; at Ascension, seen to be fed on average for 17 weeks after fledging (Simmons 1967).

**SUCCESS** Complex, varying, affected by brood reduction. At Christmas I. (Ind.), 68% of clutches hatched at least one egg; 81% of hatchlings fledged; in all, only 58% of clutches produced a fledgeling. Rate much lower at Ascension: 10% of clutches succeeded (Dorward 1962a; Simmons 1967). On Christmas I. (Pac.), breeding failed during El Niño Southern Oscillation; increased sea surface-temperature, deepened thermocline and high sea-level preceded failure of food supply and heavy rainfall may have inhibited breeding activity and flooded nests (Schreiber & Schreiber 1984). **PREDATORS.** Humans are major predator in Aust., taking eggs, chicks and some adults for food. Native rats *Melomys rubicola* a menace on Bramble Cay (Limpus et al. 1983) and *Rattus rattus* on SW Cay (Hindwood et al. 1963). Silver Gulls, Buff-banded Rails, possibly frigatebirds and possibly Rufous Night Heron *Nycticorax caledonicus* take unattended eggs, small chicks on Raine I. (B.R. King). Land crabs *Birgus latro* may do likewise on Christmas I. (Ind.) (Nelson 1978) and Cocos-Keeling Is (Gibson-Hill 1950).

**PLUMAGES** Subspecies *plotus*.

**ADULT** Age of first breeding unknown. Adult plumage attained c. 32–33 months as in *S. dactylatra* (Dorward 1962a; Nelson 1978). **HEAD AND NECK**, dark brown (219). **UPPERPARTS**, dark brown (119A), including scapulars. **TAIL**, dark brown (121); rachis, cream (54) merging to black-brown (119). **UPPERWING**. Humeral, dark brown (119A), rest of remiges, dark brown (121); rachis, black-brown (119). All coverts, dark brown (119A). **UNDERPARTS**. Upper breast, dark brown (219); lower breast and rest of underparts, white; sharp square-cut demarcation occurs between light and dark of underparts. Axillaries, white. **UNDERWING**. All marginal, outermost lesser coverts, median and lesser primary coverts, dark brown (119A). Median and lesser primary coverts fringed brown (119B). Greater primary coverts, glossy light-grey (85) with brown-grey (80) shade. Rest of coverts, white.

**DOWNTY YOUNG** Mostly naked at hatching, with sparse white down on head, back and flanks; remaining till c. 8 days, thicker at c. 14–26 days. At this stage, down absent on throat and sides of face. Primaries visible at c. 37–40 days, contra MacGillivray (1910), who states 4 weeks. MacGillivray (1910) gives sequence: primaries, followed by scapulars, head-feathers, secondaries and tail-feathers.

**JUVENILE** Similar to immature (see below); differs in: **HEAD AND NECK**. Lower neck-feathers, dark brown (119A) with narrow brown (119B) fringes. **UPPERWING**. Tips of primaries, more pointed. **UNDERPARTS**. Demarcation less prominent. Upper breast to vent, including thighs, brown-grey (80) with brown (119B) shade and white fringes; white bases to feathers not so prominent.

**IMMATURE** Similar to adult; differs in: **HEAD AND NECK**, paler; dark brown (119A). **UPPERWING**. Lesser, median and marginal coverts narrowly fringed brown (119B), fringes

becoming paler light grey-brown (119C) with wear. UNDER-PARTS, white, with brown-grey (80) and light grey-brown (119D) tips, from upper breast to vent; white bases of feathers prominent, some feathers may have white fringes, though largely juvenile feature. Demarcation of breast not so sharp, particularly during moult. Outer thighs, sides of vent and under tail-coverts, light grey-brown (119C). UNDERWING. Greater coverts, glossy light-grey (85) with brown-grey (80) shade. Tips of primaries slightly less rounded than adult.

**ABERRANT PLUMAGES** Hybrids with Masked Booby known (Worcester 1911). Albinistic birds have been recorded (Harrison 1985).

### BARE PARTS

**ADULT** Bare parts insufficiently recorded for details of seasonal variation; intensity of colours varies in breeding season (Hindwood *et al.* 1963). In Coral Sea: iris, cream, grey, yellow to dark brown in both sexes; no apparent sexual difference; requires study. Eye-ring, blue in males; chrome-yellow in females. Facial skin, blue in males; chrome-yellow in females. Bill, lime-green to yellow; in most males during breeding, base of upper and lower mandibles, blue; base in females, chrome-yellow with small blue patch in front of eye. Rest of bill in both sexes, cream or grey with faint yellow or green tinge. Legs and feet, lime-green to yellow; in most males during breeding, green-yellow; in females, almost chrome-yellow (Hindwood *et al.* 1963; HASB). At Christmas (Ind.) and Cocos-Keeling Is, in both sexes; iris, grey or yellow-grey; eye-ring, dull blue. Facial skin in males, dull purple or dark purple-grey; in females green-yellow. In males, bill, greenish grey; in females, greenish yellow, with slate-blue patch in front of eye. Gular pouch in both sexes, same as facial skin colour for each sex. Legs and feet in males, pale arsenic green; in females, pale yellowish green (Gibson-Hill 1947, 1950). Iris in two females, red (Vooous 1964).

**DOWNTY YOUNG** Insufficiently recorded. Skin, grey (87), Hoskyn Is, Qld; slate-grey, Christmas I. (Ind.) (Gibson-Hill 1947). Iris, dark brown, grey. Bill, grey (87). Gular pouch and throat, pink-brown (219D). Legs and feet, dark grey; later lightening when feathers develop; feet orange-pink at fledging (Simmons 1967). Downy young have grey bill with blue tinge towards base; separable from *S.d. personata* with grey-black bill.

**JUVENILE** Iris, light grey-brown (119D), light grey. Bill, dark grey; light blue-grey (88) at Christmas I. (Ind.). Base of bill, yellow-green. Facial skin, grey, flesh-brown at 5–8 weeks after fledging, lemon-yellow at 11–15 weeks. Feet orange becoming dull yellow at 20–30 weeks (BWP).

**IMMATURE** Iris, white inner ring, narrow grey outer. Bill, green-white. Facial skin, gular pouch, and feet, yellow-green (skin at ANWC). At Christmas I. (Ind.), bill, pale grey with slight blue colour. Feet, pale lemon-yellow. At end of sixteenth week, feet pinkish and bill, slate-grey (Gibson-Hill 1947). From N. Keeling I. (Gibson-Hill 1950): iris, grey; bill, pale grey-blue; gular and facial skin, dark grey-blue; legs and feet, light orange-pink. Elsewhere, locality not stated, gular skin greenish. Bill, blue-grey or pale olive-buff, yellow at base. Facial skin and gular pouch, blue-grey, sometimes with yellow tinge. Feet, pale yellow; sometimes tinged pink, or olive-buff (BWP).

**MOULTS** Undescribed in A'sia. Details for moult in *S.l. leucogaster* at Ascension I. in Dorward (1962a); summary in Nelson (1978).

**ADULT** Primaries moult outwards in staffelmauser. Each primary replaced at rate of 2 months. Up to three generations of feathers present at one time. Moult suspended before egg-laying and probably during chick-rearing; agrees with findings of Nelson (1978) at Christmas I. (Ind.). No details on duration of moult (Nelson 1978). Rest of moult similar to *S. dactylatra* (*q.v.*).

**POST-JUVENILE** First series of primaries starts at c. 10 months, second series at c. 15 months, when first has reached p8 (Dorward 1962a).

**MEASUREMENTS** (1) Christmas I. (Ind.), adults; methods unknown (Chasen 1933). (2) Cocos-Keeling Is, adults; BILL(G) = bill length from gape, other methods unknown (Gibson-Hill 1950). (3) Christmas I. (Ind.), adults; methods unknown (Nelson 1978). (4) Manowar I., Qld, adults, live; methods unknown (ABBBS). (5) MacLennan Cay and No. 8 Sandbank, Qld, adults (ABBBS). (6) Adults, skins (QM; ANWC; MV; data from B.R. King). (7) Locality unspecified, adults, skins (BWP). (8) Raine I., adults (B.R. King).

		MALES	FEMALES
WING	(1)	390.0 (379–400; 4)	405.0 (385–418; 3)
	(2)	395.0 (2.71; 392–398; 5)	417.5 (7.76; 406–426; 4)
	(3)	405.5 (384–428; 10)	429.0 (418–440; 8)
	(4)	389.1 (9.6; 373–409; 31)	394.4 (12.2; 375–416; 39)
	(5)	387.1 (9.92; 377–405; 6)	404.8 (10.82; 387–418; 8)
	(6)	384.3 (361–400; 14)	405.8 (394–418; 12)
	(7)	385.0 (15.8; 363–404; 7)	413.0 (11.5; 400–422; 3)
	(8)	381 (360–397; 17)	400 (386–417; 17)
TAIL	(1)	203.0 (196–209; 4)	194.0 (190–200; 3)
	(2)	206.4 (4.31; 198–210; 5)	216.0 (9.02; 204–227; 4)
	(3)	221.0 (204–236; 8)	214.0 (207–220; 6)
	(4)	195.6 (9.4; 176–211; 31)	194.9 (9.0; 176–214; 39)
	(5)	194.5 (12.39; 178–209; 6)	191.3 (8.10; 184–210; 8)
	(6)	205.6 (187–235; 12)	200.9 (185–250; 10)
	(8)	187 (171–222; 17)	194 (178–210; 17)
	(9)		
BILL	(1)	97.7 (97–99; 4)	104.6 (100–110; 3)
	(2)	98.6 (2.05; 96–101; 5)	104.0 (1.87; 102–107; 4)
	(3)	96.2 (88.2–99.5; 15)	102.0 (95–107.1; 22)
	(4)	97.2 (3.2; 91.8–106; 31)	98.9 (3.2; 90.1–104.8; 40)
	(5)	97.3 (2.44; 93.3–100; 6)	101.0 (1.86; 96.7–102.6; 8)
	(6)	97.3 (93.3–102; 14)	99.7 (95–102.6; 12)
	(7)	96.0 (1.77; 92–98; 8)	96.7 (5.82; 87–101; 6)
	(8)	97.5 (92.4–104.6; 18)	100.9 (92.9–108.3; 17)
BILL(G)	(2)	117.4 (1.65; 115–120; 5)	126.6 (1.98; 125–130; 4)
	(1)	42.0 (40–44; 4)	45.0 (44–47; 3)
	(2)	42.2 (0.74; 41–43; 5)	44.8 (0.54; 44–45.5; 4)
	(4)	47.4 (8.3; 43.3–52.6; 31)	50.3 (2.3; 45.1–54.6; 40)
	(5)	47.9 (1.75; 45.6–50.9; 6)	50.4 (0.95; 49.2–52.5; 8)
	(6)	46.4 (44–50; 14)	48.8 (42–52.5; 12)
	(8)	47.8 (42.2–55.4; 18)	50.8 (42.1–54.4; 17)
	(9)		
TARSUS	(2)		
	(4)		
	(5)		
	(6)		
	(8)		
	(9)		
	(10)		
	(11)		

Additional measurements in Vooous (1964); full details of growth rates of chicks in Dorward (1962a) and Nelson (1978).

**WEIGHTS** (1) Manowar I., Qld, adults, live, July (ABBBS). (2) Christmas I. (Ind.) (Nelson 1978). (3) MacLennan Cay, Qld, breeding adults, July (ABBBS). (4) Adults, skins (label data taken by B.R. King at QM, ANWC, MV). (5) Raine I., adults (B.R. King).

Additional weights in Vooous (1964) and BWP. No data on seasonal changes. Maximum weight of chicks at c. 30–70 days: 600–1400 g, weight varies according to food supply

	MALES	FEMALES
(1)	1188.6 (90.1; 1055-1400; 11)	1343.6 (177.6; 1055-1535; 11)
(2)	962.0 (850-1190; 20)	1260.0 (970-1480; 29)
(3)	1086.6 (75.42; 980-1140; 3)	1350.0 (90.00; 1280-1500; 4)
(4)	1066.2 (980-1140; 6)	1198.5 (897.5-1500; 7)
(5)	1056 (940-1220; 18)	1175 (1040-1430; 17)

(Dorward 1962a). Nelson (1978) also gives full details on effect of reduction of food supply on chick weights. For details of weight changes in chicks see Dorward (1962a) and Nelson (1978).

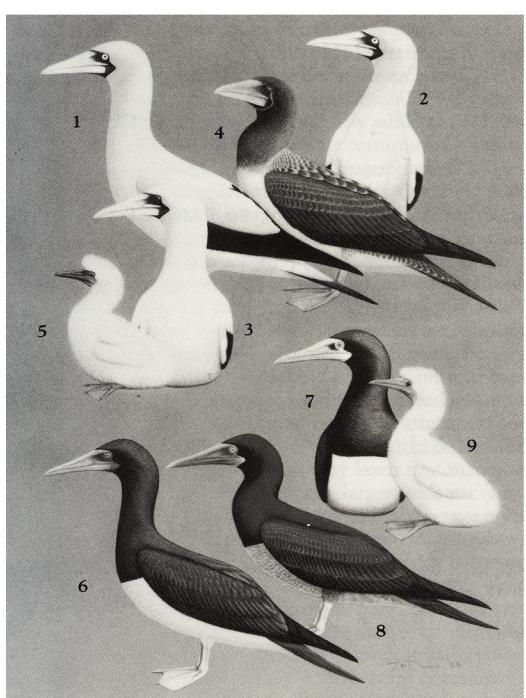
**STRUCTURE** Wing, long and slender. Eleven primaries: p10 longest, p9 0-23 mm shorter, sometimes longest when p10 replaced in moult. P8 21-31, p7 52-89, p6 84-122, p5 115-153, p4 143-181, p3 170-201, p2 189-209, p1 243-276, p11 minute. Inner web of p10 emarginated; slight on inner web of p9 and p8. Tail, wedge-shaped; 12 rectrices, t1 longest, t6 102-120 mm, occasionally 14 or 16 rectrices. Bill shape differs between sexes; broader and heavier in females, thinner in males (Gibson-Hill 1947). Bill, longer than head, conical, high at base, tapering towards tip, where slightly curved. Backward serrations on upper and lower mandibles. Upper mandible composed of culminicorn and latericorn, with secondary external nostril near gape. No external nostrils. Tarsus, short and stout. Claws strongly curved; middle longest, pectinate. Outer toe c. 70% of middle, inner c. 50%, hind c. 26%.

**GEOGRAPHICAL VARIATION** Subspecies *plotus* breeds A'asia. Subspecific separation based on colour of bare parts and plumage (Nelson 1978); males of *plotus* said to be pale headed (BWP).

RMO

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**Volume 1 (Part B), Plate 56**

Masked Booby *Sula dactylatra*

1. Adult male
2. Adult female
3. Adult female, subspecies *fullagari*
4. Juvenile
5. Downy young

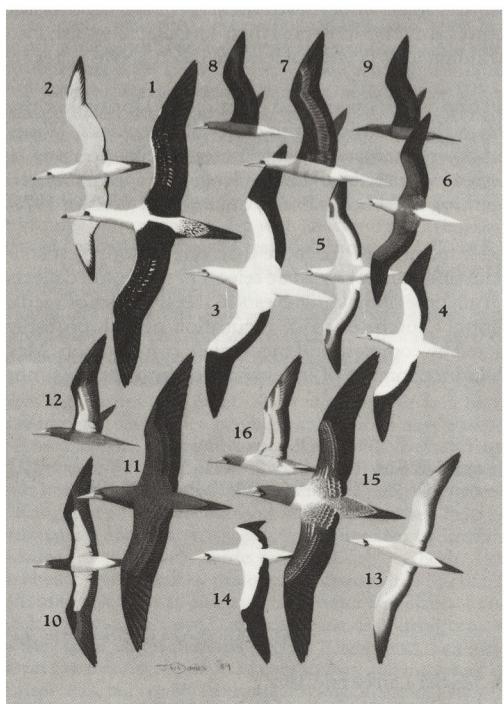
Brown Booby *Sula leucogaster*

6. Adult male
7. Adult female
8. Juvenile
9. Downy young

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**Volume 1 (Part B), Plate 58**

Abbott's Booby *Sula abbotti*

- 1. Adult
- 2. Adult

Red-footed Booby *Sula sula*

- 3. Adult, white morph
- 4. Adult, white morph, Christmas I. (Ind.)
- 5. Adult, white morph
- 6. Adult, intermediate morph
- 7. Adult, intermediate morph
- 8. Adult, white-tailed brown morph
- 9. Juvenile

Brown Booby *Sula leucogaster*

- 10. Adult
- 11. Juvenile
- 12. Juvenile

Masked Booby *Sula dactylatra*

- 13. Adult
- 14. Adult
- 15. Juvenile
- 16. Juvenile

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