

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 pterygiae 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.

REFERENCES

Brisson 1760. *Orn.* 1: 60, 6: 511.

Cottam, 1957. *Bull. Br. Mus. nat. Hist. Zool.* 5: 49-72.

Linnaeus, C. 1758. *Systema Naturae* Ed. 10, Vol. 1.

Olson, S.L. 1985. *Av. Biol.* 8: 79-238.

Schmidt-Nielson, K. 1959. *Sci. Am.* 200: 109-16.

Siegel-Causey, D. 1990. *Auk* 107: 110-18.

van Tets, G.F. 1965. *AOU orn. Monogr.* 2.

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 *Papasula* 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. Eggshells 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.

REFERENCES

- Bourne, W.R.P. 1976. *Ibis* 118: 119–23.
 Ewart, J.C. 1881. *J. Linn. Soc., Lond.* 15: 455.
 Macdonald, J.D. 1960. *Proc. zool. Soc., Lond.* 135: 357–63.
 Nelson, J.B. 1974. *Ibis* 116: 368–9.
 Nelson, J.B. 1978. *The Sulidae: Gannets and Boobies*.
 Olson, S.L. 1977. *Smithson. Contrib. Palaeobiol.* 35: 1–33.
 Olson, S.L. 1985. *Av. Biol.* 8: 79–238.
 Olson, S.L., & K.I. Warheit. 1988. *Bull. Br. Orn. Club* 108: 9–12.
 van Tets, G.F. 1965. *AOU orn. Monogr.* 2.
 van Tets, G.F., *et al.* 1988. *Notornis* 35: 35–57.
 van Tets, G.F., *et al.* 1989. *Publ. Geol. Res. Dev. Centre, Bandung, Palaeont. Ser.* 5: 57–75.

Sula dactylatra Masked Booby

COLOUR PLATE FACING PAGE 757

Sula dactylatra Lesson, 1831, *Traité Orn.* 8: 601 — Ascension Island.

The specific name is an unhappy compound of Greek δάκτυλος (finger) and Latin *ater* (dull black) and refers to the black primaries and alula.

OTHER ENGLISH NAMES Blue-faced, White or Whistling Booby, Masked Gannet.

Though **White** and **Blue-faced** have been commonly used, Nelson (1978) gives good reasons for preferring **Masked**.

POLYTYPIC Nominate *dactylatra*, Atlantic Ocean and Caribbean Sea; *melanops* Heuglin, 1859, w. Indian Ocean; *personata* Gould, 1846, central and w. Pacific Ocean, Aust.; *granti* Rothschild, 1902, Pacific Ocean; *bedouti* Mathews, 1913, e. Indian Ocean; *fullagari* O'Brien & Davis, 1990, Tasman Sea.

FIELD IDENTIFICATION Length 75–85 cm; wingspan 160–170 cm; weight 1.2–2.2 kg. Largest booby; typically sulid characters of streamlined body, long narrow wings, longish neck, pointed bill and pointed tail, with powerful flight, flapping and gliding and plunge-diving for food. Brilliant white and black plumage and dark facial mask distinguish adults but juveniles and immatures brown and white and more likely to be confused with other species. Sexes alike. No seasonal variation in plumage. Juveniles and immatures separable.

DESCRIPTION ADULT. Body plumage, entirely white above and below. Upperwing, white contrasting sharply with black remiges, greater coverts and humerals; tail, usually all black though central feathers sometimes white. Under wing-coverts, all white contrasting with black remiges. Facial skin, from base of bill to behind eye, blue-black, conferring distinctive masked appearance and forming gular patch under bill. Iris, bright yellow or dark brown (depending on subspecies). Bill varies much: yellow, yellow-green, rosy pink or orange. Legs and feet, usually leaden grey but vary and can be olive or dull orange. **JUVENILE.** Above, mostly grey-brown; head and most of neck, grey-brown streaked and mottled paler, separated from grey-brown mantle by diagnostic white collar, giving dark-hooded appearance at sea. Remiges and greater coverts, dark brown; rest of upperwing, dark brown with fine pale edges to feathers giving finely streaked or mottled appearance. White below with darker mottling on lower flanks. Underwing, mostly white with dark trailing-edge (dark remiges), mottled coverts, a dark patch near carpal joint and a varying fine bar across outer lesser-coverts sometimes extending to carpal joint. Bill, yellowish with blue-green tinge. Facial skin, dark blue-grey. Iris, dark brown. Feet, dark blue-grey. **IMMATURE.** Brown body feathering gradually replaced by white: white collar broadens, broader white tips develop on upperwing, white band develops on rump and under wing-coverts gradually whiten; median primary coverts remain streaked and are last area to become white. Adult plumage not attained until end of third year.

SIMILAR SPECIES Australasian *S. serrator* and **Cape** *S. capensis* **Gannets** differ by yellowish head, shorter tail, white humerals, no conspicuous dark mask and grey-black (not yellowish) bill. **Abbott's Booby** *S. abbotti* has almost entirely black (not black-and-white) upperwing, with white marginal coverts and a few white spots, and longer-winged, longer-tailed and larger-headed jizz. **Red-footed**

Booby *S. sula* smaller, with white tail (in our region), yellowish wash on head, more white on upperwing lacking black tertials and greater secondary coverts, red legs and feet, and blue and pink bill. **Juvenile and immature Australasian and Cape Gannets** differ from juvenile and immature Masked by heavily spotted white upperparts, white band on upper tail-coverts and without diagnostic white collar and dark-hooded appearance; also no blackish mask. **Adult Brown Booby** *S. leucogaster* differs from juvenile Masked by clean-cut brown-and-white plumage with sharp demarcation between dark head, neck and upper breast, and white lower breast and belly (demarcation indistinct on Masked and on throat), all-dark primary coverts and no white collar. **Juvenile Brown Booby** has abdomen mottled dark brown and underwing-pattern similar to adults.

Tend to be more solitary than Australasian Gannet or Brown Booby; sometimes in loose congregations, particularly when returning to breeding islands. Fly with strong, steady wing-beats alternating with glides; usually rather high (7+ m) and fast (to 70 km/h). At Raine I., birds dive into colonies at high speed to avoid pursuing frigatebirds (B.R. King). Feed by plunge-diving, usually nearly vertically. Rest and swim on sea, floating high; also perch on buoys and marine structures (drilling rigs, etc.). Juveniles at least occasionally pursue flying fish. May come to ships but usually do not follow them. Apparently silent at sea, but noisy at breeding colonies: male gives thin whistling call, prolonged and descending in pitch; female honks loudly; both sexes give series of loud honks as alarm (when pursued by frigatebirds).

HABITAT Marine, pelagic and aerial; in tropical and subtropical waters but off Peru, where warm water extends into Subtropical Zone, found farther S than usual. Distribution may be determined by distribution of flying fish (Murphy). In Tropical Zone, possibly forage at upwellings of cool nutrient-rich waters (Bourne 1963), especially when breeding; decline in numbers and breeding failure on Christmas I. (Pac.) during El Niño Southern Oscillation, when sea-surface temperature high and food supply poor (Schreiber & Schreiber 1984). Often far from land; usually over deep water.

Breed on tropical oceanic islands, atolls and cays, mostly far from mainland; proximity to clear deep water important (Nelson 1978); on Raine I., surrounded by waters of 180–3700 m depth (King 1986). Can use very small low-lying cays,

washed over by highest tides and storm waves (King 1985) and sometimes physically unstable; cays changing size, shape and vegetation under action of winds, currents, waves and tides (Limpus & Lyon 1981; Walker & Jones 1986e). Prefer areas of level open ground for nests, often exposed; on cays and atolls, from central areas to water's edge, just above high-water mark, on bare surface of sand, guano, coral fragments or lava, or among low cover of grasses, herbs or shrubs (Gibson-Hill 1948; Serventy 1959; Bush & Lodge 1977; Nelson 1978; Limpus & Lyon 1981; King *et al.* 1983; King 1985, 1986); may be restricted to smaller and smaller areas of bare ground by encroaching vegetation (Kepler 1969).

Non-breeding birds roost in congregations near breeding colonies; on Raine I., on flat open central depression with some sparse low vegetation (King 1986); sometimes on beaches (Warham 1961).

Fly fairly high, often above c. 7 m; circle in thermals over atoll lagoons (Stokes *et al.* 1984). Dive into water as shallow as 1.5 m, but in deeper water can penetrate 2–3 m or more. Diving height 12–100 m; higher than many other boobies.

Guano digging at Raine I. in last century badly affected breeding colony, but now recovering. Mining may have improved breeding habitat in long-term by providing flat bare exposed ground.

DISTRIBUTION AND POPULATION Widespread in tropical waters between approximately 30°N and 30°S usually near deep water. Extralimittally in Atlantic from Caribbean to Ascension I.; in Indian Ocean, in W off e. Africa and Arabian Pen. but not in central area: then widely from Indonesia (Sumatra) through n. Aust. waters across Pacific to w., central and s. America.

AUST. Occur from Dampier Arch., WA, to near Brisbane, Qld and sometimes farther S: Newcastle, NSW, Sept. 1979 (Morris *et al.* 1981); Barrow I., WA (Aust. Atlas); Granite I., Victor Harbour, SA, Dec. 1966 doubtfully (van Gessel 1968; Cox 1978). Very few records NT region, only one unconfirmed report between 125°E and 142°E, Melville

Bay (Humphries 1947).

NZ Few records: Gannet I. (Reischek in NZCL), W of North Cape (NZCL); Firth of Thames, 30 Oct. 1977 and possibly sightings off Miranda, 19 Oct. 1977 and 5 Mar. 1978 (Brown & Laurie 1979).

Regular occurrence round breeding islands in our area: Lord Howe, Norfolk, Kermadec, and Cocos-Keeling Is.

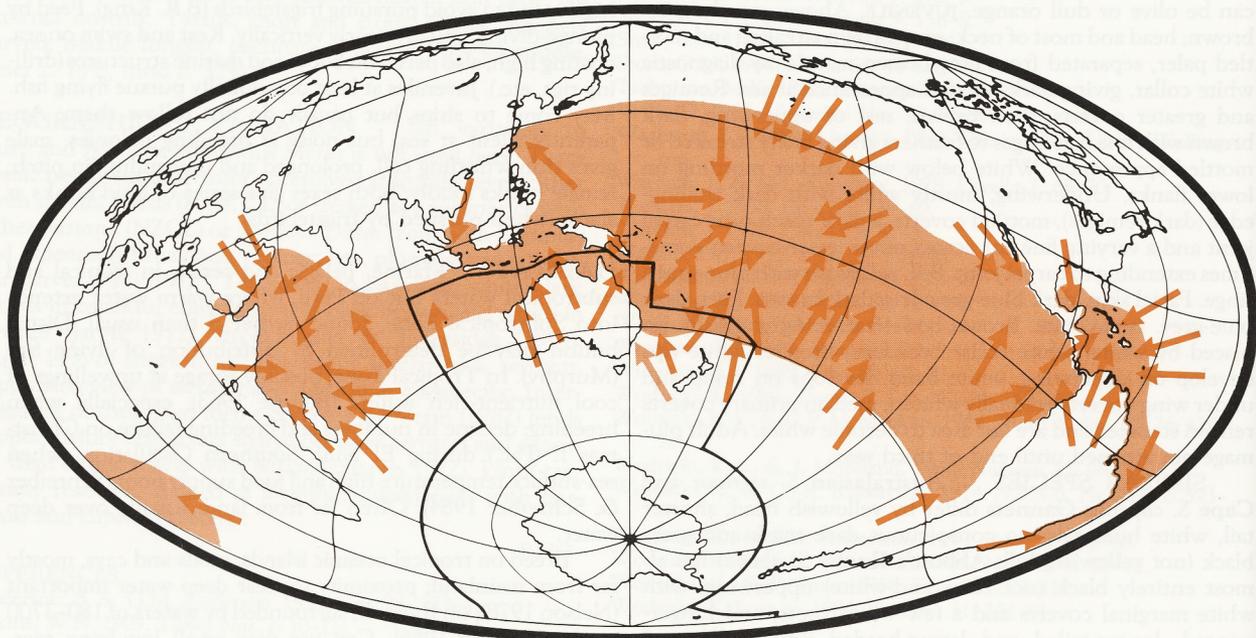
BREEDING Breeding sites summarized Table 1. Lord Howe I. is southernmost colony in world. Extralimittally, breed widely throughout tropical waters (see map).

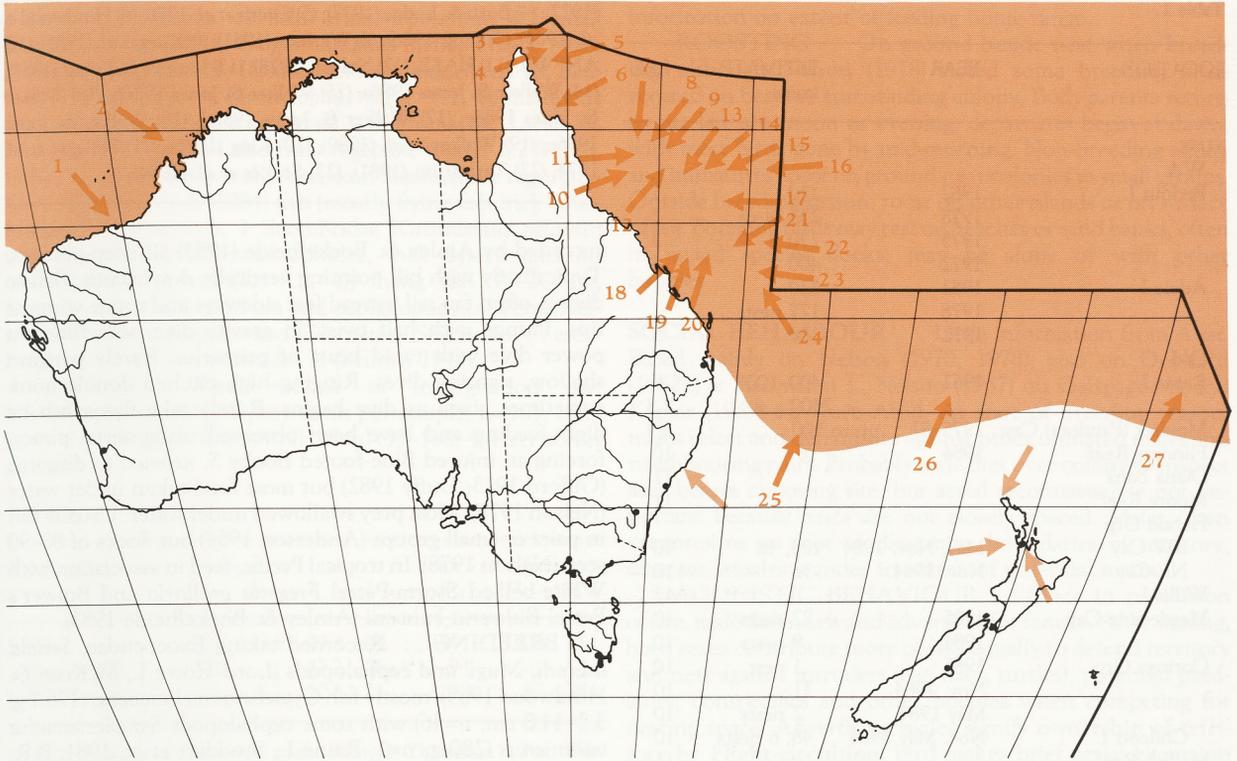
Nesting density, one pair to 42 m² (0.024/m²) (Nelson 1978).

Status, probably stable but persecuted throughout range by man and introduced predators. Extralimittally in Indian and Pacific Oceans, persecution by man and by introduced predators has caused decline and even extinction of some colonies (Nelson 1978; Feare 1984; Garnett 1984; Gallagher *et al.* 1984).

MOVEMENTS Migratory or dispersive. Fledge Norfolk I., 2 Jan.–29 Mar. (Hermes *et al.* 1986), most young fledge Christmas I. (Pac) by Dec. but breed throughout year (Schreiber & Ashmole 1970). Most immatures appear to return to natal island to breed (Nelson 1978) though one banded Kure Atoll, n. central Pacific, bred Midway I. (Woodward 1972); once established, individuals usually faithful to breeding locality (Dorward 1962a,b). Immatures and non-breeders disperse widely (see Banding) mostly to N with little overlap between populations on different islands: most birds from Kermadec Is recovered Vanuatu and New Caledonia, those from Lord Howe I. on e. coast Aust., those from Raine I. in se. PNG. During breeding season forage offshore: off Hawaii seen more often >80 km from shore than nearer land (King 1970) and in Indian Ocean most adults 160 to 320 km from breeding islands (Bailey 1968).

BANDING All returns ABBBS; from Norfolk I. summarized Fig. 1, Lord Howe I. Fig. 2, Raine I. Fig. 3.





- (1) Bedout I.; (2) Adele I.; (3) Bramble Cay; (4) Moulter Cay; (5) Raine I.; (6) Sandbank No 1; (7) Moore Reef; (8) Diana Bank; (9) Willis Is, Magdelaine Cay; (10) Flinders Reef; (11) Herald Grp; (12) Coringa Grp; (13) Diamond Is; (14, 15) Lihou Reefs; (16) Mellish Reef; (17) Marion Reef; (18) Bell Cay, Swain Reefs; (19, 20) Swain Reefs; (21) Saumarez Reef; (22) Kenn Reef; (23) Wreck Reef; (24) Cato I.; (25) Lord Howe I.; (26) Norfolk I.; (27) Kermadec Is.

FOOD Mostly fish with some cephalopods. **BEHAVIOUR.** Food obtained by deep-plunging from 12–100 m (Anderson 1954), mostly 15–35 m to depths probably exceeding 3 m, though sometimes in water as shallow as 1.5 m. Of 12 dives

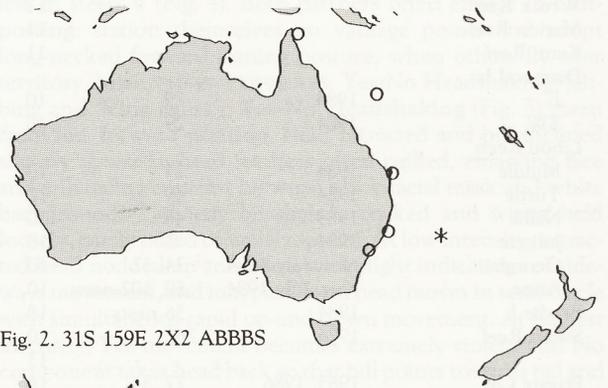


Fig. 2. 31S 159E 2X2 ABBBS

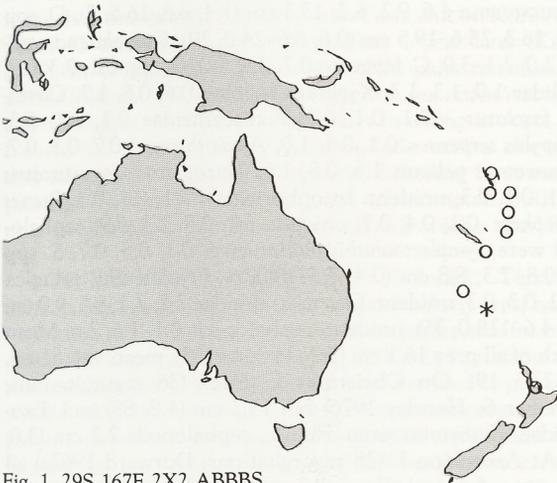


Fig. 1. 29S 167E 2X2 ABBBS

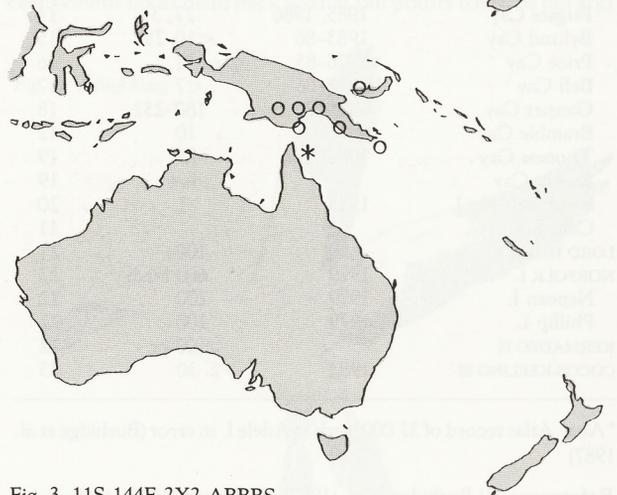


Fig. 3. 11S 144E 2X2 ABBBS

Table 1.

LOCATION	YEAR	ESTIMATE (pairs)	REF
AUST.			
WA			
Bedout I.	182	120	1
	178	235 birds	2
	175	270	3
	172	400	4
Adele I.	182	320	1*
	178	177 nests	2
	172	100	5
Qld			
Raine I.	161	400-1000 c. 2500 p.a.	6 7,8
Moulter (Pandora) Cay	175-82	up to 100	8,9
Flinders Reef	184	6	10
Diana Bank			11
Moore Reef			11
Herald Grp			
SW Cay	May, Nov. 1984	123, 48	10
NE Cay	Nov. 1984	36	10
Willis I.			12
Magdelaine Cay	185	22 nests	10
	184	9 nests	10
Coringa Grp	185	1 nest	10
	Nov. 1984	31	10
	May 1984	2 nests	10
	Nov. May 1984	48, 6 nests	10
Chilcott I.			11
Mellish Reef			11
Saumarez Reef			11
Wreck Reef			11
Marion Reef			11
Kenn Reef			11
Diamond Is			
E	184	29	10
SW	184	29	10
Lihou Reefs			
Middle	184	21	10
Turtle	184	49	10
Nellie	184	48	10
Juliette	184	3	10
Georgina	Nov. July 1984	34, 32	10
Anne	Nov. July 1984,	50, 102 nests	10
Brodie I.	184	36 nests	10
Swain Reef	176	260	10, 13
Frigate Cay	185, 1986	27, 34	14
Bylund Cay	183-86	<10-29	15
Price Cay	176-85	up to 51	16
Bell Cay	176-86	<7	17
Gannet Cay	185-86	180-232	18
Bramble Cay		10	12
Thomas Cay	186	25	19
Bacchi Cay		few	19
Sandbank No 1	184	1	20
Cato I.			11
LORD HOWE I.		100s	21
NORFOLK I.	179	600 birds	22
Nepean I.	179	200	22
Phillip I.	179	100	22
KERMADEC IS		<100 pr	12
COCOS-KEELING IS	182	c. 30	23

* Aust. Atlas record of 32 006 birds at Adele I. in error (Burbidge *et al.* 1987)

References: (1) Burbidge *et al.* (1987); (2) Abbott (1979); (3) Kolichis

(1977); (4) Bush & Lodge (1977); (5) Smith *et al.* 1978; (6) Hindwood *et al.* (1963); (7) King (1986); (8) Warham (1961); (9) King *et al.* (1983); (10) ANPWS; (11) HASB; (12) Nelson (1978); (13) Limpus & Lyons (1981); (14) Walker & Jones 1986a; (15) Walker & Jones 1986b; (16) Walker & Jones 1986c; (17) Walker & Jones 1986d; (18) Walker & Jones 1986e; (19) Walker *et al.* (1989); (20) King (1985); (21) Fullagar *et al.* 1974; (22) Tarburton (1981); (23) Stokes *et al.* (1984).

recorded by Ainley & Boekelheide (1983) all deep-plunges. Typically fly with bill pointing vertically downwards. Before diving, often fan tail, spread feet sideways and rotate wings at tips. Plunge with half twist, in gravity dive, sometimes in power dive with rapid beats of primaries. Rarely perform shallow, slanting dives. Ringing high-pitched double honk sometimes given as dive begins. Rarely take flying fish by flight-feeding and have been observed using aerial piracy, forcing an injured Blue-footed Booby *S. nebowxi* to disgorge (Gifford 1913; Duffy 1982) but most food taken under water (Nelson 1978). Most prey swallowed under water. Usually fish in pairs or small groups (Anderson 1954) but flocks of 80-90 seen (Nelson 1978). In tropical Pacific, feed in association with White-bellied Storm-Petrel *Fregetta grallaria* and Bulwer's Petrel *Bulweria bulwerii* (Ainley & Boekelheide 1983).

BREEDING Recorded taking Exocoetidae, *Seriola lalandi*, *Mugil* and cephalopods (Lord Howe I.; McKean & Hindwood 1965); mostly fish *Cypselurus melanocerus* (176.7 g; 3.2-44.0 cm; n=46) with some cephalopods *Symplectoteuthis oulaniensis* (280 g; n=1; Raine I.; Stoddart *et al.* 1981; B.R. King); flying fish 37.5 cm, Willis I. (Davis 1923); flying fish 41.3 cm, Kermadec Is (Nelson 1978).

Only detailed analysis extralimital; summarized Table 2. In **nw. Hawaiian Is** (305 regurgitations, adults 76%, subadults 7%, chicks 16%; 2097 food items; Harrison *et al.* 1983) fish consisted of *Cheilopogon atrisignis* 0.3% vol., 0.1% no., 0.3% freq., *Cheilopogon/Hirundichthys* 22.7, 11.5, 26.2, 23.1 cm (6.1; 13.4-34.3; 22), *Exocoetus volitans* 3.7, 5.8, 6.2, 14.4 cm (0.4; 9.5-18.4; 30), *Hirundichthys speculiger* 0.8, 0.8, 2.0, *Par-exocoetus brachypterus* 1.0, 2.7, 2.3, 13.6 cm (0.3; 12.5-15.3; 11), unident. Exocoetidae 29.5, 26.2, 43.9, *Euleptorhamphus viridis* 2.7, 4.0, 7.2, 26.7 cm (1.4; 16.9-30.1; 9), unident. Hemiramphidae 0.1, 0.5, 0.7, *Ablennes hians* <0.1, 0.1, 0.3, *Platybelone argalus platyura* 0.1, 0.4, 0.7, unident. Belonidae <0.1, 0.1, 0.3, *Cololabis saire* 0.1, 0.3, 0.3, Echeneidae 0.1, 0.3, 0.3, *Decapterus macarellus* 1.7, 1.3, 2.0, 20.7 cm (0.5; 18.5-22.4; 8), *D. macrosoma* 4.6, 9.2, 6.2, 13.3 cm (1.4; 6.6-16.5; 8), *D. spp* 22.7, 16.3, 25.6, 19.5 cm (0.6; 6.6-24.0; 29), *Coryphaena equiselis* 2.0, 2.1, 3.0, *C. hippurus* 0.7, 0.4, 1.0, *C. spp* 0.1, 0.3, 0.7, *Mullidae* 1.0, 1.3, 1.3, *Kyphosus bigibbus* 0.6, 0.8, 1.3, *Cirrhioptus fasciatus* <0.1, 0.1, 0.3, Pomacentridae 0.3, 0.1, 0.3, *Gempylus serpens* <0.1, 0.4, 1.0, *Auxis thazard* 0.7, 0.3, 0.7, *Katsuwonus pelamis* 1.5, 0.8, 1.6, *Tetrapterus angustirostris* <0.1, 0.1, 0.3, unident. Istiophoridae <0.1, 0.1, 0.3, *Psenes cyanophrys* 0.1, 0.4, 0.7, unident. fish 0.8, 2.3, 5.9; cephalopods were *Symplectoteuthis oulaniensis* 0.1, 0.5, 0.7, *S. spp* 0.2, 0.8, 2.3, 8.8 cm (0.4; 7.3-10.0; 6), *Hyaloteuthis pelagica* <0.1, 0.3, 0.3, unident. Ommastrephidae 2.2, 7.5, 8.5, 9.0 cm (0.3; 4.6-128.0; 35), unident. cephalopods 0.1, 1.6, 2.6. Mean length of all prey 16.1 cm (2.9-34.3; n=193), mean vol. 51 ml. (0.7-220; 19). On **Christmas I. (Pac.)** (36 regurgitations; Schreiber & Hensley 1976) fish 15.2 cm (4.8; 89) incl. Exocoetidae, *Euthynnus yaito* 3% no., cephalopods 7.2 cm (3.0; 19). At **Ascension I.** (28 regurgitations; Dorward 1962a) all large items fish incl. *Exocoetus volitans* 9% no., *Scomberesox*

saurus <1, *Fistularia* <1, *Selar crumenophthalmus* <1; small items incl. *Engraulis* 6, *Oxyporhamphus micropterus* 3, *Holocentrus ascensionis* <1, *Ophioblennius steindachneri* 70, *Benthodesmus simonyi* 9, *Centrolophus niger* <1, cephalopods *Hyaloteuthis*. In Tuamotu Arch. (16 stomachs; Lacan & Mougín 1974) samples also incl. vegetable matter 6.2% freq. **Other records:** Rose Atoll, American Samoa (four regurgitations; Harrison *et al.* 1984) fish (mostly flying fish incl. *Cheilopogon/Hirundichthys*, 1 Scombridae *Katsuwonus pelamis*) and cephalopods (Ommastrephidae, incl. *Symplectoteuthis oualaniensis*) 7.4 cm (5.6–8.9; 4); flying fish 15–20 cm, Ecuador; flying fish \leq 28 cm and cephalopods off Peru (Nelson 1978); cephalopods and *Exocoetus*, Seychelles (Vesey-Fitzgerald 1941) and Hawaiian Is (Munro 1944).

INTAKE Mean volume of regurgitation nw. Hawaiian Is, 167 ml (2.5 prey items per sample, n=305; Harrison *et al.* 1983); at Rose Atoll, 93 ml (35–168; 4; Harrison *et al.* 1984).

Table 2.

Percentages	vol.		wt.		no.	freq.	
	1	2	1	2		3	2
FISH	97.4	93.8	89.4	79	99	100	75
Exocoetidae	58.0		47.2	76	9		
CEPHALOPODS	2.6	6.2	10.6	21	<0.1	47	38

(1) NW. Hawaiian Is (Harrison *et al.* 1983); (2) Christmas I., Pac. (Schreiber & Hensley 1976); (3) Ascension I. (Dorward 1962a); (4) Tuamotu Arch. (Lacan & Mougín 1974).

SOCIAL ORGANIZATION Breeding birds feed at sea round breeding islands, tending to travel far to feed in deep waters. Outside breeding season, juveniles and at least some adults disperse widely at sea. At Raine I., some birds may retain breeding sites throughout year; elsewhere, some adults may move between colonies but there is evidence for fidelity to colonies, e.g. Kepler (1969) at Kure Atoll, Nelson (1967, 1978, 1980) and Dorward (1962a,b) at Ascension I. Tend to be solitary when flying and feeding, but occasionally associating in pairs or loose flocks when feeding. Birds returning to colony often form flocks usually of less than 20, possibly to avoid piracy by frigatebirds.

BONDS Monogamous. Mates often retained for more than one season. No data from A'asia, but on Kure Atoll, 23 of 42 breeding pairs bred together 1 year later (Kepler 1969); in Galápagos, at least eight of 22 pairs remained together (Nelson 1967). No information on sex ratios nor age at pair-formation. No data on age at first breeding in Aust., but Nelson (1978) summarized available information elsewhere and suggested 4 years old. Reported breeding in immature plumage (Nelson 1978) has not been substantiated. Both parents incubate and tend young until 4–8 weeks after fledging.

BREEDING DISPERSION Colonial. Territorial pairs in distinct groups within bounds of colony area; may be indication of strong social tendencies or preference for use of particular nesting habitat or both. At Raine I., nest in areas that are flat, free of vegetation and most exposed to prevailing winds; exposure to wind lowers ambient temperatures and assists take-off and landing. Nest and small area round it defended and used for pair formation and maintenance, reproduction and feeding of chicks and post-fledging juveniles. No

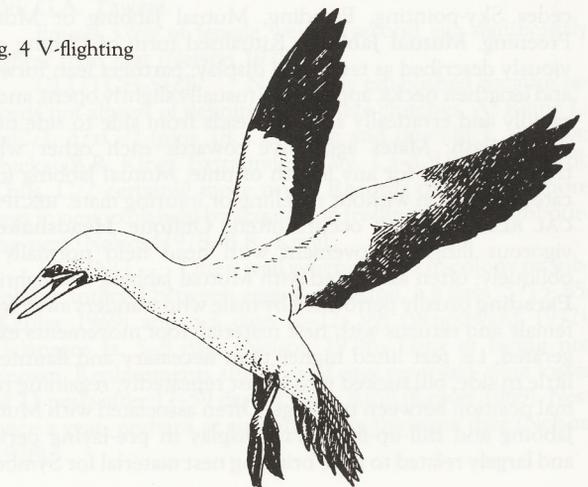
information on extent of feeding home-range.

ROOSTING On ground beside nest when breeding, although Nelson (1978) noted some breeding birds roosted on beaches surrounding colony. Both parents return to site late afternoon or evening; departures begin at dawn, with most birds gone by mid-morning. Non-breeding adults and immatures roost on ground near colonies in small groups. Outside breeding season, roost on other islands or on surface of sea. Foraging birds may rest on beaches or sand banks, often in mixed species flocks; may be alone or with other boobies.

SOCIAL BEHAVIOUR Little information from Aust. Based mainly on Nelson (1970, 1978); also on Dorward (1962b) at Ascension I., Nelson (1967) on Galápagos Is and Kepler (1969) on Kure Atoll. At start of breeding season, males select and defend site against other unmated males and neighbouring pairs. Probably male flies over colony to inspect area before choosing site, but aerial reconnaissance not important because nests are not closely spaced. Males often reconnoitre on foot to determine boundaries of territory, whereas females wander in search of potential mates.

AGONISTIC BEHAVIOUR Once in possession of site, male defends it and advertises for female. After mating, both sexes contribute more or less equally to defend territory and nest against intruders (e.g. man, turtles), potential predators, conspecifics and other boobies when competing for nesting space. Advertising males signify ownership of territory by **Flight-circuiting**: bird makes brief aerial excursion and returns with landing call and wings held almost motionless in steep V (Fig. 4). Both partners often engage in **Out-posting**: station themselves on vantage points and adopt long-necked forward-leaning posture, when others fly over territory. Main **THREAT DISPLAYS**: Yes-No Headshaking, Jabbing and Wing-flailing. **Yes-No Headshaking** (Fig. 5) given from low forward position, head retracted and bill inclined slightly upwards; head feathers often ruffled, enlarging face and enhancing contrast between black facial mask and white background. Tail may be slightly cocked and wings held loosely, partly raised or widely spread. At low intensity, retracted head nodded up and down with slight indications of sideways movement, and in typical form head moves in semi-circle with simultaneous rapid up-and-down movement. At highest intensity, **Yes** movement becomes extremely violent and **No** component takes head back so that bill points towards tail and

Fig. 4 V-flying



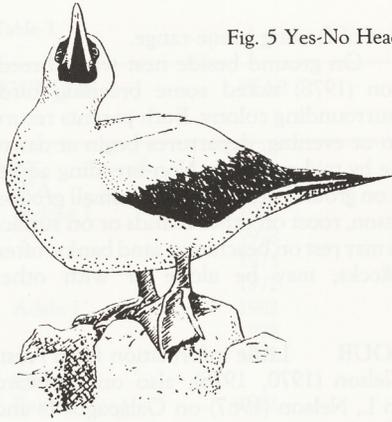


Fig. 5 Yes-No Headshaking

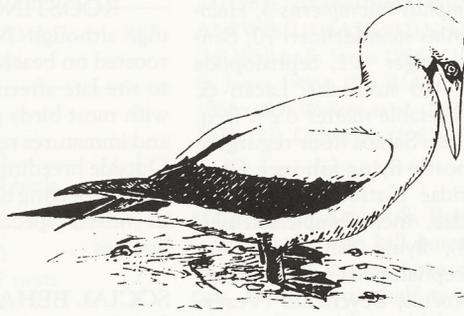


Fig. 7 Pelican Posture

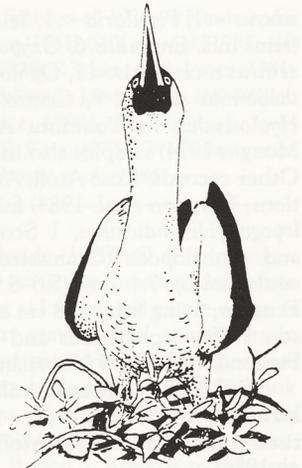


Fig. 6 Skypointing

whole movement inclined forwards and downwards. Display strongly orientated towards opponent. **Jabbing**, usually between neighbours and delivered from forward leaning posture; often with partly raised wing and tail, the latter sometimes spread widely. Jab is a flinging motion and may impart twist to head so that bills clash side to side, often loudly; feathers may be sleeked or ruffled. Sometimes, birds stand too far apart for physical contact. **Wing-flailing**. Wings lifted and brought down smartly without hitting opponent, often accompanied by Jabbing or biting, performed from forward crouching position with bill slightly inclined upwards. Usually single swift movement, but can be repeated. Directed against rival conspecific, intruder or another species, or mate or potential mate that temporarily elicits aggression. **FIGHTING** uncommon and usually brief; birds face each other, lock bills and push with extended necks; may be some associated wing-movements. At end of fight, either bird retires to its own site, with **Parading** (see below) and **Yes-No Headshaking**, or one may take flight; no pursuits recorded.

SEXUAL BEHAVIOUR PAIR-FORMATION. Displays involved in initiation and maintenance of pair-bonds: Sky-pointing, Gazing, Mutual Jabbing, Reciprocal Allopreening, Oblique Headshake, Parading, Pelican Posture, Bill-up-face-away Display and Symbolic Nest-building. **Sky-pointing** (Fig. 6) (**ADVERTISING**): neck stretched, bill pointed upwards c. 45° (sometimes vertically), wings lifted; bird whistles through slightly open bill between repetitions, bill horizontal but neck remains elongated; movement of female towards or away from site elicits Sky-pointing in male. **Gazing**: one bird intently stares at another, often maintained until reciprocated; precedes Sky-pointing, Parading, Mutual Jabbing or Mutual Preening. **Mutual Jabbing**. Ritualized form of Jabbing previously described as territorial display; partners lean forward and lengthen necks, appose bills (usually slightly open), and by rapidly and erratically shaking heads from side to side mandibles clash. Mates aggressive towards each other when together at site for any length of time; Mutual Jabbing indicates aggression without repelling or injuring mate. **RECIPROCAL ALLOPREENING** occurs often. **Oblique Headshake** is vigorous flinging movement with head held normally or obliquely; often associated with Mutual Jabbing and fighting. **Parading** usually performed by male who wanders away from female and returns with nest material; foot movements exaggerated, i.e. feet lifted higher than necessary and flaunted a little to side; bill tucked into breast repeatedly, regaining normal position between tuckings. Often associated with Mutual Jabbing and Bill-up-face-away Display in pre-laying period, and largely related to male bringing nest material for Symbolic

Nest-building. **Pelican Posture** (Fig. 7): bill tip tucked into upper breast and head held slightly backwards, occurs in both agonistic and epigamic interactions; frequently observed in aggressive individuals running to attack or who have repelled intruder, and in males that are advertising or offering female nesting material. May function to remove bill from pointed position, thus reducing possibility of Jabbing. **Bill-up-face-away Display** occurs in birds turning and moving away from mate and probably ritualized intention-movement of locomotion; involves cocking of head to one side as though squinting at sky. **Symbolic Nest-building** is gathering, presentation and building in of nesting material even though it does not significantly contribute to structure; material usually collected by male, who peers long-necked and holds material at tip of mandibles when presenting to female. Apposing bills often stimulates Mutual Jabbing and nesting material dropped. No conspicuous soliciting by female before copulation. **COPULATION**: male mounts standing or sitting female from side and holds wings close to body, laying bill alongside female's head and sometimes changing it from side to side. Male treads, moves tail from side to side; female's wings loosened and tail raised; she may gape slightly with head forward and down. Copulation followed by more Symbolic Nest-building. Boobies sometimes molested in flight by pirating frigatebirds; reaction is to flee with rapid flight and swoops, accompanied by loud honking calls. Booby often forced to crash into sea, but may regurgitate instead, after which it is left alone. Frigatebird attacks prevented by flocking, usually in flocks of fewer than 20 birds, and by diving whereby birds returning to colony, rise high, then dive with half-folded wings at considerable speed, the dive ending abruptly close to ground. Incubating bird makes head movements towards ground in front of them if disturbed by approach of intruder.

RELATIONS WITHIN FAMILY GROUP Both parents share incubation, brooding and guarding of chicks and post-fledging juveniles. Eggs hatch 4-5 days apart; older chick attacks smaller sibling, which dies 2-4 days after hatching; younger sibling may also be pushed out of nest or eaten. Parents play no part in process and do not retrieve ejected chick. At Raine I., in four seasons each with about 2000 nests, two chicks three times survived to 2 months old (B.R. King). Young take food directly from adult's crop. Very young chicks beg for food by nudging parent's lower mandible; older chicks lunge at parent's bill, while wings held out and thrashed wildly.

VOICE Reasonably well known; summarized by Nelson (1978) with some information from elsewhere in Dorward (1962b) and Kepler (1969); information supplied by B.R. King from observations at Raine I., Qld. Mostly silent at sea; very vocal and noisy at breeding colonies, particularly at nest-sites. Main call of males, thin descending whistle; of female, repeated loud strident honks. Most calling during breeding season, particularly early and late in season, when males perch on vantage points throughout colonies (Outposting) and call, mostly during morning and evening (Nelson 1978); call much during agonistic and sexual interactions, calling becoming frenzied in intense encounters; voice occasionally breaks (Nelson 1978). Distinct sexual differences in calls because structure of syrinx differs (Nelson 1978); however, both sexes may utter loud honks when alarmed because, during attacks by frigatebirds, no bird ever observed to whistle (B.R. King); juvenile and subadult males honk till about 3 years old (B.R. King). Non-vocal sounds: bills clash loudly during Jabbing and Mutual Jabbing; chicks rattle mandibles. No information on individual differences or geographical variation.

ADULT MALE Whistle. Loud two-syllable flute-like whistle *whee-oo* or *whee-ee-oo*, sounding rather thin and descending in pitch, c. 2–3 s duration; sometimes sounds like hiss. Uttered singly or repeated several times. Given in various circumstances: as Landing Call after Flight-circuiting, and as part of Outposting, Skypointing, Symbolic Nest-building, Wing-flailing, Head-shaking (though no calling if low-intensity interaction), Mutual Jabbing (less so than female) and during change-over. Functions in advertising and signifies ownership of territory. During Skypointing, Whistles repeated several times: at Kure Atoll, five Whistles per bout with up to 52 uttered in one encounter; interval between bouts 7.4 s (Kepler 1969). **Alarm Call:** Whistle at nest-site but also appear to give loud honks when attacked by frigatebirds and when defending nest-site (B.R. King; but see above). Non-vocal sounds. Loud clashing of bills during Jabbing but no calls associated with display; males Jab more often than females.

ADULT FEMALE Honk (= Shout of Nelson 1978): loud strident honking *aaah-aah-a-yah*, varying in pitch and amplitude; either uttered singly or repeated; if repeated, syllables usually descending in pitch (Nelson 1978). Calls given in various circumstances: as for male (including Skypointing, but only rarely; see Dorward 1962b), and also frenzied repeats given as Alarm Call. During Mutual Jabbing, female calls more than male, up to once every 10 s for up to 10 min at a time, early in season. Nelson (1978) also reports short soft conversational notes given by females at nest-site but not described. Non-vocal sounds: loud bill-clashing during Jabbing (Nelson 1978).

YOUNG Beg for food with rattling series of 'chuck' notes (B.R. King) described as rapid *aa-aa-aa*. . ., varying in pace and loudness (Nelson 1978); also said to utter softer honking notes when begging. Chicks rattle mandibles when threatened (B.R. King). Calls of juvenile males and females like Honk of adult female; juvenile males utter honking calls till c. 3 years old (Nelson 1978).

BREEDING No Aust. studies; extraliminally, major studies at Ascension I. (Dorward 1962a,b), Galápagos Is (Nelson 1967, 1970), Kure Atoll (Kepler 1969), various Pacific islands (Amerson 1971; Woodward 1972). Breed in simple territorial pairs, colonially, on islands well offshore or oceanic.

SEASON Throughout range, laying recorded in every month. In Aust. region: Cocos-Keeling Is, laying Jan.–July, peak in June, young Apr.–Dec. (Gibson-Hill 1950); Coral Sea, Pandora Cay, whole year with peak of laying Sept. to early Nov., young all year, mostly in summer (B.R. King); Raine I., no eggs June–July 1980–83, laying starts during or after Aug., probably peaks Sept. to early Nov., no evidence of peak Apr.–May as per Hutchinson (1950), young Nov.–May (King 1986); Lord Howe I., peak in Dec. (McKean & Hindwood 1965).

SITE On flat open unvegetated ground, usually exposed to wind. Same area used year after year; at least one member of pair may use same site or nest nearby. Some nests isolated on edges of island or colony. Usually associated, even mixed with nests of Brown Booby. Density of nests varies; small loose groups of nests may be isolated. At Raine I., density averaged 4.07 (0–12) nests/100 m² in 28 quadrats of 100 m² each (B.R. King); extraliminally, 1 pair/3.3 m² to 1 pair/201 m² (Nelson 1978).

NEST, MATERIALS Nil. Not always even a slight scrape. Twigs and debris may be brought to site, mostly by male in early stages, dropped but later removed by sitting bird within reach, leaving cleared circular area, 0.75–1 m across, round eggs, which becomes white with guano. At Raine I., some nests are small circular depressions in cleared area, 25 cm across, 1–2 cm deep, with sharply defined edges, suggesting some excavation (B.R. King). At Bedout I., nests c. 30 cm across and c. 4 cm deep (Kolichis 1977).

EGGS Elliptical; chalky surface, not glossy; dull-white outer layer on pale-blue inner layer; outer layer becomes scratched and chipped to show inner layer, stained.

MEASUREMENTS:

Cocos-Keeling Is 66.5–69 x 43–45 (Gibson-Hill 1950); Bedout I., WA 62 (55–68; 10) x 44 (40–45) (Bush & Lodge 1977); 63.2 (3.51; 55.9–68.4; 15 eggs ex 7 clutches) x 45.5 (5.08; 39.5–57.4) (Kolichis 1977); Coral Sea 63 (61–68.5) x 45.9 (43–49) (n=3 x C/2; Hindwood *et al.* 1963); Willis I. 64.84 (62.8–73.5) x 46.05 (44.4–47.8) (n=4 x C/2; Serventy 1959).

Macauley I., Kermadec Is 66.3 (2.57; 61.7–71.1; 12) x 46.5 (0.94; 45.1–47.9) (A.J.D. Tennyson; G.A. Taylor).

WEIGHTS:

Willis I. 77.5 g (70–85; 6); Macauley I., Kermadec Is 75.1 (5.33; 68–85; 12) (A.J.D. Tennyson; G.A. Taylor).

Equals 3.6% of female weight; second egg significantly lighter than first (Nelson 1978).

CLUTCH-SIZE Not clearly established because records not always of definitely complete clutches. At Raine I.: 2xC/1, 37xC/2 (plus 18 x one egg and one chick, 4 x two chicks) (B.R. King). Extraliminally; av. 1.3–1.9 (Nelson 1978). Thus, C/2 certainly more usual. Records of three or more eggs in nest explained by acquisition (rolling) from neighbouring nest (Nelson 1978; B.R. King).

LAYING Often well synchronized in colony or sub-colony. Interval between eggs: Kure Atoll, 5.6 days (3–15; 85) (Kepler 1969) and 5.3 days (2–12; 99) (Woodward 1972); Galápagos Is, 5–8 days (Nelson 1978). Time of laying not known. Replacements after loss of eggs recorded: nine losses of 21 nests after 17–59 days at Kure Atoll (Kepler 1969). Nest once a year, perhaps at almost exactly the same date (Nelson 1978).

INCUBATION By both sexes, under webs. Starts with laying of first egg but may be desultory till second egg laid and first egg may be unattended sometimes (Nelson 1978). Length of shifts (not recorded Aust.) 8–30 h. Eggshells stay in nest till dislodged or blown away or parents may put them outside cleared area. **INCUBATION PERIOD.** First egg: Kure Atoll: 43.78 days (40–49; 58) (Kepler 1969) and 43.6 (Woodward 1972). Second egg: 42.76 (38–47) and 42.7. Hatching asynchronic: 4.7 (2–9) days apart (Woodward 1972). At Ascension, period 42–46 days, hatching about 5 days apart (Dorward 1962a).

YOUNG Altricial, nidicolous. Brooded and guarded by both parents continuously till 3–4 weeks old, then left alone for longer and longer periods. When brooding, parent may cover chick or simply shade it. Small naked chicks may die after only 20 min exposure to tropical sun (B.R. King). Chicks cannot thermoregulate by gular flutter till 5–6 days old, till then depend on shelter from parent, perhaps wind. Shifts of brooding at Ascension averaged 11.6 h ($n=20$; Dorward 1962a). At night, both parents usually roost beside chick. Fed by both parents by incomplete regurgitation; chicks begs actively, even violently; most often fed in late afternoon or evening. Rate of feeding varies according to locality and doubtless availability of food; chicks adapted to survive long periods of starvation (Nelson 1970, 1978). No Aust. data on rate of feeding; at Ascension, slightly less than 2 feeding bouts/day (Dorward 1962a); Galápagos, 1.4 bouts/day (Nelson 1967, 1978). Bouts can be short or consist of 4–7 meals. No nest sanitation; chicks defecate away from nest in nesting circle. Vigorous defence of nest-site by adults, older chicks and juveniles, by calling, wing-flailing, lunging, pecking. Brood reduction: when two chicks hatch, the second invariably dies in first 3–4 days by persecution from sibling, eviction, chilling or overheating, unless first dies young (Nelson 1978). **NESTLING PERIOD.** In spite of great variation in rates of growth in different localities, young fledge about same time everywhere: c. 120 days (Ascension; Dorward 1962a); 113–120 days (Galápagos Is; Nelson 1978).

GROWTH Weight fluctuates according to conditions of time and place. At hatching, chicks c. 100 mm long, weight 40–60 g, skin grey or slightly pinkish, with very sparse white down, eyes fully open, dark blue-brown, bill grey with some pink, white egg-tooth, feet grey. Reach max. weight at Kure Atoll at c. 80 days and c. 114% of mean adult weight; at Galápagos Is, max. weight approximately equals only adult weight. Weight generally decreases to fledging. Summary of other development:

- Week 1, tiny with little down;
- Week 2, thin short down on back, flanks;
- Week 3, covered with down, not thickly, egg-tooth lost 26–35 days (Kepler 1969);
- Week 4, covered with thick white down, about one-third adult size;
- Weeks 5–6, fluffy, no sign of primaries, rectrices;
- Week 8, primaries, rectrices visible;
- Week 10, primaries, rectrices prominent, scapulars growing;
- Week 11, scapulars meet across mid-back;
- Weeks 12–14, losing down, juvenile plumage showing;
- Weeks 15–16, down all gone (Nelson 1978).

Dependent period 3–4 weeks (Dorward 1962a); at Galápagos 30–62 days (Nelson 1978). Once independent, juveniles disappear to sea.

SUCCESS No Aust. data. Elsewhere, data complex,

varying, affected by brood reduction and conditions: e.g. at Kure during six seasons total success varied from 51.1 to 90.3% (Woodward 1972). See Nelson (1978) for details. 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; heavy rainfall may have flooded nests and inhibited breeding activity (Schreiber & Schreiber 1984). **PREDATORS.** Man takes or has taken eggs, chicks, and caused general disturbance, e.g. NW Shelf (Serventy 1952), Cocos-Keeling Is. Rats are menace where present. Silver Gulls *Larus novaehollandiae* and Buff-banded Rails *Gallirallus philippensis* take eggs, small chicks. At Raine I. and Pandora Cay, Green Turtles *Chelonia mydas* destroy some nests (King 1986).

PLUMAGES

ADULT Adult plumage attained at 32–33 months (Dorward 1962a; Nelson 1978). **HEAD AND NECK,** white. Feathering adjoining base of gular pouch varies in shape; inverted V or U, clean cut or slightly wavy. **UPPERPARTS.** Entire mantle, back, rump and upper tail-coverts, white. Scapulars, dark brown (121); feathers, white at base on both webs, forming inverted V-shape. **TAIL,** sepia (119); base of feathers and rachis, white. **UPPERWING.** Primaries, sepia (119), fading to dark brown (121) with wear; inner webs, white at base. Humeral, secondaries, tertials, greater coverts, greater primary coverts, tertial coverts and alula, dark brown (121). Inner webs of secondaries and tertials, white at base to two-thirds length of feather, decreasing to one-third closer to body. Humeral and alula feathers, white at base on both webs, forming inverted V-shape. Rest of upperwing; median, lesser and marginal upper wing-coverts, white. **UNDERPARTS,** including under tail-coverts, white. **UNDERWING.** All coverts, white. Underside of tertials, secondaries and primaries, paler.

DOWNY YOUNG Largely naked at hatching, with sparse white down on back and flanks. For development of feathering, see Breeding.

JUVENILE At Ascension I., replacement of juvenile feathers begins at c. 5.5–7 months of age (Dorward 1962a). **HEAD AND NECK.** Crown to lower nape, dark brown (119A), extending as broad band to mid-point of neck on ventral side; where, with border of white underparts, forms an inverted V. Forehead, dark brown (119A), fringed white, behind thin line of white feathers adjoining base of culmen. Behind gape, narrow band of white feathers, with dark brown (119A) speckled centres, extends along rim of skin at base of bill. Lower nape and mantle separated by broad white collar, where some feathers tipped drab (119B). **UPPERPARTS.** On mantle, back and rump, all feathers white at base. Mantle, dark brown (119A) with drab (119B) fringes. Back- and rump-feathers similarly coloured with fringing absent on back; drab (119D) fringes on rump. Scapulars, sepia (219). Upper tail-coverts, dark brown (119A). **TAIL,** sepia (119); rachis, white at base. **UPPERWING.** Primaries, sepia (119); more pointed than in adult. Secondaries, tertials and alula, sepia (219). All coverts, dark brown (119A). Tertial coverts, greater upper wing-coverts, greater primary coverts and marginal upper wing-coverts narrowly fringed drab (119B); median and lesser upper wing-coverts fringed drab (119C). **UNDERPARTS,** white; thighs and outermost vent-feathers tipped pale dark-brown (119A). Axillaries, white; some may show narrow brown edge on both webs. Under tail-coverts, white with dark brown (119A) outer webs; most prominent on outermost feathers, reduced in innermost. **UNDERWING.** Most coverts, white, with varying

amounts of dark brown (119A) on webs. Greater primary-coverts, brown on outer web for half length, diminishing in extent towards body. Median and lesser primary-coverts have brown centres. Marginal coverts next to alula, brown with white fringes; brown shaft-streaks, above primaries and near axillaries; elsewhere, white. Greater coverts, similar in pattern to greater primary-coverts. Median and lesser coverts, white.

IMMATURE Similar to juvenile plumage; involves whitening of plumage, differences only described here. **HEAD AND NECK** whiten first with numerous white feathers scattered among dark-brown (119A) ones, producing mottled appearance. Head entirely white by 14–15 months (Dorward 1962a; Nelson 1978). Inverted V on neck indistinct or shallow. **UPPERPARTS**. Mantle also has mottled appearance with white feathers scattered among dark brown (119A). **UNDERPARTS** from lower neck, including thighs and outer vent-feathers, white. See Nelson (1978) for summary of whitening of plumage.

BARE PARTS

ADULT Dark-eyed birds from Lord Howe, Norfolk and Kermadec Is. Iris, dark brown (219). Eye-ring, black (82). Bill, yellow (53); greenish yellow (Oliver). Unknown if any sexual difference in bill colour. Gular pouch, facial skin, including lores and base of upper and lower mandibles, black (82). Legs and feet vary; usually grey (87) with blue-grey (88) tone; dull yellow (skin ANWC); greenish grey, yellowish on webs (Oliver).

DOWNY YOUNG Iris, dark brown (119). Eye-ring, dark grey (83). Bill, dark grey-brown (84) with grey (79) tone. Gular pouch, pale drab (119D). Facial skin, including lores, dark grey (83). Legs and feet, light grey (85); whitish (Oliver).

JUVENILE Iris, dark brown (219). Eye-ring, black (82). Bill, yellow (123D), green (59) at base. Gular pouch, facial skin, legs and feet, similar to adult.

IMMATURE Similar to juvenile.

Birds in e. Aust waters, based on photos in Lindsey (1986).

ADULT Iris, orange-yellow (18). Eye-ring, black (82). Bill, yellow (53); varyingly coloured, orange and often pink, especially in female (NZRD); creamish green (skin ANWC). Sexual difference in colour of bill claimed in Coral Sea; yellow in male and yellowish green in female (Hindwood *et al.* 1963). Gular pouch, facial skin, including lores and base of upper and lower mandibles, black (82). Legs and feet, dark grey (83). Feet and webs described as leaden grey with dull purplish tinge (Hindwood *et al.* 1963).

DOWNY YOUNG, JUVENILE, IMMATURE Similar to dark-eyed birds from Lord Howe, Norfolk and Kermadec Is.

Birds from w. Aust. and e. Indian Ocean waters (from Gibson-Hill 1950).

ADULT Iris, yellow in male; yellowish grey in female. Eye-ring, jet-black. Bill, yellow with hint of greenish grey at base in male; yellowish grey, greyer base in female. Gular pouch and facial skin, jet-black. Legs and feet, dull olive in male, lead-grey in female.

DOWNY YOUNG, JUVENILE Not known.

IMMATURE Similar bare parts to adult females; in youngest, iris, grey; gular pouch and facial skin blue-grey (Gibson-Hill 1950).

MOULTS Undescribed in A'asia. In nominate *dactylatra*, full details in Dorward (1962a) and summarized in Nelson (1978). Mode of moult, staffelmauser.

ADULT Up to three generations of feathers present at one time; each primary replaced annually. Duration of moult, till completion, is over a year. Each primary replaced at rate of two months. Moult suspended before laying and during incubation; resumed when egg hatches or chick being fed. Moult suspended anywhere within series; duration may exceed 2 months per year. Moult asynchronous among members of colony. Rate of moult subject to individual variation, through natural causes or injury. Tail-moult irregular and asymmetrical.

POST-JUVENILE Primary moult begins at about 7 months old. Primaries replaced from p1-p10 at rate of 1/month. At c. 15 months at p6 or p7, innermost primaries begin second series of replacement; p10 reached c. 18 months, during first series. On onset of second series, replacement rate slows to one feather about every 2 months. Moult continuous.

MEASUREMENTS (1) Lord Howe I., adults, live; Mar. 1971, June 1978 (ABBBS). (2) Kermadec Is, adults, skins (NMNZ; AMNH). (3) Norfolk I., adults, skins (AMNH). (4) Lord Howe I., adults, skins (ANWC; AM; MM; AMNH). (5) Raine I., adults, skins (*S.d. personata*) (ANWC; SAM; QM; BMNH). (6) Raine I., live adults (B.R. King). (7) Bedout I., adults, skins (*S.d. bedouti*) (SAM; AMNH).

	MALES	FEMALES
WING	(1) 462.2 (13.51; 446–490; 7)	477.0 (11.47; 465–495; 6)
	(2) 441.2 (7.08; 429–455; 7)	450.7 (14.5; 430–468; 4)
	(3) 441.5 (6.5; 435, 448; 2)	
	(4) 444.0 (3.34; 440–450; 5)	454.3 (8.99; 443–465; 3)
	(5) 421.8 (2.56; 418–425; 5)	
	(6) 404 (400–428; 39)	422 (405–455; 32)
	(7) 413.0 (8.52; 401–420; 3)	425.6 (3.29; 422–430; 3)
TAIL	(1) 183.5 (2.29; 180–186; 4)	184.6 (0.47; 184–185; 3)
	(2) 180.0 (5.20; 170–186; 7)	180.7 (3.26; 177–186; 4)
	(3) 174.0 (1; 173, 175; 2)	
	(4) 187.2 (11.6; 175–202.7; 5)	190.3 (12.7; 174–205; 3)
	(5) 174.9 (3.50; 170–179.7; 4)	
	(7) 171.0 (4.32; 165–175; 3)	177.6 (6.01; 172–186; 3)
	(1) 109.0 (2.21; 105.5–113; 7)	109.4 (2.21; 105–112.2; 6)
BILL	(2) 107.2 (3.10; 104–112; 7)	108.0 (1.87; 105–110; 4)
	(3) 105.0 (0; 105, 105; 2)	
	(4) 111.2 (1.65; 109.1–114; 5)	112.4 (2.63; 109–115.4; 3)
	(5) 104.5 (2.17; 102–108; 4)	
	(6) 103.8 (97.1–108.0; 39)	104.4 (99.9–109.7; 32)
	(7) 104.3 (1.25; 103–106; 3)	103.9 (2.09; 101–105.8; 3)
	(1) 61.3 (1.03; 59.9–63.5; 7)	62.3 (3.53; 55.6–67.7; 6)
TARSUS	(2) 60.4 (3.61; 55–65; 7)	61.5 (2.29; 59–65; 4)
	(3) 56.5 (3.5; 53, 60; 2)	
	(4) 57.8 (0.96; 56.5–59; 5)	60.5 (4.72; 54–65; 3)
	(5) 61.8 (2.86; 57.8–66; 5)	
	(6) 60.2 (57.9–63.4; 39)	62.3 (57.2–65.8; 32)
	(7) 53.9 (2.80; 51–57.7; 3)	54.4 (2.81; 52–58.4; 3)
	(2) 96.8 (2.53; 93–100; 7)	100.2 (5.35; 95–109; 4)
TOE	(3) 95.0 (2; 93, 97; 2)	
	(4) 100.1 (2.09; 97.6–104; 5)	95.0 (5.97; 89–103.2; 3)
	(5) 94.0 (1.96; 91–96.3; 5)	
	(7) 95.4 (2.04; 93–98; 3)	96.1 (4.36; 90–100; 3)

See Gibson-Hill (1950) and Nelson (1978) for measurements of adults and immatures at Cocos-Keeling Is. For

measurements of adults at Kure Atoll see Kepler (1969). Full details of growth rates of chicks in Dorward (1962a), Kepler (1969) and Nelson (1978).

WEIGHTS Lord Howe I., live (ABBBS): males: 2000 (122.47; 1900–2200; 4), females: 2533.3 (124.72; 2400–2700; 3). Few details available. Lord Howe I., adult male, Feb.: 2500. Raine I., adult males: 1677 (1510–1930; 39), adult females: 1852 (1520–2270; 32) (B.R. King). Moore Reef, Coral Sea, male: 2000; female: 2160 (Hindwood *et al.* 1963; ANWC; QM). No details of changes of weight available for A'asia. At Kure Atoll: range of 27 males: 1503–2211; 27 females: 1616–2353; difference significant (Kepler 1969). At Kure Atoll and Ascension I., weight of chicks at 5 weeks c. 1100 and c. 1550 respectively; weight varies according to supply of food (Kepler 1969; Dorward 1962a; Nelson 1978). See Dorward (1962a), Kepler (1969) and Nelson (1978) for details of change of weight in chicks.

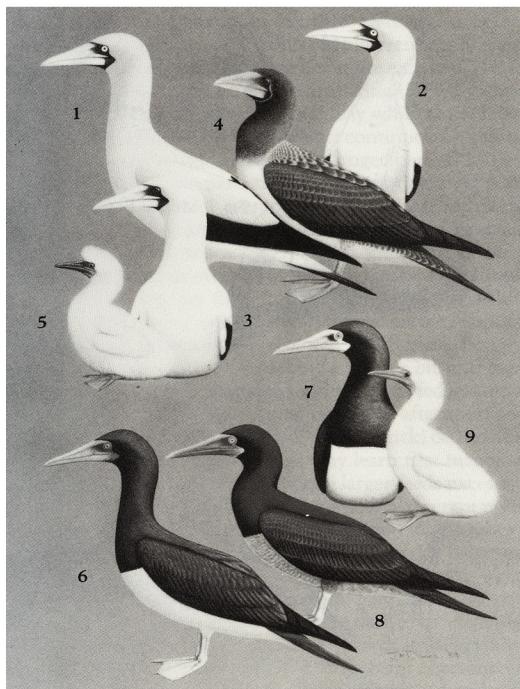
STRUCTURE Wing, long and slender. Eleven primaries, p10 longest, p9 0–38 mm shorter, p8 23–65, p7 57–101, p6 89–166, p5 122–192, p4 152–217, p3 181–219, p2 206–243, p1 231–257, p11 minute. Fifteen secondaries including four tertials. Inner web of p10 emarginated; slight on inner web of p9. Tail, long and wedge-shaped. Fourteen rectrices, sometimes 16, (x=3, n=12): t1 longest, t7 61–93 mm shorter. Bill longer than head, backward serrations on upper and lower mandibles. Bill, conical, high at base; tapering to tip where slightly curved. 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. 91% of middle, inner c. 68%, hind c. 34%.

GEOGRAPHICAL VARIATION Four to six subspecies recognized: *dactylatra*, *melanops*, *personata* and *granti*, *bedouti* and *fullagari*. Validity of *bedouti* disputed (see Nelson 1978) and needs assessment; *fullagari* occurring Lord Howe, Norfolk and Kermadec Is (O'Brien & Davies 1990); differs from adult *personata* in having dark-brown (not yellow) iris and larger wing. Subspecies claimed to be differentiated on measurements and coloration of bare parts (Nelson 1978). Hybrids with *S. leucogaster* are known (Worcester 1911).

REFERENCES

- Abbott, I. 1979. *Corella* 3: 93–102.
 Ainley, D.G., & R.J. Boekelheide. 1983. *Studies avian Biol.* 8: 2–23.
 Amerson Jr., A.B. 1971. *Atoll Res. Bull.* 127: 1–348.
 Anderson, W.G. 1954. *Elopeia* 14: 80–4.
 Bailey, R.S. 1968. *Ibis* 110: 493–519.
 Bourne, W.R.P. 1963. *Proc. Int. orn. Congr.* XIII: 831–54.
 Brown, B., & D.A. Lawrie. 1979. *Notornis* 26: 304–305.
 Burbidge, A.A., *et al.* 1987. *Emu* 87: 128–9.
 Bush, T.E., & G.A. Lodge 1977. *West. Aust. Nat.* 13: 189–90.
 Cox, J.B. 1978. *S. Aust. Orn.* 28: 18–20.
 Davis, J.K. 1923. *Emu* 22: 180–7.
 Dorward, D.F. 1962a. *Ibis* 103b: 174–220.
 Dorward, D.F. 1962b. *Ibis* 103b: 221–4.
 Duffy, D.C. 1982. *Cormorant* 10: 71–80.
 Feare, C.J. 1984. *ICBP Tech. Publ.* 2: 457–71.
 Gallagher, M.D., *et al.* 1984. *ICBP Tech. Publ.* 2: 421–56.
 Garnett, M.C. 1984. *ICBP Tech. Publ.* 2: 547–58.
 Gibson-Hill, C.A. 1948. *J. Malay. Br. R. Asiatic Soc.* 21: 68–103.
 Gibson-Hill, C.A. 1950. *Bull. Raffles Mus.* 22: 212–70.
 Gifford, E.W. 1913. *Proc. Calif. Acad. Sci. (IV)* 2: 1–132.
 Harrison, C.S., *et al.* 1983. *Wildl. Monogr.* 85.
 Harrison, C.S., *et al.* 1984. *Ibis* 126: 588–90.
 Hermes, N., *et al.* 1986. *Notornis* 33: 141–9.
 Hindwood, K.A., *et al.* 1963. *Tech. Pap. Div. Wildl. Res. CSIRO Aust.* 3.
 Humphries, C.P. 1947. *Emu* 47: 130–6.
 Hutchinson, G.E. 1950. *Bull. Am. Mus. nat. Hist.* 96.
 Kepler, C. 1969. *Nuttall orn. Club* 8: 1–97.
 King, B.R. 1985. *Corella* 9: 87–8.
 King, B.R. 1986. *Corella* 10: 73–7.
 King, B.R., *et al.* 1983. *Corella* 7: 71–3.
 King, W.B. 1970. *US Fish. Wildl. Serv., Spec. Scient. Rep. — Fish.* 586.
 Kolichis, N. 1977. *West. Aust. Nat.* 13: 1–4.
 Lacan, F. & J.-L. Mouglin. 1974. *Oiseaux Revue fr. Orn.* 44: 191–284.
 Limpus, C.J. & B.J. Lyon. 1981. *Corella* 5: 101–5.
 Lindsey, T.R. 1986. *The Seabirds of Australia.*
 Mathews, G.M. 1913. *Austral avian Rec.* 1: 187–94.
 McKean, J.L. & K.A. Hindwood. 1965. *Emu* 64: 79–97.
 Morris, A.K., *et al.* 1981. *Handlist of the Birds of New South Wales.*
 Munro, G.C. 1944. *Birds of Hawaii.*
 Nelson, J.B. 1967. *Ibis* 109: 194–231.
 Nelson, J.B. 1970. *Oceanogr. Mar. Biol. Ann. Rev.* 8: 501–74.
 Nelson, J.B. 1978. *The Sulidae.*
 Nelson, J.B. 1980. *Seabirds: Their Biology and Ecology.*
 O'Brien, R.M., & J. Davies. 1990. *Mar. Orn.* 14: 1–7.
 Palmer, R.S. (Ed.) 1962. *Handbook of North American Birds.* 1.
 Schreiber, R.W., & D.A. Hensley. 1976. *Pac. Sci.* 30: 241–8.
 Schreiber, R.W., & N.P. Ashmole. 1970. *Ibis* 12: 363–94.
 Schreiber, R.W., & E.A. Schreiber. 1984. *Science* 225: 713–16.
 Serventy, D. 1952. *Emu* 52: 33–59.
 Serventy, V. 1959. *Emu* 59: 167–76.
 Smith, L.A., *et al.* 1978. *West. Aust. Wildl. Res. Bull.* 7: 29–41.
 Stoddart, D.R., *et al.* 1981. *Atoll Res. Bull.* 254: 1–44.
 Stokes, T., *et al.* 1984. *Emu* 84: 23–8.
 Tarburton, M.K. 1981. *Notornis* 28: 209–19.
 van Gessel, F.W.C. 1968. *S. Aust. Orn.* 25: 55.
 Vesey-Fitzgerald, D. 1941. *Ibis* 41: 518–31.
 Walker, T.A., & M.E. Jones. 1986a. *Corella* 10: 89–90.
 Walker, T.A., & M.E. Jones. 1986b. *Corella* 10: 91–2.
 Walker, T.A., & M.E. Jones. 1986c. *Corella* 10: 93–4.
 Walker, T.A., & M.E. Jones. 1986d. *Corella* 10: 95–7.
 Walker, T.A., & M.E. Jones. 1986e. *Corella* 10: 98–100.
 Walker, T.A., *et al.* 1989. *Corella* 13: 49–52.
 Warham, J. 1961. *Emu* 61: 76–93.
 Woodward, P.W. 1972. *Atoll Res. Bull.* 164: 1–318.
 Worcester, D.C. 1911. *Philipp. J. Sci. Biol.* 6: 167–82.

RMO



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

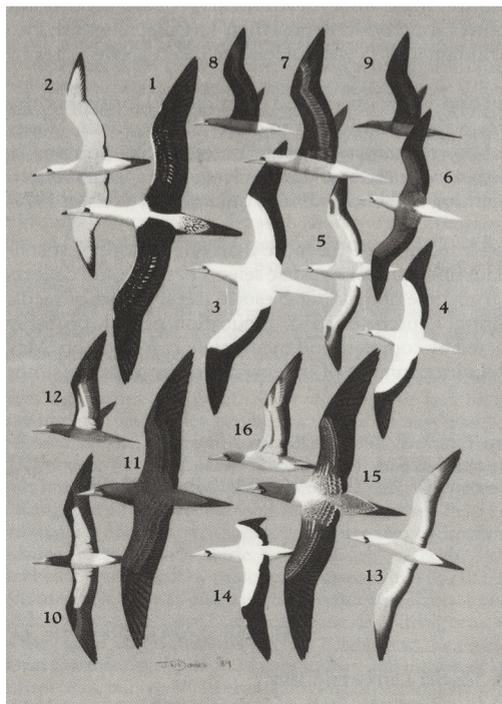
Brown Booby *Sula leucogaster*

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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