

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*.

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Family FREGATIDAE frigatebirds

Medium-sized to large tropical seabirds; among the most aerial of birds. Five species, all in genus *Fregata*; three in our region. Body, slender; neck, short; tail, long and forked; female larger than male. Wings, very long, narrow, pointed, held flat and high above body with short humeri raised. Often soar for long periods in thermals or in wind, constantly manoeuvring with deeply forked tail and occasional deep wing-beats. Also sustained flight, sometimes in unorganised flocks, with strong deep wing-beats. Eleven primaries; p10 longest, p11 vestigial; c. 23 secondaries; diastataxic. Tail deeply forked, but forking not obvious except when tail fanned during manoeuvres; 12 rectrices, outer longest. Bill, long, slender, deeply hooked; no serrations on cutting edges. Nostrils as thin slits. Face, fully feathered. Legs, extremely short, feathered; foot, small, weak, totipalmate, with reduced webs; middle claw pectinate. No aftershaft. Barely able to walk but perch in trees and sometimes on edges of cliff tops. Plumage, predominantly black or black-and-white, females typically showing more white than males. No seasonal changes, though males of all species inflate and deflate bright-red gular sacs during courtship. Moult, poorly known; primaries replaced in staffelmauser. In some populations may be suspended during breeding. Young, altricial, nidicolous, naked at hatching, develop down. Juveniles usually have varying amount of rufous or russet on head and neck, which fades with age; typically abdomen and lower breast white, separated from white or russet throat by dark breast-band, which disappears with age. Much variation between populations of same species in colour of soft parts and extent of russet and white plumage of juveniles, which makes specific identification difficult. Change towards adult plumage poorly known but perhaps begins from end of second year and is complete by 4–5 years old.

Throughout all tropical oceans. Strictly marine and all species pelagic except *F. magnificens*, which tends to feed inshore. Entirely aerial feeders with poor ability to take off from water; rarely, if ever, settle on sea. Feed either by surface-dipping in flight, taking mostly flying fish, or squid, or by piracy from other seabirds such as boobies, though this habit often over-emphasized in the literature. Foraging range from breeding localities unknown but certainly up to 500 km from land. Parents may be absent from chick for 10 days but many birds appear to return nightly to land to roost; others could spend night on the wing.

Pair-bond monogamous; probably maintained for only one breeding attempt. At start of breeding season, males take up display positions on site of future nest and direct conspicuous displays to passing females: visual display consists of presenting inflated gular sac and trembling outstretched wings towards female; auditory display may be entirely non-vocal, by bill-clattering, with or without accompanying calls. Defence of display-site varies between species and within populations of same species, there apparently being none in *F. ariel*, whereas in *F. minor* it may include threat and fighting. Copulation occurs within a few hours of attracting the female; then male leaves to begin collecting material. One member of pair stays on site to prevent pilfering of material or loss of site. Gular sac of male rarely inflated after incubation starts. Voices of sexes differ, male being more vocal during courtship and when landing. Comfort-behaviours include: drinking on the wing by skimming bill through water; dissipation of heat by gular-fluttering; sunning of ventral parts by lying or sitting back on tail facing sun and turning wings upside down; true yawning; and head-scratching at rest indirectly or in flight directly.

Breeding stations typically on remote oceanic islands. Prefer to nest in trees or on bushes, if available but often on ground on poorly vegetated islands where nothing better. Colonies large, up to 5000, but arranged in smaller groups of nests, usually 10–30 but up to 100, derived from clusters of displaying males. Breeding usually every other year and seasonal, though laying may extend over 6 months. In some species males try to breed every year by abandoning care of chicks to female, perhaps especially where food is abundant. Sex-ratios unequal, either sex predominating in different species. Nest of loosely woven sticks, becoming cemented with guano. Most material brought by male; most building by female but neither role exclusive. Only one egg per clutch. Re-laying after loss said to occur in some species. Egg, white, ovate and 6–7% of female's mass. Courtship lasts for 1–4 weeks; incubation, for 41–55 days, with equal share by both sexes; egg brooded under breast. Chick guarded by parents for 4–6 weeks after hatching. Feeding by incomplete regurgitation and insertion of head by chick into parent's mouth and throat. Nestling period lasts for 5–6 months. Rate of feeding varies with supply of food but rarely more than every second day. All species have long (5–14 months) period of post-fledging dependence on parents. Age of maturity not known but probably 4–5 years. Adult mortality and longevity not known but one female *F. minor* known to have lived for 38 years.

Fregata ariel Least Frigatebird

COLOUR PLATE FACING PAGE 933

Atagen ariel G.R. Gray (ex Gould MS), 1845, *Genera Birds*, 3: 669, Pl. 183 — no locality; Raine I., Queensland, designated by Mathews, 1914, *Austral Avian Rec.* 2: 121.

No doubt named after Shakespeare's and Milton's fairy spirit, Ariel, for the bird's fairy-like qualities.

OTHER ENGLISH NAMES Lesser Frigatebird or Man-o'-war Hawk.

Being the smallest species of *Fregata* it is best named **Least**; **Lesser** could lead to confusion with *F. minor*.

POLYTYPIC Nominate *ariel*, central and e. Indian Ocean, Aust., w. and sw. Pacific Ocean; *iredalei* Mathews, 1914, w. Indian Ocean; *trinitatis* Miranda-Ribeiro, 1919, s. Atlantic Ocean.

FIELD IDENTIFICATION Length 70–80 cm; wing-span 175–195 cm; weight c. 1 kg. Large black-and-white seabird, markings varying with age and sex; smallest frigatebird. Typical frigatebird structure and actions: long pointed wings, carried well forward, long bill with hooked tip and very long, deeply forked tail. Sexes differ. No seasonal differences except red gular pouch of male develops during courtship. Juveniles and immatures separable.

DESCRIPTION **ADULT MALE.** Mostly black with metallic green and purple gloss on head and back; bright red gular pouch, inflated like balloon during displays in breeding season. Wings, glossy blackish with slightly brown greater coverts forming indistinct bar across inner upperwing. Underparts, black; narrow white stripe on either side of abdomen runs transversely from middle of flanks and extends onto subhumeral in wing-pit. Bill, long, slender with hooked tip, grey to dark grey with darker tip. Iris, dark brown. Eye-ring, black-brown. Legs and feet, black or reddish brown; soles, flesh. **ADULT FEMALE.** Head, throat and foreneck, black forming dark hood separated from mostly black upperparts by white nuchal collar; rest of upperparts, black apart from obvious scaly buff wing-bar across inner upperwing (said to be lacking in some extralimital populations; see Nelson 1975). On foreneck, black hood extends in V-shape from base of neck to middle of upper breast, contrasting sharply with white breast and anterior flanks; white nuchal collar continuous with white of upper breast; spur of white extends from flanks onto subhumeral of wing-pit. Underwing, lower abdomen, vent and undertail, black. No gular pouch. Bill, pink; pale purplish also recorded. Eye-ring, red. Feet and legs, flesh to reddish. **JUVENILE.** Head, throat and upper neck, reddish brown with white bases to feathers; when worn, bases exposed giving mottled appearance. Upperparts, black except for pale wing-bar on inner upperwing, slightly paler than that of female; broad black breast-band, thinnest at centre of chest; from breast, below dark band, to legs, white; white extends as spurs onto bases of otherwise black underwings. Undertail and underparts behind legs, black. Bill, pale grey, tipped cream. Eye-ring, brown to dull white. Legs and feet, brown-grey to flesh. **IMMATURE.** Sequence of plumage changes, from juvenile to adult, not known; see Harrison (1983) for possible sequence. At first, lose dark breast-band, in females, feathering of head, chin, throat and abdomen, darkens gradually until adult plumage attained; in males, after disappearance of breast band, gradual darkening of chin and throat and plumage of central abdomen and mid-breast, at first, mottled

black, eventually darkening to leave only thin white spurs on sides of breast extending onto underwing.

SIMILAR SPECIES Only likely to be confused with other frigatebirds; **Christmas** *F. andrewsi* and **Great** *F. minor* in our area. In all plumages, smaller and lighter than other species but size difficult to judge in birds soaring at great heights. **Adult male** distinguished by pattern on underparts. Christmas Frigatebird differs in having large white patch on abdomen; Great has all-black underparts; subadults of Great often have remnants of white along flanks, but running laterally and not reaching subhumeral (in Least, underparts, black with diagnostic thin white stripe leading from flanks onto subhumeral of wing-pit). All other ages and sexes separated from adult male Least by greater amount of white in plumage. **Adult female.** Christmas has white abdomen and black spur extending onto white upper breast; white spur extending onto underwing parallel with edges of wing (curves forward in Least). Great has grey throat and no white collar (and so does not have hooded appearance of Least), and all-black underwing (in Least, white spurs extend onto underwing). All juveniles and immatures separated from adult female Least by white or rusty brown heads. **Juvenile.** Pose greatest identification problem and field characters not fully determined; probably not always possible on present knowledge. Size may be only character to separate Great and Christmas Frigatebirds from Least. Presence or absence of white spurs extending onto inner underwing useful: never present in Great in our region (Hawaiian birds show this character; Harrison 1983); but present in many (possibly female?) Christmas Frigatebirds. **Immature.** Sequence of plumage changes not known properly and, because of this, field identification uncertain. Gradual attainment of adult characters (either to male or female) allows separation on those characters.

General behaviour of all frigatebirds similar. Solitary or gregarious in loose congregations at sea; exclusively tropical blue-water seabird, observed close inshore and well out to sea. Usually seen flying high at sea, gliding and soaring gracefully; very manoeuvrable, especially when chasing other seabirds while trying to pirate food. Feed in flight, catch prey from ocean surface and from beaches; often noticed chasing other seabirds, forcing them to disgorge their food and catching it before it hits water. Fly and soar gracefully with long glides and deep loose wing-beats. Readily attracted to ships and boats. Rarely on ground, except accidentally, or when nests built on ground. Perch and display from bushes and trees; do

not normally perch in daytime. Breed colonially on oceanic islands, sand or coral cays and atolls. Usually silent at sea; produce various mechanical sounds and utter high-pitched whistles, shrieks and squeals at breeding colonies.

HABITAT Marine, pelagic, aerial. In tropical waters of sea surface temperature, $>22^{\circ}\text{C}$, and varying salinities (Pocklington 1979; Ainley & Boekelheide 1983). May feed over upwellings of cold nutrient-rich water round islands (Bourne 1963). Cross wide expanses of open ocean; in central Pacific, often seen >300 km from nearest land (Sibley & Clapp 1967), but also close to continental coast; at Iron Ra., Qld, in inshore waters and occasionally flying over land up to 16 km from sea (Johnson & Hooper 1973).

Breed on isolated oceanic islands, sand cays and atolls, either sparsely vegetated or with low cover of herbs, grasses or shrubs; nest on slopes, central flats, low ridges (Gibson-Hill 1948; King & Buckley 1985; King 1986; Walker & Jones 1986a). Some cays used for nesting so low-lying that they are submerged by highest tides and storm-waves (Walker & Jones 1986a); erosion and accretion of sand by these means may change size and shape of cay and structure of vegetation (Limpus & Lyon 1981).

Perch on bushes and trees; stranded trees on beaches (Warham 1960; Stoddart *et al.* 1981; Stokes *et al.* 1984). Often fly high, soaring in thermals. Do not walk or swim.

Frequent disturbance by visitors causes desertion of nesting cays (Walker & Jones 1986b). Spoil, left after guano digging, used as nesting sites on Raine I. (King 1986). Occasionally perch on artificial structures (*e.g.* parapet of beacon, Raine I.; Stoddart *et al.* 1981).

DISTRIBUTION AND POPULATION Throughout tropical waters of Indian, w. and central Pacific Oceans with isolated population in Atlantic Ocean off Brazil.

AUST. Usually seen N of 21°S in WA, through tropical WA, NT and Qld and down e. coast to Byron Bay, NSW (Aust. Atlas), though claimed to be recorded S to Pt Cloates in WA (HASB); regularly sighted (1-7 birds) off Pt Lookout, N.

Stradbroke I. (Qld Bird Reps 1983, 1984). Vagrants reported well S of normal range, often after high winds, reaching Vic. at Mornington in 1902 (MV), Carrum, 14 Apr. 1929 (Kershaw 1929) and inland at Whitfield, 20 June 1952 (Hitchcock 1952).

NZ. Vagrant. First record, specimen taken at Kaipara Harbour, 1907; to 1955, another seven specimens including Chatham Is (Oliver) and single specimens at Day's Bay Beach, 31 Mar. 1937 (CSN 4) and Umutoi, near Apiti, Nov. 1951 (CSN 5); also several sight records during that time (Oliver). **Other records:** single sighted, S. Kaipara Head, Mar. 1959 (CSN 8); Doubtless Bay, NI, Jan. 1971; C. Maria van Diemen, NI, Jan. 1971 (NZ Atlas); two, sighted, Hauraki Gulf, 7 Jan. 1973 (CSN 20); near Papatowhi, SI, Nov. 1979 (NZ Atlas); singles sighted, Waikanae, 5 Jan. 1983 and Whangaroa, 3 Mar. 1983 (CSN 31); single sighted Farewell Spit, Nov. 1983 (CSN 32); single, Moturoa I., 8 Feb. 1987 (CSN 35).

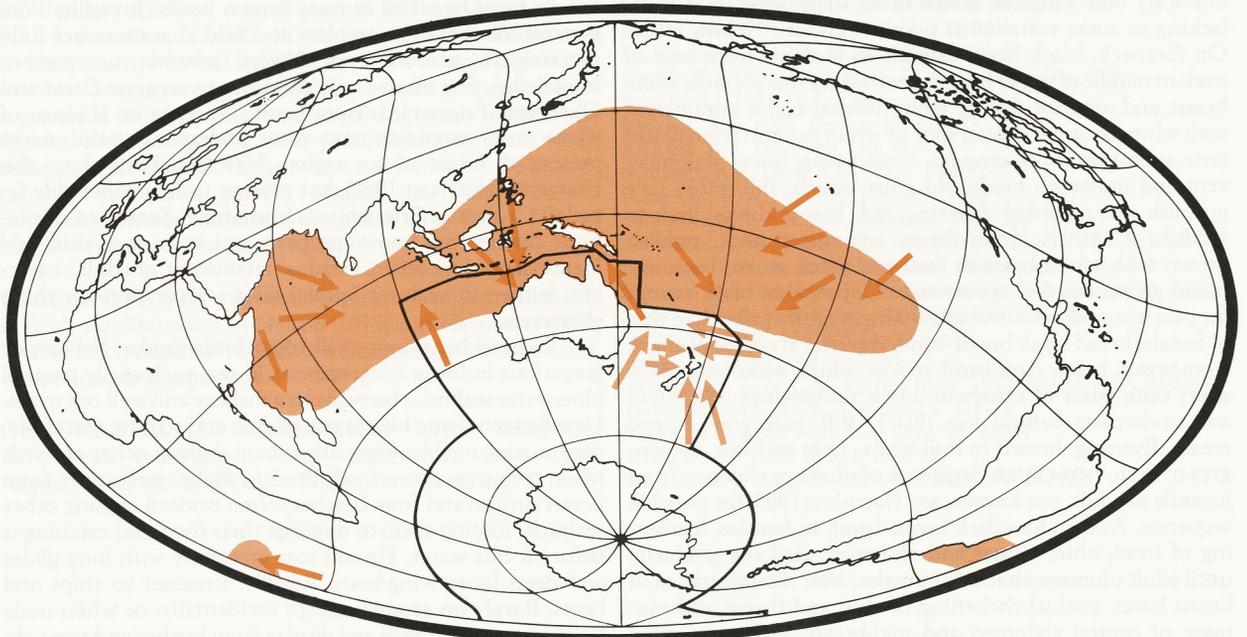
LORD HOWE I. Vagrant. Hindwood (1940) reports specimen taken by Bell, 11 Feb. 1915.

NORFOLK I. Vagrant: single female, 20 Nov. 1979 (Moore 1981); female observed regularly 1-8 Jan. 1985 (Hermes *et al.* 1986).

BREEDING Listed in Table 1. Other breeding locations listed in HASB without size of colonies: **WA:** Ashmore Reef (East, Middle Is); King Sound (Sunday, Swan Is); **Qld:** Magdelaine Is (SE Cay); Wreck Reef (Bird Islet); Cato I. Possibly breeding on or attempting to colonize Christmas I. (Ind.) (Stokes *et al.* 1987). Populations appear to fluctuate but few data (Burbidge *et al.* 1987) and colonies affected by cyclones *e.g.* breeding Rocky I. in 1965 but not since cyclone passed over island in 1974.

Status, probably stable but disturbance and continued use of birds and eggs as food by various Pacific islanders, combined with low reproductive rate suggest birds are in potential danger (de Korte 1984; Garnett 1984).

MOVEMENTS Little known. Immatures from Christmas I. (Pac.) disperse thousands of kilometres, possibly following direction of prevailing winds to W (Sibley & Clapp



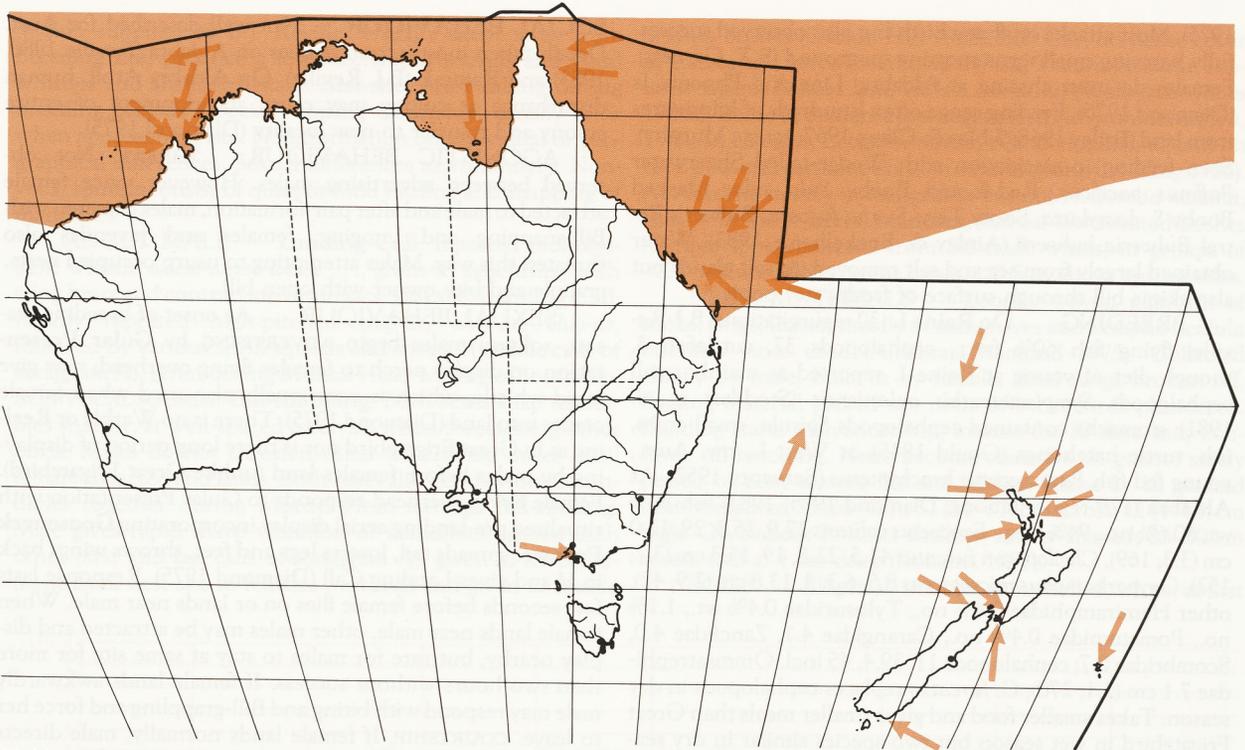


Table 1. Breeding localities of Least Frigatebird.

Locality	Year of Estimate	Estimate (pairs)	Ref.	
WA Adele I.	1982	5700	1	
	1978	>2045 nests	2	
	Bedout I.	1984	1113	1
		1982	2290	1
	West Lacepede I.	1978	300 nests	2
		1975	900	3
1972		2000	4	
QLD Rocky I., Gulf of Carpentaria		Not since 1974	5	
Manowar I.	1982	1049 nests	5	
Quoin I.		1000 birds	6	
	1981	156 nests	5	
	1982	0	5	
Raine I.	1975-85	c. 2000	5	
Swain Reefs				
Frigate Cay		No recent records	5	
Bell Cay	1976-86	max. 187	5	
Coringa Grp				
SW Islet	1986	3 nests	7	
Chilcott I.		928 birds	7	
Herald Grp				
NE Cay	1986	685 nests	7	
	1984	1337	7	
Lihou Reefs				
Anne	1984	194	7	
Nellie	1984	>188	7	
Diamond Is				
E		698	7	
SW		>481	7	
COCOS-KEELING IS	1982	3000 birds	8	

References: (1) Burbidge *et al.* (1987); (2) Abbott (1979); (3) Kolichis (1977); (4) Bush & Lodge (1977); (5) *Seabird Is Ser.*, *Corella* 9, 10, 11; (6) *Aust. Atlas*; (7) ANPWS; (8) Stokes *et al.* (1984).

1967). Not known whether movement migratory or if chicks return to natal areas to breed, though apparently attempting to colonize Christmas I. (Ind.); (Stokes *et al.* 1987). One adult from central Pacific recovered on Cocos-Keeling Is (Stokes & Dunn 1989). Periodicity of breeding not established but few observed at Aldabra Apr.-Sept. (Diamond 1975) and apparently absent Christmas I. (Pac.) Dec.-before Apr. (Schreiber & Ashmole 1970). Colony at Manowar I., Gulf of Carpentaria, surveyed from the air was occupied throughout year (S.T. Garnett). Appear to concentrate near land most frequently during stormy weather (Kikkawa 1975).

BANDING

00S176W 10 P U 7 5476 139 BBL
 00S176W 10 P U 249 3153 113 BBL
 03S170W 11 P U 4 1744 204 BBL
 03S170W 11 P U 5 approx. 1200 126 BBL
 03S170W 11 P U 5 1212 163 BBL
 03S171W 02 P U 1797 205 BBL
 03S171W 11 P U 136 10165 261 (Stokes & Dunn 1989)
 03S174W 10 P U 7 approx.1200 126 BBL
 03S174W 10 P U 7 2996 105 BBL
 03S174W 10 P U 255 1526 120 BBL
 16S149E 06 P U 14 2412 308 ABBBS

Extralimitally, numerous recoveries from w. Pacific islands of birds banded central Pacific (Sibley & Clapp 1967) and one from Aldabra recovered Bombay (Diamond 1975).

FOOD Mostly fish with some cephalopods. **BEHAVIOUR.**

All food taken while bird in flight. Flying fish taken by flight-feeding just above surface, small fish and cephalopods by dipping. Fish manipulated in bill during flight and swallowed head first. Aerial piracy (kleptoparasitism) practised on many species, particularly terns and boobies, though successful piracy thought to contribute little to total intake. On Aldabra 18% of attacks on Red-footed Boobies successful (Diamond

1975). Most attacks on flying birds but also observed successfully harrying small terns roosting on ground (S.T. Garnett). Females do most chasing at Aldabra, Line and Phoenix Is (Diamond 1975). Feeding range often hundreds of kilometres from land (Bailey 1968; Sibley & Clapp 1967; *contra* Murphy). Seen feeding in association with Wedge-tailed Shearwater *Puffinus pacificus*, Red-footed Booby *Sula sula*, Masked Booby *S. dactylatra*, Sooty Tern *Sterna fuscata*, Bulwer's Petrel *Bulweria bulwerii* (Ainley & Boekelheide 1983). Water obtained largely from sea and salt removed via salt glands but also skims bill through surface of freshwater pools.

BREEDING On **Raine I.** (30 regurgitations; B.J. Reville) flying fish 60% freq., cephalopods 37, cuttlefish 3, though diet of young at Raine I. reported as mainly small cephalopods *Symplectoteuthis oulaniensis* (Stoddart *et al.* 1981); stomachs contained cephalopods *Spirula*, small crabs, fish, turtle hatchlings (Gould 1845); at West I., nw. Aust., young fed fish *Parexocoetus brachypterus* (Serventy 1952). At **Aldabra** (179 regurgitations; Diamond 1975, 1983) fish 89% wt, 60.6% no., 94% freq.: *Exocoetus volitans* 27.9, 25.3, 29, 12.0 cm (3.3; 169), *Cheilopogon furcatus* 41.5, 22.8, 19, 15.3 cm (3.7; 152), *Oxyporhamphus micropterus* 8.5, 6.3, 3, 13.8 cm (2.9; 42), other Hemiramphidae 0.4% no., Tylosuridae 0.4% wt., 1.1% no., Pomatomidae 0.4% no., Carangidae 4.1, Zanclidae 4.0, Scombridae 0.7; cephalopods 11, 39.4, 45 incl. Ommastrephidae 7.1 cm (2.1; 270); *C. furcatus* replaces cephalopods in dry season. Takes smaller food and gives smaller meals than Great Frigatebird in wet season but two species similar in dry season.

SOCIAL ORGANIZATION Not well known for Aust. Details taken mostly from studies on Aldabra Atoll (Reville 1980, 1983) and Raine I. (B.J. Reville). Gregarious when nesting and roosting; often solitary when hunting at sea but may congregate at sources of food.

BONDS Monogamous. Probably acquire new mate each breeding season but frequency of re-mating not determined with individually marked birds; site fidelity unlikely; breed only once in two years. No known difference in sex-ratio among adults or fledgelings. Age of first breeding unknown but probably 4–5 years. Onset of display can differ between islands and between different parts of colony (Nelson 1975). After courtship parents see each other only at nest-relief and rarely when feeding older nestlings or fledgelings. Both parents incubate, and tend young until 5–8 months after fledging.

BREEDING DISPERSION Colonial; on isolated oceanic islands, sand cays and atolls in low vegetation or on ground; up to 5000 nests in colony, divided into sub-groups of up to 100 nests. Average distance between nests 0.5–0.7 m. Display-site not defended by male before acquiring female. After pair-formation, one member of pair always occupies site. Very unlikely that either member of pair occupies same site in consecutive breeding seasons. Interchange of adults between colonies occurs but no quantitative estimate available.

ROOSTING As for Great Frigatebird. Tendency for roosting groups mostly of females to form between nesting sub-groups late in breeding season. In daytime, do not normally perch and never settle on water, except accidentally. Perch on bushes and trees; stranded trees on beaches; artificial structures (Warham 1960; Stoddart *et al.* 1981; Stokes *et al.* 1984; HASB). During storms birds may rest in sheltered mangroves spreading wings out over leaves (HASB).

SOCIAL BEHAVIOUR Not well described for Aust. Details taken mostly from studies on Aldabra (Reville 1980, 1983) and Raine I. (B.J. Reville). On Aldabra Atoll, human disturbance at colony may cause abandonment of entire colony and transfer to new locality (Diamond 1975).

AGONISTIC BEHAVIOUR **THREAT.** Not observed between advertising males. However, once female attracted to male and after pair-formation, males threaten with Bill-snapping and Lunging; females and juveniles also threaten this way. Males attempting to usurp occupied nests, grapple and bite owner with open bill.

SEXUAL BEHAVIOUR At onset of breeding season, solitary males begin **ADVERTISING** by **Gular Presentation** on display perch to females flying overhead; may give rapid whistle, which is occasionally also used when female comes into land (Diamond 1975). There is no Warble or Reeling as in Great Frigatebird nor is there long period of displaying by males before females land (unlike Great Frigatebird). Female flying overhead responds to Gular Presentation with ritualized pre-landing aerial display incorporating **Gooseneck Posture**: spreads tail, lowers legs and feet, throws wings back in V and gives Landing Call (Diamond 1975). Response lasts few seconds before female flies on or lands near male. When female lands near male, other males may be attracted and display nearby, but rare for males to stay at same site for more than two hours without success. If female lands awkwardly male may respond with biting and Bill-grappling and force her to leave. **COURTSHIP.** If female lands normally, male directs Wing-trembling and Bill-rattling at female, who then moves beside male, head to head. Pair begin **Mutual Head-waving** as for Great Frigatebird; however male continues to direct Bill-rattling to female with decreasing frequency until lost by third day of courtship; occasionally during Mutual Head-waving, female gives call similar to Landing Call. During bouts of Mutual Head-waving, female often shuffles half-raised wings as male trembles wings, rattles bill, bows and whispers with gently vibrating mandibles. Pair may caress each other's body with head and bill; while doing so, female may whistle softly, but no functional preening Warble or Reeling. On Raine I., courtship begins Apr.–Mar. and is over by July (King 1986). **COPULATION** and nest-relief as for Great Frigatebird. Solitary, unpaired female may perform homologue of male Gular Presentation involving slight distension of gular area, abbreviated Wing-trembling and Bill-rattling; male may be attracted but no known cases of pair being formed.

RELATIONS WITHIN FAMILY GROUP As for Great Frigatebird. Nest material collected chiefly by male, built in by female; building starts with courtship, intense for 10 days and may continue till hatching. Parents share incubation and feeding of young equally until independence. When begging for food, chick lies prostrate before adult with outstretched wings drooped and tail cocked high while wagging head up and down behind lowered shoulders and calling with harsh, grating scream (HASB). Young recognize adults by voice or appearance when flying. When alarmed, young utter clapping sound; young defend perch by pecking, gaping and calling at rival. Chick brooded and guarded for 4 weeks after hatching; dependent on parents for 141–349 days after fledging. Chicks sunbathe by reversing outstretched wings so sun shines on undersides (HASB). Free-flying dependent juveniles spend at least quarter to half of each day at colony (Nelson 1975).

VOICE Poorly known and no detailed studies; infor-

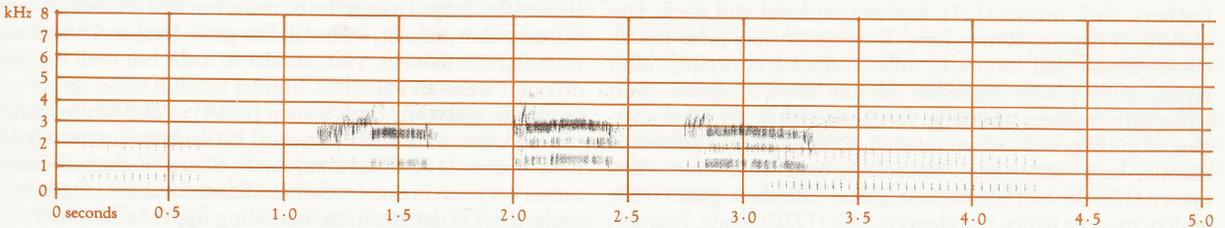
mation supplied by B.J. Reville. Usually silent away from breeding site; produce a few mechanical sounds and vocal whistles and shrill shrieks at nest-site. Most calling during breeding periods especially during Courtship, usually at or when approaching site. No information on individual or geographical differences. Sexual differences in vocabulary. Non-vocal sounds consist of quiet or loud rattling and snapping of mandibles.

ADULT MALE Landing Call: repeated monosyllabic whistle *weese-weese-weese* . . ., given in synchrony with wing beats and contraction of air-sacs. **FEMALE Landing Call:** rapidly repeated high-pitched *chip-ar, chip-ar, chip-ar*, followed by various shrill squeals and shrieks (middle calls of sonagram A), given during Mutual Head-waving of courtship. **NON-VOCAL SOUNDS. Bill-snapping.** Both sexes snap mandibles sharply, at well-spaced intervals when threatening other birds. Males do not threaten other advertising males until female attracted and lands. Both sexes also gently vibrate mandibles together during Mutual Head-waving. **Bill-rattling.** Male gives rapid sharp vibration of mandibles against each other (first and last calls of sonagram A); given as advertisement from nest-site to females overhead and given to female

acidula bushes (Gibson-Hill 1948); Bell Cay, on dense cover of grasses and herbs (*Boerhavia diffusa*, *Theura involuta*, *Lepturus repens*, *Salsola kali*, *Cakile edentula*) (Walker & Jones 1986a); Raine I., on dense low vegetation (*Achyranthes aspera*, *Tribulus cistoides*, *Lepturus repens*, *Abutilon indicum*), and on rock piles and earth mounds on central guano flat (King 1986). At Aldabra, mostly in mangroves but not *Avicennia marina*; usually in lower lateral branches; not on low stunted bushes (*Ceripos* spp); sheltered from SE trade winds; in groups of <20 within colony; some nests <0.5 m above spring tides.

NEST, MATERIALS Loosely woven platform of sticks, twigs, leaves; mostly of mangroves and *Pemphis acidula* but also vines used (Aldabra; Diamond 1975). Collected chiefly by male, built in by female, dead twigs broken off, floating material picked up, nests of other birds plundered. Building starts with courtship, intense for 10 days, may continue till hatching. Nests become coated with guano; rarely persist to next season. No site fidelity. Raine I.: 12 ground nests measured 35 (26–45) x 31 (21–37) cm across, 11 (4–18) cm high. On Bedout I.: nests shallow, saucer-shaped, 25–30 cm across and c. 4 cm deep (Kolichis 1977).

EGGS Elliptical; smooth, thin shelled, white; at first



A B.J. Reville; Aldabra I., Indian Ocean, July 1977; C130

after she lands near displaying male; male stops Bill-rattling to female at nest after second day of courtship. Much more rapid snapping of mandibles than Bill-snapping during threatening and easily distinguished. Sometimes, solitary unpaired females may produce abbreviated Bill-rattling.

YOUNG Beg with harsh grating scream; begging seems less rhythmic than begging of Great Frigatebird. Juveniles Bill-snap when threatening other birds.

BREEDING No detailed Aust. studies. Quantitative studies at Aldabra (Diamond 1975; Reville 1980, 1983). Breed in simple pairs, colonially. Most s. breeding station, Bedout I., WA.

SEASON Protracted, varying in different localities. Raine I., Coral Sea, said to breed mid-year; courtship begins as early as Apr. (sometimes Mar.), finished by July with eggs and downy young in nests; well-feathered chicks and flying young, Nov.–Dec. (King 1986); also at Raine I., eggs recorded Feb.–Aug., peak laying in May (B.J. Reville); at Bell Cay, breeding said to occur all year with lowest numbers Nov.–Feb. and highest, Apr. and July (Walker & Jones 1986a); at Quoin I., off C. York Pen., Qld, courtship and nesting, Mar.–Apr.; by mid-year, downy young and some eggs; by Dec., large numbers of juveniles (King & Buckley 1985); at Manowar I., Gulf of Carpentaria, in July, eggs, downy young and juveniles all seen (Garnett & Crowley 1987). Christmas I. (Pac.), main laying probably Apr.–May (Schreiber & Ashmole 1970); Aldabra, display starts early June, laying Aug.–Nov. (Diamond 1975).

SITE On trees, bushes, low shrubs, mats of vegetation or ground. On N. Keeling I., on dense belt of *Pemphis*

with thin limy coating.

MEASUREMENTS:

Bedout I. 63 (56–72; 10) x 45 (41–48) (Bush & Lodge 1977) 64.5 (4.85; 58.5–71.2; 6) x 42.9 (1.97; 39.6–45.4) (Kolichis 1977).

Raine I. 64 (60–70; 18) x 44 (41–47) (HASB)

Aldabra 60.8 (2.5; 8) x 42.1 (0.9) (Diamond 1975)

WEIGHTS:

Aldabra

59 (n=1) or 6.9% of female weight (Diamond 1975).

CLUTCH-SIZE One. Replacement laying probable, not quantified. Successful pairs breed only once in 2 years.

LAYING Not synchronized, except perhaps in sub-colonies. Time of day not known.

INCUBATION By both sexes equally and alternately. At Raine I., 32 shifts averaged 2.7 days (8–139 h); at Aldabra, 4 shifts averaged 3 days (1–6); also at Aldabra, shifts 5.5 days (B.J. Reville). **INCUBATION PERIOD.** Said to be c. 41 days (HASB).

YOUNG Altricial, nidicolous. Brooded and guarded by both parents; lengths of shifts not recorded. Fed by both parents by incomplete regurgitation; on average once every 1.8 days; mostly in afternoon and equally often by both parents.

GROWTH Rate of growth $K = 0.039$ for Gompertz curve (Ricklefs 1967, 1968). Reaches half asymptotic weight in 60 days (Diamond 1975). Egg-tooth lost when 7 days old; 14 days old, white down extensive except on throat, neck; 21 days old, dorsal feathers, scapulars burst sheaths; 21–25 days

old, russet feathers on face; by 42 days old, secondary greater wing-coverts emerge; by 49 days old, primary greater upper wing-coverts emerge; by 56–60 days old, secondaries and rectrices emerge; 60–70 days old, primaries emerge. NESTLING PERIOD: Aldabra: 161 days (145–179; 14). Depend on parents for 203 days (141–179; 19 wing-tagged fledgelings) after fledging.

SUCCESS At Aldabra: 59 (20%) of 297 eggs hatched, 36 chicks fledged, for total success of 12%; success inversely correlated with density of nests; at least 29% of loss of chicks by usurpation of nests by unpaired males. Raine I., no evidence of conspecific interference, no quantified data. Increased sea surface-temperature, deepened thermocline, high sea-level and heavy rainfall led to high adult mortality and breeding failure on Christmas I. (Pac.) during El Niño Southern Oscillation (Schreiber & Schreiber 1984). **PREDATORS.** Menaced by feral cats *Felis catus* at Christmas I. (Pac.) to possible extinction (Schreiber & Ashmole 1970).

PLUMAGES *Nominate ariel.*

ADULT MALE Age of first breeding unknown. **HEAD AND NECK.** Crown and sides of head, glossy pale black-green (162) with glossy purple (172B) shade; concealed bases of feathers, dark brown (121); feathers on head and neck, lanceolate; at nape c. 40 mm long. Bare distensible gular pouch covers throat and foreneck, inflated during courtship; after laying, gular pouch regresses; narrow rows of sparse short lanceolate feathers similar to foreneck visible on outer margins of gular pouch, when inflated. **UPPERPARTS.** Feathers of mantle, back and rump, lanceolate; concealed bases, dark brown (121) for half length; rest, glossy pale black-green (162), which, in some lights, has glossy purple (172B) shade. Feathers at middle of mantle are c. 75 mm long, at lower margins of mantle, c. 100 mm long. Scapulars, moderately short, but lanceolate and black-brown (119); outer webs, glossed pale black-green (162) with glossy purple (172B) shade. Subscapulars similar, but with more rounded tips and faint purple (172B) gloss on outer webs. Upper tail-coverts similar, but with less gloss. When worn, tips of feathers on upperparts, dark brown (119A). **TAIL,** strongly forked and black-brown (119); outer margins of webs have slight pale black-green (162) gloss, with glossy purple (172B) shade; rachis, black (89). When worn, tips of rectrices, dark brown (119A). **UPPERWING.** All remiges, black-brown (119); rachis, black (89). Inner webs of remiges, dark brown (121); outer webs have faint gloss of pale black-green (162) with glossy purple (172B) shade. When worn, tips of remiges, dark brown (119A). Alula feathers, black-brown (119) with faint gloss of pale black-green (162), with glossy purple (172B) shade. All coverts similar to alula feathers, but more strongly glossed; coverts often have worn dark-brown (119A) to dull white fringes. **UNDERPARTS.** Breast-feathers, black-brown (119); tips of feathers slightly pointed and glossy pale black-green (162); some outer breast-feathers lanceolate, with glossy purple (172B) shade; concealed bases, dark brown (121). Abdominal feathers similar to breast-feathers, but concealed bases, light grey-brown (119D). Most flank-feathers, black-brown (119) with faint gloss of pale black-green (162) with glossy purple (172B) shade; outer flank-feathers, lanceolate and c. 60 mm long. On each flank, adjoining base of axillaries, single horizontal oval-shaped patch of white feathers; strongly contrasts with rest of underparts; demarcation moderately sharp, but some white feathers variously streaked and suffused dark-brown (119A) to pale dark-brown (121); some white feathers have pale dark-brown (121) bases. Under

tail-coverts and thighs, glossy pale black-green (162) with glossy purple (172B) shade; concealed bases, dark brown (121). Axillaries, black-brown (119) with pale black-green (162) gloss, suffused with gloss of purple (172B); axillaries have slightly pointed tips. **TAIL.** Rachis on underside of tail, white basally, merging to brown (219B) distally. **UNDERWING.** Greater primary and greater coverts, glossy dark-grey (83) with dark-brown (121) shade. All other coverts, black-brown (119) with gloss of pale black-green (162), with glossy purple (172B) shade.

ADULT FEMALE **HEAD AND NECK.** Feathers on crown and hindneck similar to adult male; at nape, lanceolate feathers c. 31 mm long. Feathers at side of neck, glossy pale black-green (162). Chin bare with rudimentary gular pouch. Throat to lower foreneck, dark brown (121), tipped black-brown (119); in some lights, tips glossy pale black-green (162); feathers lanceolate. **UPPERPARTS.** Feathers of upper mantle vary, but most often light brown (39) to dark brown (119A), tipped dull white through wear. Lower mantle feathers, back, rump and upper tail-coverts, black-brown (119) with gloss of pale black-green (162) with glossy purple (172B) shade; concealed bases, dark brown (121); gloss less evident on rump and upper tail-coverts. Mantle-feathers, slightly pointed, but not lanceolate. Scapulars similar to male, but less glossed on webs. Subscapulars, similar, with still less gloss; long and broad with rounded tips to webs. **TAIL,** similar to male, but with less gloss on outer webs. **UPPERWING.** Similar to adult male; tips of coverts often worn and dark brown (119A) to dull white; greater coverts often have black-brown (119) centres, surrounded by dark brown (119A). **UNDERPARTS.** Sharp V-shaped demarcation between breast-feathers and dark foreneck; feathers on underparts at demarcation, including upper breast, buff (124) to orange-buff (118). Feathers of lower breast, including thighs, to abdomen, black-brown (119); black-brown (119) feathers have faint gloss of pale black-green (162) with purple (172B) shade on webs. Most of rest of underparts, white, extending to base of axillaries. Demarcation between white and dark underparts vary; feathers, white, tipped black-brown (119); feathers at middle of outer flanks, dark brown (121), tipped white; towards lower flanks, white tips become broader. Axillaries, black-brown (119) with pale black-green (162) gloss with glossy purple (172B) shade. **UNDERWING,** similar to adult male.

DOWNY YOUNG Naked at hatching. Down, woolly; long and thin on crown, white; short and light-brown (39) round eye, on malar region, ear-coverts and forehead; throat and chin, bare. Rest of body covered in thick white down. At c. 21 days old, feathers on outer mantle and scapulars; feathers, short and black-brown (119) with faint gloss of pale black-green (162) on webs; feathers have rounded tips; when worn, tips dark-brown (119A).

JUVENILE **HEAD AND NECK.** Feathers on crown to hindneck, and side of head, rufous-brown (340); feathers, long and slightly lanceolate at nape; rachis, brown (119B). Feathers paler at lores and forehead; sometimes also at nape (Gibson-Hill 1950). **UPPERPARTS.** Most feathers, black-brown (119) with worn dark-brown (119A) to brown (119B) tips; feathers on mantle have rounded tips to webs. Scapulars, black-brown (119), tipped dark brown (119A); faint gloss of pale black-green (162) on webs. Subscapulars, black-brown (119). **TAIL,** black-brown (119); slight to no pale black-green (162) gloss on outer webs, and tipped brown (119B). **UPPERWING.** Remiges, black-brown (119); outer margins of webs of tertials and humerals, brown (119B). Marginal and median primary coverts,

black-brown (119), fringed dark brown (119A). All greater, rest of median, and lesser coverts, dark brown (119A), fringed dull white through wear; marginal coverts near carpal joint, similar. Marginal coverts and lesser coverts near humeral joint, black-brown (119) with faint pale black-green (162) gloss on webs. Dull white fringes on coverts occur in diagonal bar from elbow to carpal joint. **UNDERPARTS.** Upper breast-feathers, tipped pale rufous-brown (340); concealed for three-quarters of length, light grey-brown (119C); rachis, dark brown (119A). Across lower breast, varyingly distinct black-brown (119) band of feathers with concealed light grey-brown (119C) bases; distal tip, black-brown (119) for quarter to half length. Lower flanks, inner thighs and under tail-coverts, similar. Abdomen and extending to base of axillaries, white, forming large heart-shaped patch. Demarcation between white patch and rest of underparts moderately sharp; feathers at demarcation varyingly streaked as in adult female. Outer thighs, black-brown (119) narrowly tipped white. Axillaries, black-brown (119) with faint pale black-green (162) gloss on webs. **UNDERWING.** Greater coverts and greater primary coverts, glossy grey (84) with dark-brown (119A) shade. Rest of coverts, black-brown (119) with very faint pale black-green (162) gloss on webs, or gloss absent. Nelson (1975) states as general remark that juvenile plumage in frigatebirds may be retained for at least 30 months; further study needed for this species.

BARE PARTS Based on photos in Lindsey (1986), except where stated. Bare parts of adults during breeding, brighter; for full details of bare parts of all age classes at Cocos-Keeling Is, see Gibson-Hill (1950).

ADULT MALE Iris, dark brown (219). Eye-ring, black-brown (119). Bill, dark grey (83) merging to grey-black (82) at tip; grey, greyish blue and reddish also recorded (Hindwood *et al.* 1963). Gular pouch, red (12). Legs and feet, black or reddish brown (HASB).

ADULT FEMALE Iris, dark brown (219). Eye-ring, red (10). Bill, pink (7); pale purplish grey also recorded (HASB). Legs and feet, flesh coloured to reddish (HASB).

DOWNY YOUNG Iris, black-brown (119). Bill, pale grey (86) to dull white; bare skin on throat and gular pouch similar. Legs and feet, light grey-brown (119D). Naked skin of chicks, pale blue-grey, almost white (Gibson-Hill 1950).

JUVENILE Iris, black-brown (119). Eye-ring, brown (119B) to dull white. Bill, pale grey (86), tipped cream (54); light pinkish mauve recorded in males (Gibson-Hill 1950). Legs and feet, brown-grey (80); very pale mauve recorded in males (Gibson-Hill 1950).

MOULTS Based on skins (MV, AM), except where stated.

ADULT Primaries moult outwards in staffelmauser. Duration and onset of moult-series unknown. Moult may be delayed until at least towards end of fledging period, as inferred at Aldabra (Nelson 1967; Diamond 1975).

POST-JUVENILE No data. Further study of moult required.

MEASUREMENTS (1) Cocos-Keeling Is, adults, live; BILL G = from gape, other methods unknown (Gibson-Hill 1950). (2) Bramble Cay, Qld, adult females, live; methods unknown (ABBBS). (3) Cocos-Keeling Is, immatures, live;

BILL G = from gape, other methods unknown (Gibson-Hill 1950).

	MALES	FEMALES
WING	(1) 533.5 (13.73; 518-550; 4) (2) 560.0 (6.04; 551-566; 4) (3) 536.0 (8.79; 529-555; 6)	547.0 (9.35; 534-562; 5) 546.3 (30.14; 491-581; 6) 318.4 (3.38; 314-324; 5)
TAIL	(1) 316.5 (9.81; 307-331; 4) (2) 356.2 (6.41; 347-364; 4) (3) 291.3 (22.90; 244-314; 6)	315.6 (19.51; 278-342; 6) 89.4 (2.57; 86-93; 5) *
BILL	(1) 82.2 (2.77; 79-85; 4) (2) 90.1 (1.61; 87.5-91.9; 4) (3) 82.8 (1.57; 80-85; 6)	88.4 (1.36; 87-90.5; 6) *
BILL(G)	(1) 99.7 (2.61; 96.5-103; 4) (3) 100.7 (1.28; 99-102; 6)	109.4 (2.24; 106-113; 5) *
THL	(2) 99.7 (1.61; 97-101; 4)	107.4 (1.78; 105-109.5; 6) *
TARSUS	(1) 22.7 (0.75; 22-23.5; 4) (2) 17.9 (0.66; 17.3-18.8; 4) (3) 22.9 (0.83; 22-24.5; 6)	24.9 (0.48; 24-25.5; 5) *
		24.1 (0.37; 24-25; 6) *

Additional measurements in Gibson-Hill (1950), Hindwood *et al.* (1963), Nelson (1976) and HASB.

WEIGHTS Few data. Adult females at Bramble Cay, Qld, Mar.: 942.2 (116.66; 780-1107; 4) (ABBBS). Label data from adult skins (MV, AM, QM): female, Groote Eylandt, NT, July: 970 g; female, N. Stradbroke I., Qld, Mar.: 1246 g; male, Qld, no date: 499 g; male, Vic., straggler, June: 555 g. No data on seasonal changes. Further study required. For details of changes at Aldabra, see Diamond (1971, 1975).

STRUCTURE Wing, long, narrow and pointed. Eleven primaries: p10 longest; outer web, narrow, p9 28-34, p8 66-88, p7 110-119, p6 154-165, p5 196-208, p4 231-244, p3 254-277, p2 292-305, p1 311-372, p11 minute. No emarginations. Eight short humerals. Twenty-two secondaries, including five of tertial form. Underside of webs of remiges and tail, glossy. Tail, forked; 12 rectrices, t6 longest, t1 165-203 mm shorter. Bill, slender; maxillary unguis hooked. Bill smooth in adults, flaky in juveniles. Nostrils slit-like, in groove of culminicorn and latericorn, near base of bill. Gular pouch in male highly distensible during courtship and at breeding; gular pouch regresses after laying; narrow rows of sparse feathers visible on outer margins of gular pouch when inflated; when inflated, heart-shaped. Tarsus, short and feathered. Toes totipalmate. All claws curved. Middle claw, long, curved outwards; serrated on inner margins. Outer toe c. 84% of middle, inner c. 58%, hind c. 34%.

RECOGNITION Juvenile frigatebirds virtually impossible to distinguish in field; see discussion given in Nelson (1975) and Harrison (1987).

GEOGRAPHICAL VARIATION Three doubtful subspecies: *ariel*, *iredalei* and *trinitatis*; based on measurements of bill and wing. On Aldabra I., females show dimorphism in colour of bill and eye-ring (Diamond 1971). Similar dimorphism occurs in females of other Indian Ocean populations; no details given (Nelson 1975); not known whether such dimorphism occurs in A'asia (R. O'Brien).

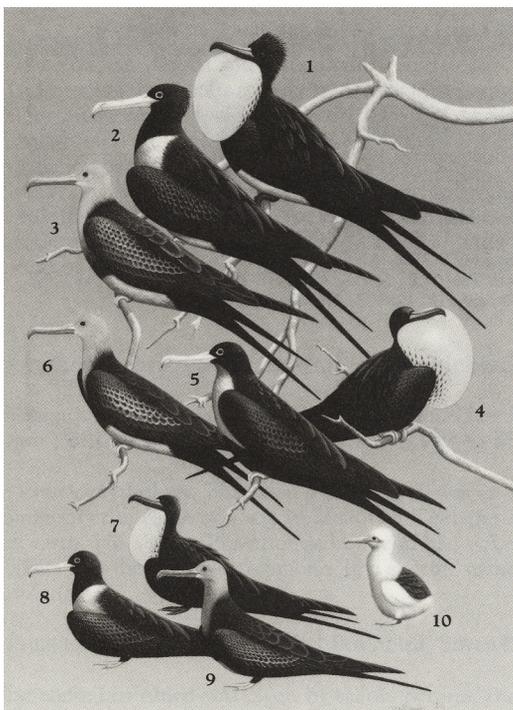
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Volume 1 (Part B), Plate 66

Christmas Frigatebird *Fregata andrewsi*

1. Adult male
2. Adult female
3. Juvenile

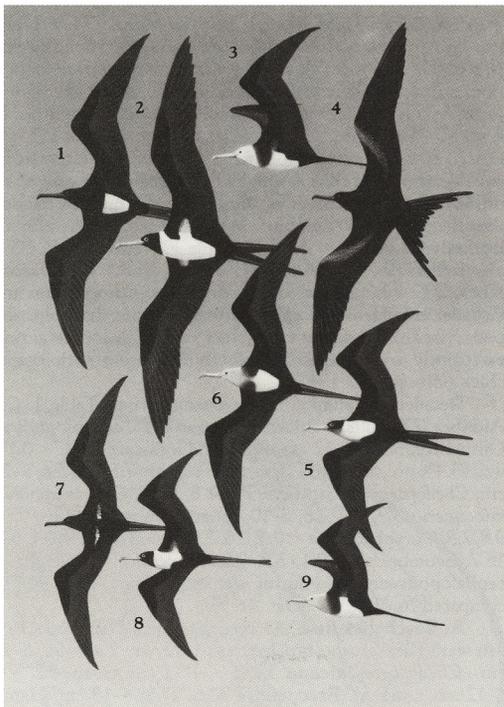
Great Frigatebird *Fregata minor*

4. Adult male
5. Adult female
6. Juvenile

Least Frigatebird *Fregata ariel*

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

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Volume 1 (Part B), Plate 67

Christmas Frigatebird *Fregata andrewsi*

- 1. Adult male
- 2. Adult female
- 3. Juvenile

Great Frigatebird *Fregata minor*

- 4. Adult male
- 5. Adult female
- 6. Juvenile

Least Frigatebird *Fregata ariel*

- 7. Adult male
- 8. Adult female
- 9. Juvenile

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