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648 Charadriiformes

Order CHARADRIIFORMES

A large, diverse assemblage of small to medium-large (12–75 cm long) limicoline, pratincoline, aquatic or terrestrial birds. Cosmopolitan from Arctic to Antarctic regions; in all sorts of maritime, freshwater and open terrestrial habitats (including deserts) with a few (woodcocks and snipes) even using dense forests. Once known as Limicolae or Laro-limicolae (e.g. Mayr & Amadon 1951); colloquially, the assemblage (excluding alcids, skuas, gulls, terns and skimmers) is often referred to as waders (especially in Britain) or shorebirds (especially in North America).

About 350 species in 19 families, though taxonomic treatments vary. Following families recognized (mostly based on

recent reviews of Order [Sibley et al. 1988; Sibley & Ahlquist 1990; Sibley & Monroe 1990]):

Thinocoridae seedsnipes; four species, S. America. Pedionomidae Plains-wanderer; monotypic, Aust.

Scolopacidae sandpipers, snipes and allies; c. 85 species, cosmopolitan. Rostratulidae painted snipes; two species, s. America and Old World.

Jacanidae jacanas; seven species, pantropical.

Chionididae sheathbills; two species, Antarctica and subantarctic islands.

Burhinidae thick-knees, stone-curlews; nine species, widespread in Old World and two in Neotropics.

Haematopodidae oystercatchers; c. 11 species, worldwide in tropics and temperate regions.

Recurvirostridae avocets and stilts; about seven species, worldwide in tropical and temperate regions.

Ibidiorhynchidae Ibisbill; monotypic, central Asia.

Charadriidae plovers and lapwings; c. 60 species, cosmopolitan.

Pluvianellidae Magellanic Plover; monotypic, S. America.

Crab Plover; monotypic, Arabian region.

Glareolidae pratincoles, coursers, and Egyptian Plover; c. 15 species, widespread in Old World. Stercorariidae skuas and jaegers; about seven species, mostly in Arctic and Antarctic regions.

Rhynchopidae skimmers; three species, pantropical. Laridae gulls; c. 47 species, cosmopolitan. Sternidae terns; c. 42 species, cosmopolitan.

Alcidae auks; c. 20 species, Arctic and temperate regions of n. hemisphere.

Apparently monophyletic. Pteroclididae (sandgrouse) probably sister-group of Charadriiformes (e.g. Fjeldså 1976, 1977; Sibley & Ahlquist 1990; BWP), though whether best placed within Charadriiformes or in separate order is debated. Flamingoes (Phoenicopteridae) and divers (Gaviidae) have also been treated as Charadriiformes (Olson & Feduccia 1981; Fjeldså 1976, 1977) but DNA–DNA hybridization studies (Sibley & Ahlquist 1990) inconsistent with these theories. Affinities to other orders still controversial; DNA–DNA hybridization has suggested closest links are to large waterbirds, such as storks, herons and allies, Pelicaniformes, Procellariformes, penguins, grebes, divers (Gaviidae) and also Falconiformes.

All these were combined in huge order Ciconiiformes by Sibley & Ahlquist (1990).

Taxonomy and relationships reviewed in Sibley & Ahlquist (1990), Christian et al. (1992) and BWP (and references therein). Recent reviews have included: patterning of downy young (Jehl 1968; Fjeldså 1976, 1977), osteology (Strauch 1978; Mickevitch & Parenti 1980; Olson & Steadman 1981), DNA—DNA hybridization (Sibley et al. 1988, Sibley & Ahlquist 1990) and electrophoresis of tissue proteins (Christian et al. 1992). The studies of allozymes, DNA—DNA hybridization and the most recent osteological study of the entire order (Strauch 1978) have agreed in finding two or three well-knit, monophyletic assemblages within the Charadriiformes: scolopacids and allies (Thinocoridae, Pedionomidae, Scolopacidae, Rostratulidae, Jacanidae) and charadrids and allies (Chionididae, Burhinidae, Haematopodidae, Recurvirostridae, Ibidorhyncidae, Charadriidae, Pluvianellidae, Dromadidae, Glareolidae, Stercorcariidae, Rhynchopidae, Laridae, Sternidae, Alcidae); Strauch (1978) treated Alcidae as separate lineage, but skeletons may be so highly modified for foot-propelled diving that they do not reflect relations well (Sibley & Ahlquist 1990); gulls and allies have also been regarded as a separate lineage (Christian et al. 1992) or as allied to charadrids (e.g. Sibley & Ahlquist 1990). Further relationships within the Order discussed in introductions to families.

Because the Order comprises so many species and adaptations are so diverse, few characters shared by all species; those that are shared are mostly anatomical features of the skull, e.g. most or all have schizorhinal nostrils, schizognathous palates, well-developed vomer, lachrymals fused with ectethemoid and pre-frontal bones, well-developed supra-orbital grooves; see Olson & Steadman (1981) for more information on osteological characters. Wings usually have 11 primaries, with p10 longest and p11 minute; 15–24 secondaries; diastataxic except in *Scolopax minor*, as far as is known. Usually 12 tail-feathers. Necks usually rather long with 15–16 cervical vertebrae. Oil-gland bilobed and tufted. Syrinx, tracheo-bronchial; two carotids (type A-1 of Glenny 1955); caeca present. Legs usually rather long; hind toe small or lacking in most but all toes greatly elongated in Jacanidae. Feathers with small thin afterfeathers. Normally two moults annually: complete post-

breeding and partial pre-breeding; some jacanas and alcids have flightless periods when moulting remiges. Young, downy, usually with intricate cryptic patterns on upperparts of three chief types: pebbly, spotted and striped, matching characters of habitat (Fieldså 1976, 1977): precocial, nidifugous usually, self-feeding or not depending greatly on parents.

Thirteen families recorded in HANZAB region, with 54 species breeding, 41 occurring as regular non-breeding migrants and c. 38 as accidentals or probable accidentals. Scolopacidae, Stercorcariidae, Laridae and Sternidae will be dealt with in Volume 3 of HANZAB.

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Family LARIDAE skuas, jaegers, gulls and terns

A large assemblage of small to very large charadriiform seabirds. We recognize four subfamilies within the Laridae following Mayr & Amadon (1951), AOU (1983).¹

Stercorariinae Skuas and jaegers; about six species; cosmopolitan.

Larinae Gulls; c. 47 species; cosmopolitan. Sterninae Terns; c. 42 species; cosmopolitan.

Rynchopinae Skimmers; three extralimital species, pan-tropical.

Taxonomic rank given to above groups varies greatly. Considered four families within suborder Lari (e.g. Campbell & Lack 1985; BWP), or four tribes within subfamily Larinae (e.g. Sibley et al. 1988; Sibley & Ahlquist 1990; Sibley & Monroe 1990). Others have divided Lari into three families (Stercorariidae, Laridae and Rynchopidae) with gulls and terns usually considered subfamilies within Laridae (e.g. Wetmore 1960; Judin 1965; Hackett 1989; Peters). Moynihan (1959) divided the group into two subfamilies, Stercorariinae, containing the skuas, and Larinae, containing gulls, terns and skimmers in three tribes. Study of skeletal and external morphology of suborder 'Lari' (our Laridae) was mostly unable to cluster gulls and terns satisfactorily and found group surprisingly uniform (Schnell 1970a,b). Despite lack of agreement on taxonomic ranking of above groups, monophyly of Laridae is not in doubt. Studies of biochemistry (Christian et al. 1992), DNA–DNA hybridization (Sibley & Ahlquist 1990), downy young (Fjeldså 1977) and skeletal morphology (Strauch 1978; Mickevich & Parenti 1980; Chu 1995) generally agree in finding close relation with Glareolidae (pratincoles) and Dromadidae (Crab Plover *Dromas ardeola*). DNA–DNA hybridization suggests Alcidae (auks) also closely related (Sibley & Ahlquist 1990), though this contradicted by studies of skeletal morphology (e.g. Strauch 1978; Chu 1995).

Body-form varies greatly, from small and slender in some gulls and terns, to robust and thickset in skuas, jaegers, some gulls and a few terns. Differences in size between sexes slight; males usually larger but females larger than males in Stercorariinae. Wings usually long, narrow and pointed, but broader and more rounded in some; 11 primaries; p10 longest, p11 minute; 17–24 secondaries. Tail has 12 rectrices; shape varies: in Stercorariinae, central rectrices project beyond rest of tail and greatly elongated in adult breeding plumages of *Stercorarius*; in most Sterninae and Rynchopinae, outer rectrices elongated and tail forked; in Larinae, usually square. Bill, varies, though usually rather short and stout, with prominent gonydeal angle; rather fine in some Larinae and Sterninae; tip pointed in Sterninae, decurved in strong hook in Stercorariinae. Bill highly modified for unique foraging methods in Rynchopinae (Zusi 1962). Lack cere, except in Stercorariinae. Nostrils schizorhinal and perforate, with no median septum. Legs, short and stout; attached near centre of body; tibiae partly bare; tarsi, short and typically scutellate in front. Four toes; hindtoe, short, raised, sometimes rudimentary or absent; front toes, fully webbed (webs somewhat incised in some). Claws, moderately long, strong, laterally compressed. Caeca ranges from large (Stercorariinae) to poorly developed (Rynchopinae, Sterninae). Supra-orbital salt-glands well developed.

Plumages mainly browns, black, white and greys. Colours of bare parts often striking and often showing marked variation with both season and age. Adults moult twice annually: (1) a post-breeding (pre-basic) moult to non-breeding plumage, which is complete (with apparent exception of *Larus sabini*); and (2) a pre-breeding (pre-alternate) moult to breeding plumage, which is almost always partial (but see *Larus pipixcan* and *L. sabini*); some terns also undergo one or two pre-supplemental moults of inner primaries. Primaries moult outwards.

Hatch in natal down, which is replaced by juvenile plumage; downy young precocial but more dependent on

¹ This treatment differs from the arrangement presented in the introduction to the Charadriiformes in Volume 2 of HANZAB (p. 648), where these four subfamilies were listed as families. Recent major studies in avian classification (particularly by Sibley and coworkers) and the publication of a revised species list of Aust. birds (Christidis & Boles 1994) since the preparation and publication of Volume 2, have brought much rearrangement. In this and subsequent volumes of HANZAB, taxonomy, nomenclature and arrangements of species follow Christidis & Boles (1994) (though they do not present subfamilial taxonomy). Their sequence of families of Charadriiformes occurring in HANZAB region is: Pedionomidae, Scolopacidae, Rostratulidae, Jacanidae, Chionididae, Burhinidae, Haematopodidae, Recurvirostridae, Charadriidae, Glareolidae and

Laridae. However, work on Volume 2 was too advanced to follow their sequence and taxonomy fully. The Scolopacidae are out of place in the arrangement of subfamilies in Volumes 2 and 3; other families follow the order of Christidis & Boles (1994).

Plate 23

Oriental Pratincole Glareola maldivarum (page 366) 1 Adult breeding; 2 Adult non-breeding; 3 Juvenile; 4,5 Adult

Australian Pratincole Stiltia isabella (page 373) 6 Adult; 7 Downy young; 8 Juvenile; 9 First immature non-breeding; 10, 11 Adult parental feeding than other Charadriiformes. Post-juvenile (first pre-basic) moult complete or partial, varying within and between families; moults of subadults complicated and vary between subfamilies (see subfamily accounts). Generally slow to mature, attaining adult plumage when 2–4 years old and first breeding at 2–4 years (smaller gulls and terns) to 4–9 years (many skuas and larger gulls and terns); some may breed in first year (e.g. Sterna albifrons).

Inhabit wide range of marine and freshwater habitats from Tropics to polar regions; many species strongly migratory, especially those breeding at high latitudes, e.g. South Polar Skua Catharacta maccormicki and Arctic Tern Sterna paradisaea, which migrate between polar regions. Most nest in terrestrial colonies near water (see subfamily accounts); some species highly pelagic in non-breeding season. Use wide range of foraging methods (see subfamilies; for discussion of feeding methods, see General Introduction).

See subfamily accounts for summaries of social organization and breeding.

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Subfamily STERNINAE terns and noddies

Cosmopolitan group of seabirds, with narrow pointed wings and long pointed bills, ranging in size from Little Sterna albifrons (20–28 cm) to Caspian Terns Sterna caspia (up to 55 cm). Mostly smaller, slimmer and longer-tailed than gulls (Larinae) and more aerial. About 42 species in six genera.

GENUS NUMBER OF SPECIES

Sterna Sea terns (including commic terns); c. 32 species; 17 in HANZAB region (15 breeding, 2 non-

breeding migrants; 1 species not acceptably recorded)

Chlidonias Marsh terns; 3 species; all recorded HANZAB region (1 breeding, 1 non-breeding, 1 accidental)

Phaetusa Monotypic; Large-billed Tern P. simplex; extralimital in South America; often combined in Sterna

Anous Dark noddies; 3 species; all breed HANZAB region

Procelsterna 1 (possibly 2) species; Grey Ternlet P. albivitta breeds HANZAB region (second taxa extralimital)

Gygis Monotypic; White Tern G. alba; breed HANZAB region
Larosterna Monotypic; Inca Tern L. inca; extralimital in South America

Studies of osteology (Strauch 1978; Mickevich & Parenti 1980; Chu 1995), behaviour (Moynihan 1959), DNA–DNA hybridization (Sibley & Ahlquist 1990) and allozymes (Christian *et al.* 1992) have generally suggested that terns more closely related to gulls than to other Laridae; monophyly of the Sterninae appears not to be in doubt, and sometimes considered a full family (e.g. BWP).

Number of genera recognized varies. Moynihan (1959) recognized only three: Sterna (including Chlidonias and Phaetusa), Larosterna, and Anous (including Procelsterna and Gygis). Others have recognized as many as ten (e.g. Peters) or 12 (e.g. Wolters 1975) genera. Gull-billed Tern S. nilotica often placed in monotypic genus Gelochelidon; large terns with erectile crests (e.g. S. bergii, S. bengalensis) sometimes placed in Thalasseus; Caspian Tern S. caspia sometimes placed in monotypic genus Hydroprogne, or in Thalasseus. Anous, Procelsterna and Gygis sometimes treated as tribe Anousini (noddies). Our arrangement follows Christidis & Boles (1994) and Sibley & Monroe (1990), except that Black-fronted Tern S. albostriata placed in Sterna rather than Chlidonias (following Mees 1977; Lalas & Heather 1980; NZCL; see that account). Monophyly of genus Sterna as recognized here has been challenged by electrophoretic study of Hackett (1989).

Body-form gull-like, but slimmer and more elongate than gulls except in largest species. Males usually slightly larger than females, especially in length and depth of bill. Necks short. Wings, long and pointed, narrower than in gulls; when wing folded, primaries project well beyond tertials (tips of 5–6 outer primaries usually exposed) and often beyond tip of tail. About 18–24 secondaries; ulnar part of wing shorter than in gulls. Flight musculature differs from gulls by lack of expansor secondarium (except in Anous). Tail, long in most species, with 12 rectrices: most have deeply forked tail, with t6 often elongated as tail-streamer; Chlidonias has short tail, only shallowly forked; tail of noddies forked, but with t3 or t4 longest in Anous and t5 longest in Procelsterna and Gygis. Bill, straight, with simple rhamphotheca and no cere; slender and rather long in most species, heavier in larger species, especially Phaetusa, short and thick in S. nilotica; tip pointed, not hooked. Legs, short or very short; tarsi rather weak; scutellate. Three front toes fully webbed, though webs deeply incised in Chlidonias; hindtoe reduced or vestigial, raised. Swim less readily than gulls, and have less well developed oil-gland (vestigial in S. fuscata). Supra-orbital salt-glands well developed. Down occurs on both pterylae and apteria.

Sexes similar in plumage. Adult Sterna and Phaetusa usually uniform light grey above and white or pale grey below (with evanescent pink flush in some species), usually with contrasting black markings on head (often in form of cap) and tip of wing; some browner above (e.g. S. fuscata, S. anaethetus). Chlidonias, Larosterna and Anous mostly dark grey, dark brown or black above and below; Procelsterna, uniform ash-grey; Gygis, all white. Irides normally dark brown. Bill, legs and feet of most, yellow, orange, red or black. Phaetusa, Chlidonias and most Sterna show seasonal change in plumage: in non-breeding plumage, black caps reduced or flecked with white, many develop dark cubital bars, fork of tail usually less deep (and tail often slightly darker), underparts of grey-bellied species become paler, and bill and feet often become darker; Chlidonias also develop paler upperparts. No seasonal change in appearance of noddies. Adults typically have two moults per cycle: a complete post-breeding (pre-basic) moult to non-breeding plumage; and a partial pre-breeding (pre-alternate) moult to breeding plumage (which involves at least head, neck and some of body, and often all of body, tail and varying number of inner primaries). Primaries moult outwards. Moult of remiges, especially primaries, protracted in most; post-breeding (pre-basic) moult of primaries continues long after moult of body finished, and often overlaps with start of pre-breeding (pre-alternate) moult. Species moulting inner primaries in pre-breeding (pre-alternate) moult can thus have two concurrently active waves of moult in primaries. In some species (e.g. S. albifrons and some Chlidonias) there is often a third wave, as innermost primaries replaced a third time in a pre-supplemental moult. In two small pale tropical species (Gygis alba and Sterna

Downy young, precocial or semi-precocial; semi-nidifugous in most; nidicolous in Gygis, Anous. Natal down, ramose and woolly in most species, but long, straight, silky and very soft in Chlidonias (perhaps an adaptation to rather wet nesting sites). In some Sterna (e.g. S. dougallii), terminal barbs of down cling together to cause spiny appearance, especially on upperparts; down also very short in some (e.g. S. albifrons, S. nereis). Ground-colour of down ranges from white to grey or buff (rich orange-buff in Chlidonias), though dark, like adults, in some Anous. Dark markings on upperparts complex and diffuse: Chlidonias have bold black blotches; others varyingly streaked or speckled dark brown or black above, without distinct pattern except for three radiating lines on crown in many. Some species virtually unmarked above (e.g. S. caspia, S. nilotica). Some variation in colour and patterning of down (especially ground-colour) appears to be geographical (e.g. down of tropical populations of S. dougallii usually paler than in temperate populations) but also much individual variation, and siblings from the same clutch often look totally different (see Fjeldså 1977 for more information on downy young). Juvenile plumages typically differ from non-breeding adults in having buff or blackish tips or bars on much of upperparts and upperwing; tail generally darker than in adult, often with dark subterminal markings; many species have much individual variation in upperparts, and darkness of ground-colour and width of dark barring usually correlated. Juvenile plumages rather unusual in S. virgata, S. vittata and S. fuscata; see species accounts for details. In Anous, Gygis and Procelsterna, juvenile plumage similar to adult.

Sequence of moults from juvenile to adult plumage, complex. When recognizable traces of juvenile plumage have been lost, distinction of immatures from adults depends mainly on moult and wear of primaries. However, this of little use for ageing species in which timing of breeding and moulting vary (a frequent occurrence in Tropics) and subadult moults of such species (including all noddies) poorly known. Following generalizations based on species of Sterna and Chlidonias with regular cycles. POST-JUVENILE (FIRST PRE-BASIC) MOULT usually complete, with head and body finished several months before last outer primaries; in some species, birds can arrest moult when a few very worn outer primaries remain. In several species of medium-sized Sterna from s. hemisphere (striata, albostriata, vittata and virgata), post-juvenile moult appears to be partial, moulting almost no remiges or rectrices (though interpretation complicated because, unlike most juvenile terns, first post-breeding [second pre-basic] moult of head and body coincides with first moult of primaries, much as in typical gulls [D.J. James]); these species (and possibly S. hirundinacea) have several other unusual features in common, including heavily marked juvenile plumages, little sexual dimorphism in length of wing, and only one moult of primaries and (apparently) rectrices per cycle. They may represent a radiation from a single s. hemisphere ancestor (D.I. James). Whether first pre-basic moult partial or complete, most terns superficially resemble adult non-breeding when 3-7 months old, except for retained juvenile remiges (which are still moulting). When 9-12 months old, at least some perform partial first pre-breeding (first PRE-ALTERNATE) MOULT, often starting before post-juvenile moult finished; some attain traces of breeding plumage (especially on crown and cubital bar) but in most there is probably no change in appearance. Resultant first immature non-breeding (first alternate) plumage superficially like adult non-breeding and, in species with regular cycles, held when adults in full breeding plumage. When c. 1 year old, complete FIRST IMMATURE POST-BREEDING (SECOND PRE-BASIC) MOULT brings on plumage almost identical to adult non-breeding; this retained for much of second year, so most immatures retain non-breeding appearance from c. 5 months to c. 21 months old. Partial SECOND PRE-BREEDING (SECOND PRE-ALTERNATE) MOULT near end of second year is first moult to bring on extensive breeding plumage. In many species, second immature breeding plumage may differ from adult breeding in having a few non-breeding-like feathers in crown, cubital bar, tail or underparts; however, reliability of these ageing characters undermined in some species by similar variation in very small number of adults. Subsequent moults, as adults.

Mostly marine, inshore; some frequent both littoral and freshwater habitats; some markedly pelagic. Carnivorous; some only or mainly take fish (e.g. Black-naped Tern S. sumatrana, White-fronted Tern S. striata); other HANZAB species take mixture of fish, molluscs, crustaceans and insects; some freshwater species also take small vertebrates, such as mice or frogs (e.g. Whiskered Tern C. hybridus and Gull-billed Tern S. nilotica). Mostly diurnal but some nocturnal or crepuscular. Forage singly, in small groups or in mixed species feeding flocks, usually with other terns or seabirds, such as shearwaters. Feed mainly by surface plunging, occasionally shallow plunging; and by dipping (contact and non-contact). Also feed by hawking for insects over land and water; gleaning food while walking on ground or in shallow water; and kleptoparasitism.

¹ In Arctic Terns, the first alternate plumage was once mistaken as a separate species and named Sterna portlandica (Ridgway 1874), and the second alternate plumage was mistaken as another, Sterna pikei (Lawrence 1853). These taxonomic treatments have long since been discarded, but the terms 'portlandica plumage' and 'pikei plumage' still confusingly and incorrectly used for homologous plumages in many terns.

Highly gregarious when feeding, roosting and breeding, and will mob predators at colonies. Monogamous, with pair-bonds tending to persist from year to year. Birds may breed as early as 1 year old, but usually not till 3–4 and even older. Can live for many years. Normally breed in colonies, which can number up to tens of thousands. Nesting densities vary with species and habitat, and in large colonies of some *Sterna*, distances between nests can be a bodylength. Nesting territories used for courtship and pair-formation, courtship feeding, copulation, and nesting. Fidelity to nesting site between years high in some species, though other species move between colonies or shift site of colonies altogether (Campbell & Lack 1985). At colonies, social flights, called Mass Flights, preads, panics, or UPFLIGHTS, common. In these displays, some or all members of a colony take flight and fly round in dense flock. Many authors use the terms interchangeably. Others distinguish between Mass Flights and Dreads: In Dreads, birds take off and fly low over colony for some distance without calling, then fly upwards calling loudly; Dreads an escape response but may also be used to help synchronize breeding. In Mass Flights, all birds take off and fly upwards, calling loudly from outset; Mass Flights most common before laying and are used to help synchronize breeding cycles of individuals; resurgence of Mass Flights occurs when chicks being fed, mostly by non-breeding birds visiting colony, at least some of which are preparing to breed in the next breeding season (K. Hulsman). The distinction is often not clear in published descriptions of flock behaviour. Vocal at breeding colonies; calls raucous.

In Sterna and allied genera, displays usually elaborate and similar between species. Aerial flights and some ground displays persist after laying. In GROUND DISPLAYS, which often involve more than two birds, birds drop wings, raise tails and stretch necks upwards. Aerial displays occur in and round colonies. In HIGH FLIGHTS, several birds ascend rapidly to 100 m or more, with some birds displaying as they descend. Zigzagging flights common and especially spectacular in Crested Tern, even after nesting has finished (Gibson 1956). A male carrying a fish will execute noisy LOW FLIGHT through colony, which often stimulates others to join in. FISH-OFFERING CEREMONIES involve one bird flying round, calling loudly, usually with fish held crosswise in bill; usually, another joins it, flying

in front of first. Fish not transferred on wing, but may be passed on ground, accompanied by strutting.

Noddies (Anous, Procelsterna and Gygis) have different displays to sea terns. Similarities include ground displays before and during incubation, which involve birds droping wings so that tips on or close to ground. In courtship display at nest-site, male bobs head slightly and caresses head and neck of female with bill; male courtship-feeds female, and birds call and touch bills. In aggressive territorial displays, male raises feathers of crown slightly, gives rattling call, then thrusts stiffened neck forward and bows. In all displays, orange tongue, pale crown and markings round eyes prominent (Woodward 1972).

Within Sterninae, both sexes share nest duties. Chicks semi-precocial and, if undisturbed, semi-nidifugous (most species) or nidicolous (Anous, Gygis); older chicks occasionally form crèches in some Sterna. Food given in bill (most species) or by regurgitation (e.g. S. fuscata, Anous). Parental feeding continues after fledging, sometimes for

several months and, sometimes, after dispersal from colonies (Campbell & Lack 1985; BWP).

Breeding seasonal, though some tropical terns, notably Bridled S. anaethetus and Sooty S. fuscata Terns, breed at sub-annual intervals depending on local conditions; at some sites, breeding of population may be continuous (King & Buckley 1985; King et al. 1992; BWP). Usually breed in colonies on offshore islands or on headlands; also on or round terrestrial wetlands or in coastal habitats, such as sand dunes, beaches and on islands and sandspits in estuaries; some species nest on cliffs (e.g. Grey Ternlet P. albivitta); Black-fronted Terns nest in shingle beds in streams; Whiskered Terns in vegetation in freshwater swamps; occasionally nest on man-made structures, such as jetties and wrecked ships (HASB; Aust. NRS). Will nest with other species of terns. Ground-nesting birds make unlined or poorly lined scrape in sand or gravel, sometimes under vegetation or in crevice of rock; most noddies nest in trees and bushes, and build bulky nests out of plant material, though many Common Noddies A. stolidus nest on ground; Whiskered Terns build mounds or platforms of vegetation; White Terns make no nest, laying egg on bare branch or leaf of a tree (Fjeldså 1977; HASB; Aust. NRS). Ground-colour of eggs varies from cream or stone-grey to greenish stone, buff or light brown, with markings of black or dark brown, occasionally dark purple (HASB). Clutchsize, 1-3; most species breeding temperate zones average two eggs per clutch, most in tropical areas only one. Incubation period ranges from 19 to 36 days; species that lay 2-3 eggs per clutch incubate for shorter periods, mostly between 19 and 23 days, while those that usually lay one egg incubate for longer, from 28 to 36 days. Both sexes incubate. Adults defecate away from nest. Both sexes feed young, mostly bill to bill or by dropping item beside chick, though noddies, Procelsterna and some tropical Sterna fed by regurgitation. Young of ground-nesting species leave nest within 1 week of hatching but may remain near nest for a few more days; usually seek shelter in nearby cover, though some species form crèches (Hulsman 1977; HASB); young of tree-nesting species usually remain in nest till able to fly (but see Gygis alba). Most species dependent on parents for food for up to 4 months after fledging. Age of first breeding, usually 3–4 years, some species at 2 years (BWP).

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Sterna Anaethetus Scopoli, 1786, Delic. Flor. Faun. insubr., fasc. 2: 92 — 'In Guinea' = Paney, Philippines (ex Sonnerat, 1776, Voy. Nouv. Guinée: 125, pl. 84).

Specifically named from the Greek ($\alpha \nu \alpha i \sigma \theta \eta \tau \sigma s$) senseless, stupid, an allusion to the former tameness of nesting terns and noddies, which allowed seafarers close enough to kill them.

OTHER ENGLISH NAMES Brown-winged Tern, Panayan Tern, Dog Tern, Smaller Sooty Tern.

POLYTYPIC Nominate anaethetus breeds e. Indian Ocean, from Sunda Is and Aust., into w. Pacific Ocean, E to Solomon and Palau Is and N to Taiwan; subspecies antarctica Lesson, 1831, breeds Red Sea, Persian Gulf and w. Indian Ocean S to Maldive and Mascarene Is; apparently accidental to Cocos-Keeling Is. Extralimitally: subspecies melanoptera Swainson, 1837, breeds West Indies and West Africa; subspecies nelsoni Ridgway, 1919, breeds Pacific coast of Mexico and Central America.

FIELD IDENTIFICATION Length 30–32 cm; wingspan 77–81 cm; weight 110–180 g. Medium-sized tropical tern, with stout bill about same length as head; long slender wings, with longest tertial reaching to third or fourth primary when perched; long deeply forked tail, with outer rectrices forming long tail-streamers in adult; and long legs and toes. Slightly smaller and slimmer than Sooty Tern Sterna fuscata. Adult has striking black-and-white head-pattern, dark upperparts and white underparts. Juvenile, duller, grey-brown and white, with less well defined head-pattern and with grey markings on side of breast; tail, deeply forked but without elongated tail-streamers. Flight, direct and elegant, usually with slow wing-beats. Sexes similar. Slight seasonal variation. Juveniles and first immature non-breeding distinct.

Adult breeding White band extends narrowly across lower forehead, over eye and tapers to a point behind eye. Upper forehead, crown, nape, hindneck, sides of head to just below and behind eye, and upper ear-coverts, black, forming neat cap; black loral stripe extends from bill and joins black cap at eye, separating white forehead from white underparts. Rest of head and neck, white. With wear, develop narrow white collar on hindneck. Upperparts, brownish-grey, slightly paler on mantle, and contrasting strongly with black cap, and with white sides to tail; mantle develops brown tone with wear. Upperwing: coverts, brownish grey, as upperparts, with fine white leading-edge extending from base of wing to base of leading primary; remiges, dark brown, contrasting slightly with coverts. Underparts, pale grey, palest on breast, and becoming whiter with wear. Underwing: mostly white, with grey leadingedge to outer primary and broad dark-grey trailing-edge; remiges highly reflective, and extent of grey can vary with light. Bill, glossy grey-black. Iris, black-brown. Legs and feet, dark grey. Adult non-breeding Differ from adult breeding by: Cap, dark brown, grading to paler brown on nape, spotted with white on forecrown and finely speckled white on lores and ear-coverts. Upperparts, brown, with thin white scaling; upperwing-coverts, dark brown with pale-brown scaling. Tail-streamers, much shorter, and mostly grey apart from dull-white sides. Underparts, white. Juvenile Typically, grey-brown version of adult, with white or buff streaking and scaling. Head and neck like adult, but duller: Forehead and supercilium, cream, and less well defined than in adult; cap, mostly dark brown, finely streaked white to buff on crown and nape and faintly spotted pink-buff on ear-coverts; anterior lores, dark grey, with large dark-brown spot in front of eye. Grey half-collar extends from cap to upper breast, forming distinctive wedge on underparts. Upperparts, grey, with pink-buff scaling and bold black crescents on mantle. Upperwing: coverts, grey, with pink-buff scaling, like upperparts, and with white leading-edge not as well defined as in adult; remiges mostly black, with thin greyish fringes; tertials, light grey-brown, with dark-brown subterminal band and buff tips. Tail, grey, with thin dark-grey subterminal band and broad cream to buff tip; no tail-streamers. Underparts, dull white, except for: grey wedge on side of upper breast; dirty grey flanks; and blotchy pale-grey undertailcoverts. Underwing: coverts and exposed bases of remiges, offwhite, with mottled grey leading-edge to primary coverts; rest of remiges, grey with silvery-grey stripes through centres. Bare parts, like adult, but bill, legs and feet sometimes have palergrey tinge, and bill is shorter. Some juveniles much darker: uniform grey above, with ill-defined dull-buff scaling, or even sooty grey above, with no pale scaling; in dark birds, head darker, without white-streaked forecrown and with only diffuse and obscure whitish forehead and supercilium and pale throat. First immature non-breeding Poorly known. Similar to juvenile and differs by: forehead, white; cap, dark brown finely streaked white on crown and with small white striations on nape; lores, white, finely speckled dark brown; upperparts and upperwing-coverts, generally greyer, with narrower palegrey (not buff) scaling; less grey on flanks; tail, lacks paler fringes and is still shorter than in adult. Below, primaries paler than in juvenile and more like adult. Bill, same length as adult.

Similar species Only likely to be confused with Sooty Tern; see that text for details.

Gregarious tern of tropical and subtropical seas, breeding on coral cays, rocky islands and rock stacks; more likely to be seen in harbours or from land than Sooty Tern. Usually seen singly or in loose flocks, though often in hundreds or thousands at breeding colonies. Forage almost exclusively in open sea, but also close to shore; will feed with other terns and noddies. Feed by dipping to surface and surface plunging from 2–13 m above sea, sometimes plunging vertically; rarely submerge entirely. Roost or loaf on branches of low bushes; occasionally on ground among vegetation or rubble, on shoreline or in trees; at sea, alight on floating objects, such as coconuts and flotsam. Flight, buoyant but direct, with exaggerated beats

of long pliable wings, accompanied by marked lift of body; markedly aerobatic, often wheeling and soaring. Gait similar to that of Sooty Tern. Noisy at colonies; barking wup wup in alarm and growl in anger; occasionally utter harsh kee-yarr at sea.

HABITAT Usually offshore in tropical and subtropical seas, often well away from land; during breeding season, associated with vegetated coral cays, rocky islands and rock stacks; rarely round mainland coasts, occasionally blown there by strong

winds and cyclones (Qld Bird Rep. 1990).

Usually forage in open seas, well offshore (MacGillivray 1928; Storr 1964a,b; Domm & Recher 1973; Hulsman & Langham 1985; Storr & Johnstone 1988; Dunlop et al. 1988b); occasionally within 2-3 km of breeding islands (Storr 1964a; Hulsman & Langham 1985). Recorded foraging in swell near surf-zone (Hulsman 1974) and in strait between islands (Warham 1962). Feed from or just below (<20 cm) surface of water (Warham 1962; Hulsman 1974; Hulsman & Langham 1985; HASB). Analyses of diet on Penguin I., WA, indicate pelagic Sargassum communities probably important foraging habitat (J.N. Dunlop).

Breed on offshore coral cays, rocky continental islands and rock-stacks. Nests usually concealed; in crevices or caves up to 1.5 m deep, under rocks, among talus or coral rubble; on cliff-ledges; on ground beneath low bushes or shrubs (<80 cm tall) (MacGillivray 1928; Gillham 1963; Ford 1965; Bonnin 1968; Domm & Recher 1973; Hulsman & Langham 1985; Storr et al. 1986; Dell & How 1987; Corella Seabird Is Ser.). Occasionally among grass, roots of Pandanus or vines (MacGillivray 1928; Hawken 1972), though at same sites, avoid vine-thickets (Garnett 1987). Density of vegetation varies from sparsely scattered with <25% ground-cover, to 50-75% ground-cover (Limpus & Lyon 1981). Not recorded nesting on Gannet Cay after cyclone razed vegetation (Walker & Jones 1986d). Rarely, nest on shingle or sandy beaches (MacGillivray 1928; HASB) and occasionally in old turtle carapaces (King et al. 1983a; King 1986).

On breeding grounds, roost or loaf on branches of low bushes; occasionally on ground among vegetation or rubble; rarely, on shoreline or in trees. Occasionally, on artificial structures, including posts, cray-fishing posts and buoys (Warham 1957; Bonnin 1969; Stranger 1970; Hulsman & Langham 1985; HASB). In wintering areas, do not roost or loaf on land, but will rest on floating objects at sea, including coconuts, fishing-boats and flotsam (Dunlop & Johnstone

1994).

DISTRIBUTION AND POPULATION Tropical and subtropical coasts and waters off e. and w. Africa, Asia and Aust.; also Caribbean. In Americas, from s. Florida, SW to Yucatan Pen. and S to Panama; also SE from s. Florida, through Caribbean islands (including Bahamas, Cuba and Lesser Antilles) to n. Venezuela; rare in Gulf of Mexico and farther N along e. coast of USA. In Africa, scattered in Mauritania, from sw. Senegal to Guinea-Bissau, in Gulf of Guinea and off e. South Africa and s. Mozambique; also Madagascar, Seychelles and Mauritius. Widespread e. Africa, from Tanzania, through Somalia to coast of Red Sea, extending round Arabian Pen. and Persian Gulf, to w. India; also round sw. and s. coasts of India, Sri Lanka and Maldive Is. In Asia from Malay Pen. and e. Bay of Thailand, S to Indonesia and Aust., through New Guinea and Solomon Is to Samoa and Tonga, and N through Palau and Philippines to Taiwan and islands off se. China (Ali

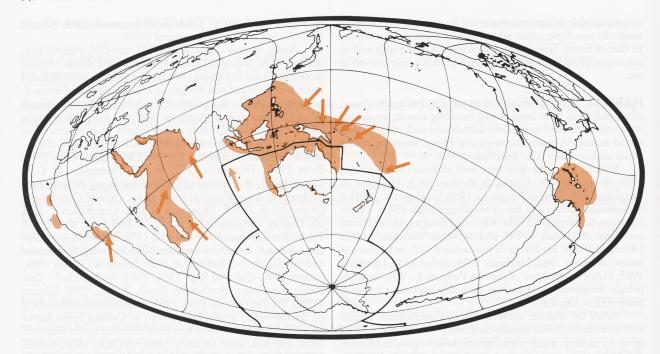
& Ripley 1969; AOU 1983; de Schauensee 1984; Coates 1985; Urban et al. 1986; Langrand 1990).

Aust. Mainly coasts of WA, NT and Qld; vagrant to s. waters. WA Vagrant, Denmark, 1 Jan. 1981 (Aust. Atlas); mostly recorded C. Leeuwin, N to Dirk Hartog I., with isolated records at Pt Maud and Ningaloo; widespread from Barrow I. to Dampier Arch., and at sea off Kimberley coast from waters W of Dampier Pen. to Ashmore Reef and Joseph Bonaparte Gulf (Aust. Atlas). Possible record inland, at Northam, Mar. 1943 after cyclone (Masters & Milhinch 1974). NT Occasional visitor to Darwin (e.g. Rix 1970; McKean & Gray 1973; Storr 1977; Thompson 1977; H.A.F. Thompson & D.K. Goodfellow), and infrequently elsewhere in sw. Arafura Sea. Widespread from Wessel Is to w. and s. Gulf of Carpentaria (Aust. Atlas; H.A.F. Thompson & D.K. Goodfellow). Qld SE. Gulf of Carpentaria but not w. C. York Pen.; widespread Torres Str., and round ne. coast to c. 18°S. Farther S, sporadically on coasts away from breeding islands; rarely, S to Fraser and Stradbroke Is (Draffan et al. 1983; Smyth & Corben 1984; Sutton 1990; Qld Bird Reps 1984, 1987; Aust. Atlas). Tas. Single, beachcast, Northdown Beach, 8 Aug. 1982 (Green 1983). SA First record, 4 Jan. 1968, when pair found breeding on Baudin Rocks within large colony of Crested Terns Sterna bergii (Bonnin 1968); up to four birds recorded seven times till 1975, but not since (Bonnin 1969, 1973a,b, 1982; Lovell 1972; SA Bird Rep. 1972-73). In 1906, Campbell (1907) reported a single Sooty Tern at Baudin Rocks, but may have been misidentified Bridled Tern (Bonnin 1968). Single reported Troubridge I., 1 Jan. 1972 (Lovell 1972). No Aust. Atlas records.

NZ Single, beachcast, New Brighton, 25 Nov. 1987 (Tunnicliffe & Langlands 1990).

Cocos-Keeling Is Single, specimen, 5 July 1941 (Gibson-Hill 1949, 1950).

Breeding (Pairs unless stated.) WA Widespread on islands from C. Leeuwin to Shark Bay; also in Pilbara region and Kimberley Div.: St Alouarn I., <15¹; Seal I. (C. Leeuwin)²; Knobby Head (C. Leeuwin), 4 nests, 1985; 2 nests, 19863; Augusta⁴; Hamelin I., 1 nest⁵; Tub Rocks⁶; Second Rock⁶; First Rock⁶; reefs off C. Bouvard⁷; Penguin I., >1000^{8,9}; Shag Rock¹⁰; Seal I.8; Bird I.11; rocks off C. Peron6; Arch Rock6; Garden I. (North Rock)⁶; Carnac I., 50–100¹²; Rottnest I., including offshore islets and rocks (Dyer I.; Joan, Phillip, Duck, Monday and Clune Rocks; Parakeet I.; Cathedral Rocks)13; Little I., off Whitford's Beach^{6,7}; Two Rocks I.⁶; Edward I., c. 50, 1976¹⁴; Lancelin I., c. 2000, 1990s^{9,15}; North and South Green I., 100s^{4,16}; Whittell I., 8 nests, 1962¹⁶; Buller I., 300 birds¹⁶; South Rosnard Bay Rock, probably 16; North and South Sandy Knoll I., c. 500 adults^{4,16}; South Essex Rock⁴; Middle Essex Rock⁴; North Essex Rock, probably¹⁶; North, Middle and South Cervantes Is, 300–400^{4,16}; Whitlock I., c. 80¹⁶; Boullanger I.⁴; South Fisherman I., c. 500¹⁷; Middle Fisherman I., a few pairs¹⁶; North Fisherman I., 2000¹⁸; North West and East Beagle Is, 200-4004,16; Houtman Abrolhos: 7046, breeding recorded on 66 islands¹⁹: Pelsaert Grp (Square I.; Gun I., c. 1000; Pelsaert I., up to 60; Arthur and Gregory Isl.; Uncle Margie, Newman, Jackson Is)19-22; Easter Grp (Rat I., formerly; islet off Rat I.; Wooded I., 250; Morley I., 1 pair, 1945; Alexander I.) 20,23,24; Wallabi Grp (Dick, Long, Pigeon and Pelican Is)²⁰; islands in Freycinet Estuary (Mary Anne, White, Double, Charlie, Friday, Slope Is)²⁵; Sunday I.²⁵; Egg I.²⁵; Dirk Hartog I.⁷; Lowendal Is, >10,000, with 3000-4000 on Bridled I.9; Montebello Is9; Kendrew I.²⁶; islets S of Hermite I.²⁶; Haycock I., 200 pairs, 1991²⁷; Goodwyn I., 70 pairs, 1992²⁸; Rosemary I., Elphick

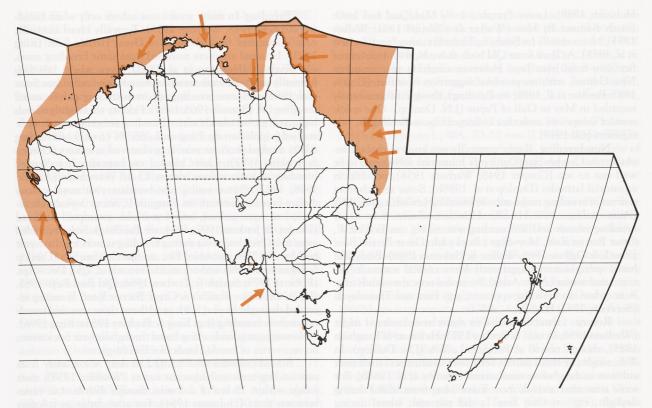


Nob^{10,26}; Elphick Nob, ≤150 pairs, 1991²⁹; Nelson Rocks, Goodwyn I. and Haycock I., in Dampier Arch. 4,27,28; Montalivet Is (Warm Rock)⁷; Low Rocks, Admiralty Gulf⁷; Lesueur I., 50– 100 old nests³⁰. **NT** Round Haul I.³¹; Sir Edward Pellew Is^{31,32}; Wellesley Is, May 199133. Said to breed on several offshore islands³². Qld Widely distributed on islands in all regions except SE (King 1993): Rocky I., Gulf of Carpentaria, 1965³⁴; Bramble Cay, c. 10, 197935; Badu I.4; Kusa (Flat) I.36; Kusamet I., 300, 1979³⁷; Tuin Rock³⁶; Channel I., 80, 1979¹⁰; Jaylag I.³⁶; Travers I.³⁶; Hammond Rock^{36,38}; Tuesday I. No. 4, 10, 1978¹⁰; East Strait I., 6 nests³⁸; Channel Rock, c. 5, 1979¹⁰; Booby I., at least 5039; Albany Rock, c. 300 birds36,38; Roko (Bushy) I.36; Cairncross I.7; Pandora Cay, <50 nests, 1976; >500 nests, 1980; <50 nests, 1982⁴⁰; Raine I., up to 150⁴¹; South-East Cay, Ashmore Banks, 1 nest, 1981⁴²; Quoin I., ≤200 nests⁴³; C. Restoration Is⁴⁴; Lloyd Bay Isl.⁷; Chapman I., ≥100 nests, 1987⁴⁵; Sherrard I., 100 nests, 1987⁴⁶; Sandbank No. 8, 100 nests, 1976⁴⁷; Fife I., c. 40 adults, 1988⁴⁸; Claremont Isl. No. 5⁷; Pelican I., up to 500 nests⁴⁹; Stainer I., ≥20, 1984⁵⁰; Davie Cay, ≥10, 1982⁵¹; Tydeman Cay, c. 10, 1982⁵²; Wharton Reef³⁸; Aye Sandbank⁷; Combe I., c. 50, 1984⁵³; Nymph I., <50 birds, 1992⁵⁴; Lizard I., many⁵⁵; Bird I., c. 300⁵⁵; Eagle I., c. 200^{55,56}; Pethebridge I.⁷; Rocky Isl., c. 300 nests⁵⁷; Three Isl., 100s⁵⁸; Low Isl., small colony, 1944³⁸; Woody I.⁴⁴; Michaelmas Cay, 1 pair⁵⁹; North Barnard I.⁷; South Barnard I., >4000 adults⁶⁰; Purtaboi I., c. 250 breeding birds, 1987–88⁶¹; Brook I., c. 1200 birds⁶²; Holbourne I.⁶³; Eshelby I., 2500–4000, 1985– 8664; Redbill I., 150 birds, 198665; Reid I.44; Beverley Grp44; Frigate Cay, >200 nests, 19766; Gillett Cay67; Price Cay, 50– 100 nests, 1976⁶⁸; Bell Cay, 300-500, 1976⁶⁹; Gannet Cay, 150, 1980⁷⁰; Tryon I., 200, 1984⁷¹; Northwest I.⁷; Wilson I., 5, 1983-8472; Wreck I.44; Heron I.10; Erskine I., 25-3573; One Tree I., 250-40074; Masthead I., 1275; Hoskyn I.7; Fairfax I., <20 birds⁷⁶; Lady Musgrave I.⁷; Lady Elliott I., >500 nesting, 1987–8877. SA One pair bred Baudin Rocks, 1968–6978

⁹ J.N. Dunlop; ¹⁰ Aust. NRS; ¹¹ Serventy & White 1943; ¹² Dunlop & Storr 1981; 13 Saunders & de Rebeira 1993; 14 Abbott 1981; 15 Abbott 1978b; ¹⁶ Ford 1965; ¹⁷ Johnstone 1978b; ¹⁸ Johnstone 1978a; ¹⁹ Fuller et al. 1994; ²⁰ Storr et al. 1986; ²¹ Burbidge & Fuller 1989; ²² Fuller & Burbidge 1992; ²³ Johnstone 1992; ²⁴ Johnstone & Coate 1992; ²⁵ Storr 1985; ²⁶ Storr 1984; ²⁷ Dunlop et al. 1994a; ²⁸ Dunlop et al. 1994b; ²⁹ Dunlop et al. 1994c; ³⁰ Abbott 1979; ³¹ Storr 1977; ³² McKean & Gray 1973; ³³ Walker 1992; 34 Garnett & Crowley 1987; 35 Elvish & Walker 1991; 36 Draffan et al. 1983; ³⁷ Garnett 1987; ³⁸ Warham 1962; ³⁹ Garnett et al. 1988; ⁴⁰ King et al. 1983a; ⁴¹ King 1986; ⁴² King & Limpus 1983; ⁴³ King & Buckley 1985a; ⁴⁴ Kikkawa 1976; 45 King 1991; 46 King & Limpus 1991; 47 King et al. 1983b; 48 King et al. 1991; ⁴⁹ King et al. 1985a; ⁵⁰ King 1985; ⁵¹ King & Buckley 1985b; ⁵² King & Buckley 1985c; 53 King et al. 1985b; 54 Smith 1994; 55 Domm 1977; 56 Smith & Buckley 1986; 57 Smith & Ogilvie 1989; 58 McLean 1993; 59 King et al. 1992; 60 Walker & Oldroyd 1991; 61 Walker 1993; 62 Thorsborne & Thorsborne 1986; 63 Walker 1989b; 64 Walker & Hegerl 1986; 65 Walker 1989a; 66 Walker & Jones 1986a; 67 Limpus & Lyon 1981; 68 Walker & Jones 1986b; 69 Walker & Jones 1986c; 70 Walker & Jones 1986d; 71 Hulsman et al. 1993; 72 Walker & Hulsman 1993; 73 Walker & Hulsman 1989; 74 Hulsman 1979; 75 Jahnke 1977; 76 Walker et al. 1993; 77 Walker 1989c; 78 Bonnin 1968, 1969.

Populations Estimates of colony sizes above. No other estimates. In WA, population has expanded and range extended S. In 1840s, not recorded S of Houtman Abrolhos, but found breeding on islets off Rottnest I. by 1889. Breeding recorded Shoalwater Bay in 1901, but still uncommon there by 1939. However, since 1940s, breeding distribution has expanded S to Seal I., E of C. Leeuwin (Storr & Ford 1962; Gillham 1963; Serventy & Whittell 1976; Storr & Johnstone 1988; HASB). On Penguin I., Shoalwater Bay, not recorded between 1940 and 1942, but colonized since; breeding colonies there have expanded since 1980s, now supporting >1000 pairs (Serventy & White 1943; Dunlop et al. 1988a; Dunlop & Jenkins 1994).

Breeding population on Penguin I., has increased despite human recreational activities over several decades (J.N. Dunlop). On some islands in sw. WA, said to compete with Rock Doves *Columba livia* for nesting sites in small caves in limestone cliffs (Aust. NRS). On Wedge I., WA, several killed



by foxes (Ford 1965). Occasionally collide with lighthouses (Stokes 1983).

MOVEMENTS Little known; migratory or highly dispersive. Two subspecies in HANZAB region, one breeding and one vagrant. Subspecies antarctica breeds w. Indian Ocean; populations breeding Red Sea and Gulf of Aden move to nonbreeding areas along e. coast Africa as far S as Mozambique; population breeding Kenya move to unknown breeding areas; populations breeding Persian Gulf and Makran Coast thought to disperse along w. coast of India as far E as Bombay; apparently accidental to Cocos-Keeling Is. Nominate anaethetus breeds e. Indian Ocean, E to Solomon and Palau Is and N to Taiwan; movements poorly known (Gibson-Hill 1949; Blake 1977; see BWP). Rest of account refers to nominate anaethetus unless stated.

Aust. birds leave many breeding areas outside breeding season. Most populations breeding on continental islands off e. and w. Aust., breed spring-summer and are considered migratory (Storr et al. 1986; HASB), though non-breeding range not known (Cooper 1948; Warham 1958) and may be dispersive. Move away from Aust. coastal waters in non-breeding season and large-scale seasonal trends apparent; reporting rates for Atherton, e. Qld, Top End and sw. Aust. regions combined: spring 1.1%, summer 3.5%, autumn 0.2%, winter 0.1% (Aust. Atlas). Banding recoveries indicate at least some Aust, young and adults move long distances from breeding areas (see Banding). Populations breeding sw. Aust. possibly move to non-breeding area in nw. Celebes Sea, 4-7°N; five birds banded sw. Aust. have been recovered there (Dunlop & Johnstone 1994). No good evidence for claim that sedentary in n. parts of Aust. range (see HASB); movement of birds in colonies where breeding occurs throughout year not known. Some occurrences on continental coasts possibly associated with cyclones or bad weather (Whitlock 1927; McKean & Gray 1973; Qld Bird Rep. 1990).

Departure WA At most breeding colonies, most adults and fledgelings usually leave early to mid-Apr.; all left by mid-Apr. to early May, though can be later in some years (see Dunlop & Jenkins 1992; Dunlop & Johnstone 1994). Leave Penguin I., Apr., though c. 1 week earlier in 1990 than in 1987 and 1988 (Dunlop & Jenkins 1992); large n. movement observed at nearby Carnac I. in first half Apr. (Dunlop et al. 1988a). Common near Swan Coastal Plain till early Mar., exceptionally mid-Apr. (Storr & Johnstone 1988). In 1960, appeared to leave Lancelin I. by mid-Apr. (Ford 1965); leave North and South Fisherman Is, late Mar. and early Apr. (Johnstone 1978a,b). In Houtman Abrolhos, birds that bred Pelican I. left early Apr. 1959-60 (Storr 1966); on Wooded I., common till early May (Johnstone & Coate 1992). Last birds left Slope I., Shark Bay, WA, 24 Feb. 1975 (Mitchell 1975). Common Gascoyne Region till late Feb. (Storr 1985); occur off Pilbara till Apr. (Storr 1984); occur in Kimberley till early May (Storr 1980). At least some WA birds move long distances, with recoveries of adults from SA and nw. Celebes Sea; also recovered in first year from nw. Celebes Sea (Smythies 1981; Dickinson et al. 1991; Dunlop & Johnstone 1994; see Banding). Peak passage, Timor Sea, Apr.; loose flocks, including fledgelings, observed moving N through Lombok and Lintah Straits and Sabu and Banda Seas, late Apr.-late May; thought to be WA birds en route to nw. Celebes Sea (Dunlop & Johnstone 1994). Old Most leave Lady Elliot I. by Feb., though a few sometimes occupy nests in Apr. (Walker 1989b); in Capricorn Grp, last fledgelings leave Tryon I. early Mar. (Hulsman et al. 1993); adults and young leave One Tree I., late Mar. or early Apr., laggards till late Apr. (Domm & Recher 1973; Hulsman 1979); leave Erskine I. soon after breeding, which is completed by Mar., few remain mid-Apr. (Walker &

Hulsman 1989). Leave Purtaboi I. by Mar., and last leave South Barnard Is, Mar. (Walker & Oldroyd 1991; Walker 1993). Not normally on Booby I., Torres Str., after Jan. (Garnett et al. 1988). At least some Qld birds move N, with recovery of first-year from Irian Jaya. However, common year round in New Guinea, with no previous suggestion of influx (Coates 1985; Beehler et al. 1986; see Banding), though influx recently recorded in May in Gulf of Papua (J.N. Dunlop). One specimen of subspecies antarctica collected Cocos-Keeling Is, July (Gibson-Hill 1949).

Non-breeding Range generally not known, though includes nw. Celebes Sea (Dunlop & Johnstone 1994); said to be well out to sea (Cooper 1948; Warham 1958), possibly in equatorial latitudes (Dunlop et al. 1988b). Some records from s. areas of breeding range outside breeding period, e.g. sw. WA (Aust. Atlas; contra HASB). However, absent from many breeding islands and surrounding waters, e.g. on Erskine I., Great Barrier Reef, May–Sept.; Rocky Isl., Great Barrier Reef (Smith & Ogilvie 1989; Walker & Hulsman 1989). Birds that breed spring–summer apparently leave coastal waters in autumn and winter (Aust. Atlas). Recorded on some islands in n. Aust. when no breeding apparent, e.g. East and Thursday Is (Serventy 1952; HASB).

Return Generally arrive en masse at colonies at night (Warham 1958; Domm & Recher 1973; Hulsman & Langham 1985), though not so at Penguin I., WA (J.N. Dunlop). In WA, singles or small parties seen over continental shelf near colonies in days before mass arrival (Dunlop et al. 1988b). For some time after arrival, most move away from island during daylight, e.g. on One Tree I., did not visit island during daylight till about 2 weeks after first arrivals; first moved into vegetation about 4 weeks after arrival (Hulsman & Langham 1985). Transition from night to day visitation of nesting areas took 7–8 days (Hulsman 1977a). Old Arrive Booby I., Torres Str., Aug. (Garnett et al. 1988). Arrive Eagle I., Oct. or Nov. (Smith & Buckley 1986). Arrive Purtaboi I., Nov. (Walker 1993). In Capricorn Grp, first arrive One Tree I., at night around mid-Sept.; not seen in daylight till second week Oct. (Domm & Recher 1973; Hulsman 1979; Hulsman & Langham 1985); arrive Tryon I., Oct. or Nov. (Hulsman et al. 1993); Masthead I., 11 Oct. 1910 (Campbell & White 1910). Begin to arrive Lady Elliot I. in Oct. (Walker 1989b). Increase of numbers on One Tree I. in Jan. possibly influx of non-breeders (Hulsman 1979). WA In Timor Sea, peak passage, assumed to be en route to WA, from late Sept. to early Oct. (Dunlop & Storr 1994). Occur off Kimberley coast from late Sept. (Storr 1980); off Pilbara coast from late Oct. (Storr 1984); common Gascoyne Region, from Sept. (Storr 1985). On Houtman Abrolhos, common Wooded I., from Oct. (Johnstone & Coate 1992) and arrive Pelsaert I., mid-Oct. (Surman 1994). Arrive North and South Fisherman Is, mid-Oct.; earliest date 13 Oct. (Johnstone 1978a,b). On Lancelin I., in 1954, first appeared 24 Oct., when small group roosted at night; on 26 Oct., small parties arrived during morning, stayed for c. 1 h before returning to sea; more and more remained to roost on island till Nov. when observations stopped (Warham 1958). Common Swan Coastal Plain, from late Sept. (Storr & Johnstone 1988). Arrive Fremantle in second week Oct. (Storr 1964a). First arrive Carnac I., late Sept.; occupy territories at night by second week Oct. (Dunlop & Storr 1981). First seen roosting during day on Penguin I., between 22 Sept. and 12 Oct. 1986– 89; influx of young and pre-breeders up to 3 years old occurs throughout breeding season, with maximum rate of recapture in Mar. (Dunlop & Jenkins 1992).

Breeding In many areas come ashore only when breeding (Cooper 1948; Warham 1958). Typically breed annually; nest in summer through most of Great Barrier Reef (King 1993). Unusual absences recorded from some breeding areas, e.g. Tryon I. (Hulsman et al. 1993). Even where breeding normally seasonal, some aseasonal breeding recorded (see Storr et al. 1986) and some breeding opportunistic, e.g. pair recorded breeding SA (Bonnin 1968, 1969). Fidelity to breeding islands high, at least on islands where breeding seasonal, e.g. in wellstudied population on Penguin I., 86.9% (n=23) of breeding adults marked previous year were observed in colony (Dunlop & Jenkins 1992); adults banded on Lancelin I. recovered breeding at same colony almost 13-16 years later (ABBBS 1978, 1982). Some young non-breeders visit natal colony during breeding season; on Penguin I., many 3-year-olds returned to natal colony, and 4-year-olds attempted to breed (Dunlop & Jenkins 1992, 1994; see Banding). Some recorded away from breeding areas during breeding season, e.g. first-year bird banded WA recovered Dec. in nw. Celebes Sea (Dunlop & Johnstone 1994) and occasional records se. Qld, Dec.-Apr. (Roberts 1979; Smyth & Corben 1984; Qld Bird Rep. 1985, 1987). On some islands on Great Barrier Reef, breeding recorded throughout year, with or without these seasonal trends in numbers breeding (e.g. King & Buckley 1985a; King 1986). Movements on islands where breed throughout year not known; no recoveries of banded birds (see Banding).

Round colonies tend to feed in deep water away from surrounding reefs and adjacent coasts (Warham 1958); most forage within 15 km of colonies, though distribution varies between years (Hulsman 1984). For attendance at colonies and roosting sites, and foraging movements during breeding period, see Hulsman & Langham (1985).

Banding, Colour-marking Recoveries indicate high fidelity of young and adults to natal colonies (see Dunlop & Johnstone 1994). On Penguin I., young birds recaptured at natal colony in third year, but first- and second-year birds also recovered; breeding confirmed in fourth year. One-, 2- and 3-year-olds tend to be present at colony late in breeding season and rarely retrapped till after main peak of laying. Of birds up to 3 years old recorded visiting Penguin I. colony (n=13), 12 were raised there, and one banded Seal I. colony, 1.1 km N (Dunlop & Jenkins 1992). Adult apparently breeding Booby I., Torres Str., recaptured over 2 years later (Garnett *et al.* 1988).

Some recoveries away from colonies in Aust.: single banded 3 Dec. 1972 found dead 225 km SSE at Fremantle on 5 Dec. 1976 (ABBBS 1977); adult banded North Fisherman I., WA, 30 Nov. 1974, recovered dead 1900 km ESE at Coffin Bay, SA, early Jan. 1985, more than 10 years after banding (ABBBS 1985). Birds banded Aust. and recovered extralimitally: banded North Fisherman I., WA: runner banded 7 Jan. 1973, recovered 3500 km N at Berau, Kalimantan-Timur, Indonesia, 28 Dec. 1973 (ABBBS 1974); runner banded 31 Dec. 1979, recovered 3834 km N in Sabah, Malaysia, 18 Aug. 1980 (ABBBS 1981); adult banded, 5 Jan. 1981, recovered 3941 km N, 15 June 1993 (Dunlop & Johnstone 1994); banded Penguin I., WA: adult banded 1 Nov. 1986, recovered dead 4305 km N at Philippines, 20 June 1991 (ABBBS 1992; Dunlop & Johnstone 1994); adult banded 7 Oct. 1988, recovered 4155 km N, at sea c. 240 km SW of Kiamba, Philippines, 11 July 1992 (ABBBS 1993); nestling banded Booby I., Torres Str., 30 Oct. 1988, recovered 1619 km NW on Misool I., Irian Jaya, 2 Sept. 1989 (ABBBS 1990).

Other records

32S115E	11	2+	U	55	4539	12	ABBBS
32S115E	11	2+	U	50	397	346	ABBBS
30S114E	12	P	U	106	225	342	ABBBS

FOOD Carnivorous; in A'asia, almost entirely fish but also crustaceans and aquatic insects; extralimitally, also take molluscs. Behaviour Diurnal, though some evidence for nocturnal feeding; daily peaks in return to colony in morning and evening, possibly birds moving to and from feeding grounds at night (Hulsman 1974; Hulsman & Langham 1985). May feed closer to colony in evening (Hulsman & Langham 1985). Usually forage in open sea; usually 2 km, but up to 16 km, from shore (Hulsman 1977a). Often feed on schools of fish forced to surface by other predators (MacGillivray 1928; Storr 1964b; Domm & Recher 1973; Hulsman 1974, 1987). Forage singly or in loose flocks; up to 25 recorded feeding together (Storr 1964a; Hulsman 1977a). Forage by (1) DIPPING: taking food from or just below (< 20 cm) surface (Warham 1962; Hulsman 1974; Hulsman & Langham 1985; HASB); and (2) SURFACE PLUNGING from 2-6 m or 3-13 m above water, and at angles of 20°-90°; rarely submerge entirely (Hulsman 1974, 1977a; Hulsman & Langham 1985; cf. Ali & Ripley 1969). May take insects blown out to sea (Henry 1971). Feed mates and young by regurgitation so rarely have food stolen because they do not carry food in bills when moving from foraging grounds to colonies (Hulsman 1976; K. Hulsman).

Adults On Lizard I., Qld (91 food items, Jan. 1992; 77, Feb. 1993; S. Blaber): MOLLUSCS: cephalopods: Sepia 1.1 freq. in 1992, – in 1993; Teuthoidae 1.1, 1.3. FISH: Apogonidae –, 9.2; Atherinidae: Atherinomorus lacunosus –, 30.3; Blenniidae: Xiphasia matsubaria 1.1, -; unident. 1.1, -; Carangidae: Gnathanodon speciosus -, 1.3; Clupeidae: Amblygaster sirm 46.2%, 30.3%; Herklotsichthys –, 1.3; unident. 1.1, 3.9; Labridae: Stethojulis strigiventer –, 1.3; Monacanthidae 2.2, –; Mullidae: Mulloides flavolineatus -, 5.3; Upeneus tragula 12.1, -; Pomacentridae: Pristotis jerdoni 2.2, -; unident. 1.1, -; Priacanthidae: Priacanthus -, 5.3; Tetraodontidae: Lagocephalus lunaris 2.2, -; unident. teleosts 27.5, 2.6. On Penguin I., WA, (45 regurgitations; J.N. Dunlop): Crustaceans: decapods: crabs (including two syngnathid crabs) 28.9%; Insects 20%; Fish 51.1 (mainly larval and juvenile) Carangidae, Gonorhynchidae,

Hemiramphidae, Monacanthidae, and Mullidae.

Other records (Including food given to young): Molluscs: gastropods; cephalopods: Spirulidae: Spirula australis; Echinoderms (possibly from fish stomachs); Crustaceans: decapods: prawns (Hulsman 1977a); Insects: Hemiptera: Gerridae; Pentatomidae; Lepidoptera (Wetmore 1916; Henry 1971). Fish (MacGillivray 1928): Acanthuridae (Hulsman 1977a); Atherinidae; Monacanthus filicauda juv. (Hulsman 1977a); Balistidae (Wetmore 1916; Henry 1971; Hulsman 1976; Hulsman 1987); Clupeidae: Spratelloides; Engraulididae: Engraulis australis; Exocoetidae (Hulsman 1976); Monocanthidae: Atorolepis filicauda; Scombridae (Smith 1993).

Young Regurgitated fish fed to chicks usually already broken into small pieces, though adults often reswallow large pieces. Whole fish may be passed tail first (Hulsman & Langham 1985; BWP). On One Tree I. fed throughout day, with modal times 05:00 to 06:00 and 16:00 to 17:00; mean feeding interval: 338 min (211; 8) in 1974-75, 171 min (146; 54) in 1979-80. Chicks received an average 4 meals/day (1-9) (Hulsman & Langham 1985).

On One Tree I., Old (53 items; Domm & Recher 1973): Fish: Engraulididae: Engraulis australis 98.1% no. (2-8 cm); Monocanthidae: Arotrolepis filicauda 1.9 (2-4 cm). Also on

One Tree I., Qld (133 items, regurgitations and obs.; Hulsman & Langham 1985): Crustaceans: prawns 0.8% no. (2-<4 cm); Fish: 'silver' species (incl. Engraulididae) 2–<4 cm, 3.8; 4–<6 cm, 9.0; 6-<8 cm, 6.0; 8-<10 cm, 3.8; 10-<12 cm, 1.5; unknown size, 33.1; Exocoetidae: 6-<8 cm, 0.8; 8-<10 cm, 0.8; Blenniidae 6–<8 cm, 0.8; Monocanthidae 2–<4 cm, 4.5; 4–<6 cm, 15.8; 6–<8 cm, 8.3; 8–<10 cm, 3.0; unknown size,

Intake Average length of food taken 58.0 mm (Hulsman 1981); on Penguin I., WA, 20–50 mm (J.N. Dunlop). Weight of food given increases with age of chicks, with mean weight of food per meal at 12 days, 8.7 g (5.3; 24) (Hulsman & Langham 1985).

SOCIAL ORGANIZATION Based on studies on One Tree I., Great Barrier Reef (K. Hulsman in BWP), and Lancelin I., WA (Warham 1958); references to BWP below refer to studies on One Tree I. unless stated otherwise. Adults and newly fledged young leave nesting colonies in loose flocks (Dunlop & Johnstone 1994); outside breeding season said to be solitary (K. Hulsman); at sea near colonies in WA before arriving in large numbers, seen singly or in small flocks (Dunlop et al. 1988b); mean group-size off WA, Apr., 3.38 (1–20; 45 flocks) (J.N. Dunlop). Feed singly (BWP) or in flocks, e.g. of 25 birds (Storr 1964a; Domm & Recher 1973); sometimes feed in mixed flocks (Warham 1962) with Black Noddies Anous minutus (Domm & Recher 1973; Hulsman 1974; Hulsman & Langham 1985), Arctic Skuas Stercorarius parasiticus (Storr 1964a), White-winged Black Terns Chlidonias leucoptera, Common Terns S. hirundo, Sooty Terns (Carter 1983), Roseate Terns S. dougallii and Fairy Terns S. nereis (J.N. Dunlop); after cyclone, seen feeding with Sooty, Common, Crested, Lesser Crested S. bengalensis and Little Terns S. albifrons (Griffin 1972). Roost in groups at colonies (Warham 1957; Garstone 1978); groups small on arrival but later hundreds roost in nesting areas during day (Warham 1958); may roost with Black Noddies (Hulsman & Langham 1985; K. Hulsman; see Roosting).

Bonds Monogamous (Warham 1958; K. Hulsman). Of six pairs, only two retained partners in successive seasons, one of these persisting for at least 6 years; change from traditional nest-sites (see Breeding) often associated with divorce or disappearance of partners (Dunlop & Jenkins 1992; J.N. Dunlop). Birds return to natal colony, most doing so in third year of life. Age of first breeding seems to depend on physiological maturity and obtaining nest-site. Breed in fourth year, when many, if not most, have returned to natal colony; many third-year birds, and some first- and second-year birds, found in colonies but usually not until late in breeding season (Dunlop & Jenkins 1992, 1994). Many birds arriving at colonies appear to be paired (Warham 1958; Domm & Recher 1973; HASB) but some pairing possibly occurs at colonies during night, when Terns active and noisy (Domm & Recher 1973). Members of some pairs may reunite at nest-sites. Late in breeding season, courtship flights seem most common (Hulsman 1977a) with unpaired birds and unsuccessful breeders of season taking part (but see Sexual behaviour). Parental care Both parents incubate and care for young, feeding them for several weeks after fledging, though not for as long as in some other Sterna (BWP; Warham 1958; Hulsman 1974, 1977a; Hulsman & Langham 1985). Juveniles practise foraging within 6 days of fledging (Hulsman 1977a). Not known if parents accompany or feed young after dispersal from colony; may become independent on leaving colony area c. 35 days after fledging (K. Hulsman). Do not form crèches (Hulsman 1974; K. Hulsman).

Breeding dispersion In small loose colonies (BWP; Warham 1958; Fien 1971; Storr et al. 1986; Dunlop & Jenkins 1992) or as single pairs (Storr et al. 1986; Walker 1989b; King et al. 1989, 1991; King 1991; Fuller et al. 1994; Campbell; Aust. NRS); sometimes apparent colonial nesting possibly concentration of solitary pairs gathering in suitable habitat (Campbell; Fuller et al. 1994; Aust. NRS). On One Tree I., behave colonially and nests not spread evenly (K. Hulsman; cf. Domm & Recher 1973). Where nests concentrated, nests not close together (Warham 1956); widely scattered (King et al. 1985b; North); 1-5 m apart (Dunlop & Jenkins 1992; BWP) but appear much closer at some sites (K. Hulsman); 20– 30 m apart (HASB). On Penguin I., WA, in one colony, c. 600-650 nests in c. 2 ha (Dunlop & Jenkins 1992); on Bridled I., WA, c. 3000-4000 breeding pairs nesting over c. 10 ha (J.N. Dunlop); on Eagle I., Great Barrier Reef, average density c. 190 nests/ha (Smith & Buckley 1986). Size of colonies varies but generally much smaller than colonies of Sooty Terns; on Great Barrier Reef, 5–1000+ pairs (e.g. Domm 1977; Jahnke 1977; Hulsman 1979; Smith & Buckley 1986; King 1993; NRS); off coast of WA, 40-2000 pairs (e.g. Abbott 1978a,b; Johnstone 1978a,b; Fuller & Burbidge 1981; Dunlop et al. 1988a). On Houtman Abrolhos, some nest in loose wellspaced colonies of up to 250 pairs (Fuller & Burbidge 1981; Burbidge & Fuller 1989; Storr et al. 1986). For further details of colonies, see Distribution. Nest-sites traditional (Hulsman 1977a; Dunlop & Jenkins 1994); see Breeding. Sub-colonies may consist of specific age-classes (see Dunlop & Jenkins 1994). Territories Defend small territory round nest, which is used for ground courtship, nesting, feeding young, and resting by off-duty bird (BWP). Home-range Feed offshore during breeding season (Warham 1958; Domm & Recher 1973; Hulsman 1977a; Dunlop et al. 1988a; Hulsman & Langham 1985). Most hunt within 15 km of colony, though some up to 28 km (Hulsman 1984); after returning in afternoon, may hunt within 2 km of colony (Hulsman & Langham 1985).

Roosting Outside breeding season, roosting behaviour not known, but probably do not roost on land (Dunlop & Johnstone 1994); feathers water-repellent and can settle on sea, though seldom do so; readily settle on floating material, which is probably important for roosting (e.g. Warham 1958; Dunlop & Johnstone 1994). At breeding areas, roost at night on land; tend to retire late and remain restless throughout night, calling (Warham 1957, 1958; HASB); active from 21:00 to midnight and again from 02:00 to dawn (05:15) (Hulsman 1977a). When first arrive at breeding grounds, activity and calling obvious but, for first 2 weeks, not seen by day (Campbell & White 1910; Domm & Recher 1973; Dunlop et al. 1988a; Walker & Oldroyd 1991); on One Tree I., during this time, roost away from future nest-site. About 3 weeks after first arrival, groups roost during day on sandbanks or similar, 2-3 km from breeding grounds; move to shoreline and other exposed places near nesting area when about to occupy nests (Domm 1977; Hulsman & Langham 1985; K. Hulsman). Both diurnal pattern of roosting and use of roosting sites alter with stages of breeding cycle; use of roosting sites also varies with time of day (Hulsman & Langham 1985). On One Tree I., before breeding, daily pattern of roosting shows strong diurnal pattern independent of tidal cycle: birds arrive at shoreline roost at 08:00 and leave at 16:30-19:00. In week before full occupation, periodic collective upflights occur from roosts on shore (Hulsman 1977a) (see Sexual behaviour). Close to start of nesting, move en masse to nesting grounds and roost overnight and, at first, are absent by day (Warham 1958; Hulsman

1977a, 1979; Dunlop & Storr 1981; Hulsman & Langham 1985; Dunlop et al. 1988a). Apparently select nest-sites after dark (Campbell & White 1910). Daytime visits begin c. 2 weeks after first visiting future nesting area (Domm & Recher 1973; Hulsman 1977a) with transition from night to day visitation taking 7-8 days (Hulsman 1977a). In WA, in some areas, daytime visits brief, at first birds staying c. 1 h at sunrise, then flying out to sea or to a roost elsewhere. On Penguin I., on return, roost at night on nesting sites; in succeeding days, spend progressively more of morning in colony before leaving, and return earlier in afternoon till pairs eventually spend most of day at nest-sites, as well as roosting at them at night (Warham 1958; Dunlop et al. 1988a; Dunlop & Jenkins 1992; J.N. Dunlop). On One Tree I., during nesting, birds spend most of their time away from island during daylight, returning to roost at night (Hulsman 1977a); in first 1–2 weeks after selection of nest-site, visit nest-areas in morning; after this, number of birds on island falls steadily from sunrise until 15:30 or 16:00 and then rises sharply c. 16:30 with most returning by 18:00– 19:00, though some appear to stay away all night (Hulsman 1974, 1977a); similiar pattern noted when feeding young, despite there being a constant stream of adults arriving at and leaving colony (Hulsman 1977a). Birds often loaf and sun themselves during day. Non-territorial birds loaf in trees or bushes (BWP; K. Hulsman). After clutch laid, off-duty breeding bird will loaf alone in territory or on habitual vantage point nearby, usually a rock, branch, or post (BWP; Warham 1958). During incubation and fledging periods, adults often roost in Argusia and Pisonia trees, particularly in early morning (soon after sunrise) and late afternoon, as well as in hotter parts of day; more often perch on bushes in nest-areas during incubation than in fledging period. By time chicks c. 40 days old, many adults spend most of day away from nest-areas, roosting communally in areas frequented before nesting, e.g. tree-tops and shoreline; round this time one-third of adult population was resting on island except between 14:00 and 17:00. Overall spend less time foraging than Crested Terns do and spend more time on other activities, such as resting on shoreline (Hulsman & Langham 1985; K. Hulsman). Chicks sometimes sun themselves (Hulsman 1977a) and have been found down burrows of Wedge-tailed Shearwaters Puffinus pacificus, apparently sheltering from heat (Dyer 1992).

SOCIAL BEHAVIOUR Fairly well known (as Social Organization). Secretive when breeding (King & Buckley 1985a). More timid than Sooty Tern. Aerial display and Butterfly Flight said to be similar to those of Sooty Terns (Warham 1958). Flock behaviour On One Tree I., c. 4 weeks after first arrival at colony, large flock returning from feeding congregates over lagoon and reef-flats at dusk, flying and soaring 1-20 m above water before entering colony (K. Hulsman); not seen in colonies in WA (J.N. Dunlop). During nesting, after dawn and at dusk, birds gather flying and calling over nestareas (Hulsman 1977a). DREADS: common early in breeding season; stimulated by Dread Call from single bird darting swiftly and low out to sea, with wings widely swept, body canting from side to side, and making violent evasive movements. Neighbouring birds repeat call, and fly seaward in like fashion; exodus silent after first call, but after birds swoop low over water they rise and return, uttering Alarm Call. Dread usually localized but may spread to whole colony (Warham 1958; Hulsman 1977a; HASB); see also Sexual behaviour and Parental anti-predator strategies. Comfort movements As for other members of genus; stretch one wing and leg over fanned

tail; preen often: rub head on shoulders and scratch head or bill with foot directly, bringing foot up from under wings; often scratch in flight (Warham 1958).

Agonistic behaviour Aggressively defend territory, nest and young against conspecifics and other species with which they nest. Territorial advertising Bird signals ownership of territory to conspecific by HEAD-NODDING (Fig. 1): standing bird tilts whole body fowards at c. 45° or more and nods rapidly, with wings held away from body; bird may give Advertising Call with bill wide open and tongue vibrating. Threat In territorial dispute on ground, opponents face one another and nod, with feathers of hindcrown raised and bill open; give Advertising Call, especially after intruder driven off. Birds often interrupt courtship on ground and copulation between another pair, displaying male usually repelling intruder as described above (Warham 1958; HASB). In disputes, birds sometimes take to air, especially in disputes between territorial neighbours. May rise vertically from ground (UPWARD-FLUT-TER), half-hovering, with wings beating rapidly and intermittently flying forward, and giving Anger Calls; birds then separate and usually return to respective territories. Birds that perch on vegetation overhanging a nest, often swooped by owners of nest. Fighting Adults grab and tug at each other with bills, and sometimes beat each other with wings, uttering Anger Calls; bird may be grabbed by nape, wing, or tail to

prevent escape (K. Hulsman). Sexual behaviour Pair-formation involves social and individual phases of aerial courtship, as well as ground displays at colony; some birds display at possible nest-sites (HASB). On One Tree I., resurgence of display flights occurs late summer, after hatching; more courtship flights, especially High-flight, occur Jan.-Feb. than in Oct.-Dec.; resurgence coincides with return of young non-breeding birds to colony, and display flights probably performed by these non-breeders and failed breeders (Hulsman 1977a). Males with young may perform Fly-up and Low-flight (Hulsman 1977a; K. Hulsman). On Whitlock I., WA, aerial displays seen late Oct. (Ford 1965); on Rocky Isl., Great Barrier Reef, courtship activity seen early Nov. (Smith & Ogilvie 1989); on Lancelin I., many pairs noted displaying, courting and exploring nest-sites in late Nov. (Aust. NRS); aerial displays also common late in season (see below). Aerial courtship Few collective upflights occur in week before regular daytime occupation of nesting grounds; birds fly up together calling, then resettle within c. 3 min (Hulsman 1977a; K. Hulsman). Individual phase includes High Flight and Low Flight. HIGH FLIGHT: Not common at colony, and may go unnoticed at sea, where it also occurs (Domm & Recher 1973; K. Hulsman). Usually two birds (rarely three) make rapid spiral ascent to c. 300 m, level off, and then begin downward glide; sway from side to side, mostly in unison, though movements of pursuer may be delayed a little; birds overtake each other (PASS CEREMONY) one or more times during glide; some calling (not described). Food rarely carried (HASB; K. Hulsman). LOW FLIGHT: Occurs before laying, mostly initiated by male but sometimes by female (K. Hulsman). Bird picks up stick or leaf, or sometimes regurgitates (and retains) a piece of fish, and flies round colony with slow exaggerated wing-beats (BUTTERFLY FLIGHT of Warham 1958) and giving Advertising Call; adopts aerial version of BENT POSTURE, with neck stretched and held slightly below horizontal and bill held down. Advertising bird pursued by up to eight others, often at high speed. Low Flight sometimes starts from a FLY-UP (K. Hulsman): male on nest-territory arches neck, with head held low, and flies up almost vertically;

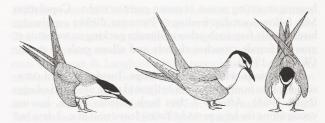


Figure 1 Head-nodding

Figure 2 Parade

after ascending, sometimes comes straight down in same posture. Courtship on ground Typically occurs on nest-territory between established or potential mates; these sites consistently occupied for 3-4 weeks before laying (Dunlop & Jenkins 1992; BWP). Birds assume BENT POSTURE: body tilted fowards, bills c. 30° below horizontal, carpal joints lowered and held slightly outwards, and wing-tips crossing above or below raised tail; plumage sleeked, except for feathers of hindcrown, which may be raised. Holding this posture, two movements occur: (1) PARADE (Fig. 2): two birds strut side by side with short steps, and heads slightly averted so that nape presented to partner; occasionally, one lightly touches back of other's head with bill; after moving short distance, birds turn to face each other and BILL-FENCING occurs: wave lowered bills from side to side, without touching, or raise heads and wave bills at 10-15° above horizontal (Cooper 1948; Warham 1958; HASB; K. Hulsman); (2) PIROUETTE: Often follows Parade and takes two forms. In first, birds circle each other alternately as they move forwards; when one circles, other is stationary. In second form, one bird (usually male; K. Hulsman & N.P.E. Langham), closely circles other, which leans forwards, shuffling to keep facing towards partner, though both keep heads tilted down and slightly averted; circling bird reverses direction repeatedly, in arc, in front of other (Warham 1958; K. Hulsman). During Parade or Pirouette, both birds sometimes pick up and mandibulate stones or bits of vegetation, and give short Kek or Growl calls (Warham 1958). Courtship feeding Male feeds female by regurgitation (Hulsman 1977a); females faces or stands beside male and adopts Hunched Posture, as in other terns; gives Begging Call and pecks repeatedly at base of male's bill. Male arches neck to regurgitate, and female takes food from bill. Courtship feeding occurs less often than in many other Sterna that carry food in their bills (K. Hulsman). Greeting Nest-relief takes several forms: (1) Incoming bird approaches on ground, with head and breast lowered and head retracted, similar to Hunched Posture; when at nest, nods, and sitting bird leans forwards and nods as it stands and moves off nest. (2) Incoming bird gives Advertising Call before landing, often eliciting same call from sitting bird, which then rises, and pair perform mutual Pirouette. (3) Incoming bird gives Advertising Call and sitting bird leaves, without interaction, in different direction to that of incoming mate. (4) Bird continues sitting despite arrival of mate, which then either regurgitates piece of fish, or picks up piece of vegetation, and flies round giving Advertising Call; sitting bird responds by moving off nest quickly and adopts Bent Posture on ground; incoming bird immediately goes to nest and reswallows fish or drops vegetation before sitting. In 97 change-overs with eggs and young on One Tree I., relieved bird left immediately (35% of cases), preened (18%), drank in flight (27%), picked up pieces of vegetation and discarded them (7%), defecated in flight (6%), or performed some other activity (7%) (K. Hulsman & N.P.E. Langham). Campbell & White (1910) reported

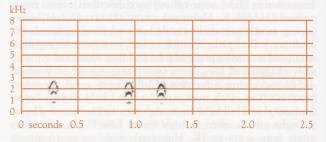
hearing crooning noises between pairs at night. Copulation May follow courtship feeding or Pirouette. Before copulating, birds usually face each other and make pecking movements at ground; female crouches slightly and allows male to mount (Warham 1958).

Relations within family groups Incubating bird occasionally flies from nest to wet belly; said to be used to cool eggs (Sales 1965). After 3-7 days both parents forage, leaving young alone for long periods. Young leave nest at c. 3 days but remain nearby until fledging (Hulsman 1977a; K. Hulsman). At night, downy young stamp feet on fallen branches and leaves on which they are perched and make tapping sounds; done only occasionally during daylight; may be form of communication with adults (Prendergast & Taylor 1987). According to Hulsman & Langham (1985) behaviour of parents and chicks during feeding of young similar to that of Sooty Tern, as described by Dinsmore (1972). Returning adult gives Advertising Call, to which older young respond by running through vegetation. If chick delayed in reaching spot, parent takes off and circles area, sometimes with slow exaggerated wing-beats, uttering Advertising Call, and lands again, if necessary alighting on vegetation then dropping to ground to find chick (K. Hulsman). Chicks fed by regurgitation. Adult often holds food in bill till chick takes all or part of it. Condition of food passed to chick varies: sometimes whole fish passed tail first and swallowed that way by chick; other times regurgitated bits of several small fish or partly digested mass. Adult swallows any regurgitate not taken by chick (Hulsman 1974; Hulsman & Langham 1985). BEGGING: Chick crouches slightly, in hunched posture, with neck retracted, and calls persistently, lifting bill to c. 30° above horizontal with each call; often pecks at parent's bill. Once fledged, young wait on shoreline or reefcrest to be fed. Begin to practise dipping (most common foraging methods of adults) c. 1 week after fledging. Fed on shore for c. 35 days. Not known if parents feed young after dispersal from colony (K. Hulsman). Anti-predator responses of young Within a day or so of hatching, conceal themselves by crawling into any nearby hole or under thick vegetation (Domm & Recher 1973; Hulsman 1977a). On hearing Alarm Call of parent, young <3 days old freeze, lying flat in nest with bill on ground. Older young leave nest and hide in nearby rocks or vegetation and are then difficult to find (Domm 1977; Hulsman 1977b). Seen scurrying down nearby burrows of Wedge-tailed Shearwater, but retreated when attacked by Shearwaters (Dyer 1992). If closely approached by person, run and seek new refuge (BWP). Parental anti-predator strategies Give Alarm Calls on approach of danger. Escape aided by tunnels under vegetation (Cooper 1948; Hulsman & Langham 1985; BWP). Aggressive towards other nesting birds (BWP). Alone or in groups of up to 30 chase or swoop at Silver Gulls Larus novaehollandiae in or over colony (Bonnin 1969; Hulsman & Langham 1985; K. Hulsman); often strike when swooping (Hulsman 1977b); a mob may form a wedge (apex pointing to ground) over Gull on ground, in or under vegetation; all birds in wedge seem to make Anger Calls and closest Terns swoop Gull (Hulsman & Langham 1985). Give Anger Calls and swoop vigorously at Buff-banded Rails Rallus philippensis, which take eggs; sometimes Tern then jumps on Rail's back causing it to withdraw (BWP; Hulsman & Langham 1985). Response to people: said to be more timid than Sooty Tern, leaving nest furtively well before arrival of person, then flying off; but at times fairly tame, allowing close approach (Cooper 1948; Warham 1956, 1958; Bonnin 1969; Serventy & Whittell 1976; BWP); can be captured on nest (Söderberg 1918; North),

especially in thick grass (North). Generally, sitting bird leaves nest and hovers or flies and calls round person (e.g. MacGillivray 1926; Bonnin 1968, 1969; Fien 1971); sometimes persistently lands near nest (Bonnin 1968; Dell & How 1987). When scrambling off nest, often get entangled in vegetation (Cooper 1948; North). Dreads may occur (Hulsman 1977a, see Flock behaviour). If person stays near nest, adult sometimes returns and tries to lure intruder away with Brokenwing Display (Cooper 1948; K. Hulsman), but this less common than dive-attacks to within 1 m with Anger Calls. Do not strike people but may defecate on them (Bonnin 1968; Hulsman 1979; Hulsman & Langham 1985; K. Hulsman). On Penguin I., sw. WA, where people have been regularly present since 1918, allow approach to within 4 m, with mode of 1.1–2 m, whereas on remote Bridled I., off Pilbara, mode 5.1-6 m, with some being disturbed at 27 m; more tolerant behaviour on Penguin I. attributed to gradual habituation to regular presence, and relatively predictable activity of, people at the colony (J.N. Dunlop). Other anti-predator features include nesting under cover, dispersion of nests, cryptic coloration of eggs and chicks, defecating away from nest, and fast initial growth of chicks (Hulsman & Langham 1985).

Well known. Account in BWP based on information from HANZAB area from Warham (1958) and K. Hulsman. Elsewhere, calls described by LeCroy (1976). On One Tree I., much calling in flight at night before and during breeding (see Social Organization, Social Behaviour); when selecting nests, call at night but not during day (Campbell & White 1910). Roosting birds call through night (Warham 1957, 1958). Vociferous when nesting colony approached (MacGillivray 1926, 1928). Often called Dog Tern because the Alarm Call is similar to the yapping of small dog (Cooper 1948; Warham 1958; Serventy & Whittell 1976; Campbell; North; HASB); reminiscent of call of Black-winged Stilt Himantopus himantopus (Fien 1971; Serventy & Whittell 1976). NON-VOCAL SOUNDS: Downy young tap feet on fallen branches and leaves; 38 counts of tapping by one chick: mean of 9.4 taps/min during day, and 64 taps/min at night; highest count 112 taps/min at 04:00. Most taps, especially at night, rapid double strike (counted as two taps in samples above) of one foot against perch. Tapping chicks more difficult to locate than calling chicks, so may serve as safe mode of communication at night (Prendergast & Taylor 1987).

Adult Based on account in BWP. ALARM CALL (= Dog Call of Hulsman & Langham 1985): Staccato barking wep wep or wup wup (Warham 1958; Serventy & Whittell 1976); see sonagram A. Increases in pitch with increasing danger (Hulsman & Langham 1985). ANGER CALL (= Tremulous Call of Hulsman & Langham 1985): Guttural tremulous GRRRrrrrr, emphatic at beginning then trailing off: heard much during swoops on ground and aerial predators (BWP); seemed to be



A A. Griffin; Middle Brook I., Qld, Jan. 1977; P39

uttered by all birds in flock attacking intruding Silver Gull (Hulsman & Langham 1985; see also Growl, below). ADVER-TISING CALL: Loud tremulous hrrr or greer, likened to whinny of horse (BWP); usually delivered with bill open and tongue vibrating (Warham 1958). Given by advertising male, and by bird arriving to relieve mate or feed young; may elicit same call from sitting mate (BWP). GROWL: Growling greer, greer during Bill-fencing (see Social Behaviour); also utter harsh growls when fighting conspecifics (Warham 1958). KEK: Utter kek or kuk in courtship on ground, apparently as contact call (Warham 1958; BWP). BEGGING CALL: Not described; given by female during courtship feeding (BWP). FISHING CALLS: Harsh grating cries when fishing (Warham 1958). DREAD CALL: mer-er-er or aah-aah-ah, falling in pitch, then rising, given by bird flying off; appears usually to be spontaneous, though sometimes caused by human intruder; causes others to fly up during or immediately after call, some also calling (Warham 1958; Hulsman 1977a).

Young Small chicks give high-pitched peep (BWP). Foot-tapping (see above).

BREEDING Fairly well known; detailed study on One Tree I., n. Old (Hulsman & Langham 1985) and on Penguin I., WA (Dunlop & Jenkins 1992, 1994). Breed on offshore islands and stacks, in loose colonies, occasionally singly; nest on mainland at one site in WA (Storr et al. 1986; Dell & How 1987; HASB).

Season In e. Old, mostly spring and summer, but appear to nest all year round at some sites; in WA, late spring and summer, probably occasionally in winter. Same pair will nest at same site and lay at about same date each year (Hulsman 1977a). QLD: One Tree I.: some synchrony in nesting within sites but overall, season protracted and not highly synchronized; arrive mid- to late Sept. but do not move to nesting areas for c. 4 weeks; laying, 5-8 weeks after arrival, between late Oct. and early Dec.; dates vary from year to year (Domm & Recher 1973; Hulsman & Langham 1985; K. Hulsman). Great Barrier Reef: Ouoin I., breed throughout year (King & Buckley 1985a); Raine I., throughout year, with no summer or winter peak (King 1986); Pelican I., in summer (King et al. 1985a); Bell Cay, mainly Nov. and Dec. but two nests with eggs found in July (Walker & Jones 1986c); Nov.-Feb., with eggs in mid-Feb. (Smith & Ogilvie 1989); laying begins, and some eggs hatch, late Oct. (Warham 1962). Found breeding Torres Str., Oct. and Nov. (Warham 1961). wa: Eggs, early Nov. to late Jan.; young, mid-Dec. to early Mar. (Sedgwick 1940; Ford 1965; Aust. NRS); Houtman Abrolhos: Nov. to early Jan.; in 1991 eggs, early Nov., and hatching, early Dec.; juveniles in Aug. probably from eggs laid in late June or early July (Storr et al. 1986; Surman 1994); Penguin I.: laying, from mid-Oct., latest in early Jan.; peak of developed brood patches, late Dec. (Dunlop & Jenkins 1992). sa: Single pair at Baudin Rocks found with eggs in late Dec. in one season and young in early Jan. in another (Bonnin 1968, 1969).

Site On ground, under vegetation or in rocky areas round edge of islands; under shrubs, Melanthera biflora, Argusia argentea, mangroves, stiff aerial roots of Pandanus, tussocks of grass, under or in hollow log; also in crevices of rocks, caves, under ledges or clefts of rock up to 1.5 m deep, under large pieces of coral rubble or stones; also in hollow carapaces of dead Green Turtles Chelonia midas; occasionally in open, on pigface or on rock; some nests found on open metal deck of scuttled ship, 50 m from shore; small colony nesting under planks of wood and bits of roofing iron among ruin of old shack (Campbell & White 1910; Hill 1913; MacGillivray 1917, 1927; Serventy 1930; White 1946; Hulsman 1977b; Hulsman & Langham 1985; King 1986; Garnett 1987; Aust. NRS). On One Tree I., nests surrounded by vegetation usually have tunnels running under vegetation to nests, often with two exits (Hulsman & Langham 1985); tunnels under vegetation on Masthead I. range from 15 cm to 180 cm long, and lead to a cleared space (Cooper 1948). Same pair returns to same nestsite year after year (Hulsman 1977a). On Penguin I., of 23 Terns colour-banded in 1987-88, 20 resighted in 1988-89 season, 16 at original site, four at new site; in 1989-90, 14 birds resighted, nine on original site, three on site to which they had moved in previous season, and two on new site; shifts involved distances of 1, 3, 5 and 15 m; re-laying sometimes leads to a shift of 1-2 m (Dunlop & Jenkins 1992); one individual now on same site for 7 years and with same mate for 6 years (J.N. Dunlop). Nest with Black-naped, Crested, Caspian and Roseate Terns, Silver Gulls and Wedge-tailed Shearwaters; some nest among nesting Silver Gulls, a few only 30 cm from nests of Gulls (Walker 1989b; Aust. NRS).

Nest, Materials Unlined scrapes or depressions in shingle or sand, or in natural cavities among rubble or coral slabs (Campbell & White 1910; MacGillivray 1928; Domm & Recher 1973; Hulsman 1977b; Hulsman & Langham 1985; Fuller et al. 1994). May dig a shallow depression but mostly lay in nests of previous seasons (Hulsman 1977b).

Eggs Typically oval but also swollen oval or almost elliptical; close-grained, smooth, lustreless; ground-colour, chalky or dull white, uniformly distributed with rounded freckles, dots, spots and a few small irregular blotches of reddish purple, and underlying markings of dull purplish-grey; on some eggs, markings only freckles and dots, others may have a cap of large confluent blotches on thicker end; rarely, eggs rich creamybuff with many conspicuous irregular blotches and blurs intermingled or scattered between the dots and spots (North). MEASUREMENTS: 46.3 (1.43; 44.5–48.5; 14) x 33.0 (0.91; 31.5– 34.5) (North); NT: 47.7 (3.01; 43–51; 6) x 32.9 (1.56; 30– 34.5) (Hill 1913). WEIGHT: Average 25 g (Langham 1983).

Clutch-size One (Hulsman & Langham 1985); occasional clutches of two (Hill 1913); clutches of two and three eggs (Aust. NRS) probably result from eggs rolling into other nests.

Laying On One Tree I., laying within a colony spread over 30-40 days, though some groups lay within a few days of each other (Hulsman 1977a); protracted, over a 40-day period, but somewhat synchronized over 15-day period in subcolonies (Hulsman & Langham 1985). May re-lay after failure (Dunlop & Jenkins 1992).

Incubation By both sexes, beginning soon after laying (Hulsman & Langham 1985). Completely observed shifts of incubation lasted 159.8 min (17.3; 48), incompletely observed shifts lasted 343.3 min (29.0; 26); change-overs most frequent between 11:00 and 15:00 (Hulsman & Langham 1985). Birds incubating at nightfall not incubating at dawn (Hulsman & Langham 1985). An egg that had blown into a crevice, was placed in an unoccupied scrape under a rock and was subsequently brooded by a female (Aust. NRS). INCUBATION PE-RIOD: 28-30 days (Hulsman 1977a). Adults defecate round territory but do not defecate in or next to nest; walk c. 1 m from nest or fly a short distance to defecate (Hulsman 1977a; Hulsman & Langham 1985). Remove egg-shells from nest, sometimes within 1 m of nest (Hulsman 1977a; K. Hulsman).

Young Semi-precocial. Within c. 1 day of hatching, young conceal themselves from intruders by crawling into nearby hole or thick vegetation (Domm & Recher 1973); if disturbed, chicks <3 days old, freeze in nest, lie flat with chins pressed to ground; older chicks leave nest and hide in vegetation (Hulsman & Langham 1985); hide down burrows of shearwaters if approached (Dyer 1992). Growth MEASURE-MENTS, WEIGHT: Summarized in Table 1 (from growth curves in Hulsman & Langham 1985). Young reach half asymptotic weight on average 13.6±1.7 days after hatching, and asymptotic weight of 128.5 g (98.8% adult weight) at c. 40 days (Langham 1983; Hulsman & Langham 1985). Parental care, Role of sexes Young brooded by both sexes for at least 3 days after hatching; average duration of shifts of brooding or chick attendance, 336.0 min (28.8; 53); most change-overs occur between 07:00 and 10:00; after 3-7 days, both parents forage, leaving young alone for long periods (Hulsman 1977a; Hulsman & Langham 1985). After at least 3 days, chicks move away from nest and hide under coral slabs or among vegetation near nests (Hulsman 1977a). Both parents feed young; regurgitate food for young and hold food in bill till young take all or part of it (Hulsman 1977a; Hulsman & Langham 1985). Young fed 1-9 meals/day, in two peaks, between 05:00 and 06:00 and 16:00 and 17:00 (Hulsman & Langham 1985); chicks most often fed between 10:00 and 11:00 and 18:00 and 19:00 (Hulsman 1977a). Mean interval between successive feedings in two seasons: 337.6 min (210.8; 8) and 171.1 min (145.6; 54) (Hulsman & Langham 1985). Average weight of meal, 8.7 g (5.3; 24) for chicks 12 days old or more (Hulsman & Langham 1985). Chicks defecate where they stand (Hulsman 1977a).

Table 1

Hatching	10	20	30	40	50	60	1
9	25	55	101	159	200	219	
13	16.5	20	24	27.5	31.5	35	
24	53	85	109	119	123	125	
	9 13	13 16.5	9 25 55 13 16.5 20	9 25 55 101 13 16.5 20 24	9 25 55 101 159 13 16.5 20 24 27.5	9 25 55 101 159 200 13 16.5 20 24 27.5 31.5	9 25 55 101 159 200 219 13 16.5 20 24 27.5 31.5 35

Fledging to maturity FLEDGING PERIOD: 58–60 days (Langham 1983), 61–63 days (K. Hulsman plus extralimital information from Diamond [1976]). On One Tree I., some young leave island 28–34 days after fledging (Hulsman 1977a). Confirmed age of first breeding, for birds colour-banded as chicks, 4 years (Dunlop & Jenkins 1992).

Success On One Tree I.: from 164 eggs laid in three seasons, 114 (69.5%) young fledged; annual variation, 17.6–96.2%; from 113 eggs laid in two seasons, 107 (94.7%) hatched, 105 (92.9%) fledged; infertile or cracked eggs or both most likely causes of failure of eggs to hatch; some eggs may have been eaten by Buff-banded Rails or broken by adults scrambling from nests when disturbed; storm-surge after a cyclone drowned some chicks; some chicks starved after cyclone reduced adult foraging efficiency; one chick taken by a Silver Gull (Hulsman 1977b; Hulsman & Langham 1985). Rats probably take eggs (Warham 1962).

PLUMAGES Prepared by K. Bartram. Extralimitally, finish post-natal moult to juvenile plumage at *c*. 9 weeks old (Diamond 1976). Undergo protracted post-juvenile (first pre-basic) moult to first immature non-breeding plumage, starting 3–6 months after fledging, and finishing *c*. 1 year after fledging. No data on sequence of plumage changes to adult plumage or when adult plumage attained; probably takes at least 3 years. Adults undergo two moults per year: a complete post-breeding (pre-basic) moult and a partial pre-breeding (pre-alternate) moult, with only slight change in appearance. Timing of moults and extent of pre-breeding moult varies with timing and fre-

quency of breeding. First breed when 4 years old. Sexes similar. Slight geographical variation. Nominate *anaethetus* breeds HANZAB region and described below.

Adult breeding (Definitive alternate). Head and neck Lower forehead and supercilium, extending well past eye and tapering to point, white. Upper forehead, crown, nape, hindneck and upper third of ear-coverts, black (89), forming neat cap. Lores, black (89), forming broad loral stripe (thicker than in Sooty Tern), extending from bill to eye, separating white of forehead and supercilium from white underparts and joining black cap at eye. Chin, throat, foreneck, sides of neck and lower two-thirds of ear-coverts, white. With wear, white bases of feathers of hindneck exposed to form narrow white collar. Upperparts Upper mantle, grey (84), contrasting strongly with black cap; develop brown tinge when worn. Rest of upperparts, dark greyish-brown (83-119A). Underparts Pale grey (86), slightly paler on upper breast; triangle of grey (84) extends from upperparts between rear flanks and uppertailcoverts. Axillaries, white. With wear, grey tips to feathers lost and underparts become whiter. Uppertail Dark greyishbrown (83–119A), as upperparts, with white outer edge. On t6, base of inner web, basal half to three-quarters of outer web, and distal outer edge, white (white distal outer edge lost with wear). Shafts, cream (pale 92). Undertail Light grey (85) with white bases and cream (54) shafts. Upperwing Coverts, brownish-grey (121-84) with smaller lesser coverts slightly darker, and smallest marginal coverts, white, forming white leading-edge from base of wing to base of primaries. Remiges, dark brown (219), contrastingly darker than coverts, and with broad pale wedges through centre of inner webs of primaries; wedges, off-white basally grading to light grey (86). Secondaries and tertials have white bases to inner webs. Shaft of p10, brown (121C). Underwing Coverts, white. Remiges, pale grey (86) to white, grading to grey (85) distal third and with darker grey (83) tip; elongated pale-grey (86) to white wedge extends onto grey distal third of inner webs of primaries. Outer web of p10, pale grey (86). Shafts of remiges, cream (92).

Adult non-breeding (Definitive basic). No Aust. specimens. Based on BWP and Olsen & Larsson (1995). Differs from adult breeding by: Head and neck Pattern of head intermediate between that of adult and juvenile. Forecrown, dark brown (119A), spotted with white; grades to dark brown (119–119A) on rear-crown and ear-coverts, and to pale brown (119A) on nape. Lores, dark brown (119A), finely speckled with white. Upperparts Brown (119A–119B) with small white fringes to feathers. Underparts White. Tail Less deeply forked than in adult breeding. Grey (84), becoming brownish grey (brown 84) with wear; basal half of outer rectrix, dull white. Shafts, dull white. Upperwing Coverts, dark brown (119A) with paler-brown (119B) fringes.

Downy young No specimens available; based on BWP. Most of body covered in long fine down; speckled dark brown, grey and buff; sometimes uniform grey. Belly and vent, dull white.

Juvenile Varies, with some much darker (see Variants, below). Typically, like adult but streaked and scaled with buff. Head and neck Pattern somewhat similar to that of adult. Forehead and supercilium, cream, less well defined than in adult. Cap and loral stripe more diffuse than in adult, dark brown, darkest in patch behind eye, giving effect of dark eyestripe. Crown, dark brown (121), finely streaked with dull white or whitish buff (white 121D); nape, dark brown (121) with faint dull-white fringes to feathers. Ear-coverts, dark brown (121) with faint pink-buff (dull 121D) tips when fresh.

Lores immediately in front of eye, dark brown (121) forming large spot; anterior lores, dark grey (82) finely speckled white. Throat, sides of neck and foreneck, white, with diffuse grey half-collar extending from rear of cap to upper breast. Upperparts Mantle, grey (83) with grey-black (brownish 82) subterminal bands and broad pink-buff (121D) fringes to feathers. Back, rump and uppertail-coverts, grey (83-84) with pinkbuff (121D) fringes, slightly paler than on mantle. Underparts Off-white, with diffuse grey (86) patch on sides of upper breast, which joins with patch on sides of neck; all feathers have light buff-brown (buff 223D) fringes. Flanks mottled grey (85-86), grading to grey (85) towards rear-flanks; undertailcoverts, off-white, with pale-grey (86) to whitish-grey bases. Uppertail Rectrices, grey (83-84) with thin irregular subterminal brownish-grey (79–84) bands, broad cream fringes and pink-buff (223D) tips; shafts, grey-black (82). Undertail Brownish grey (brownish 84–85), grading to pale grey (86) on basal quarter; shafts, pale cream (white 92). Upperwing Greater, median and most lesser coverts, grey (83-84) with pink-buff (121D) fringes, like upperparts; smaller lesser coverts, dark brown (119A) with small off-white fringes, which are gradually reduced towards leading-edge, and smallest (leading) coverts are unmarked. Marginal coverts, white, forming white leading-edge extending from base of wing to base of outer primary. Primaries and secondaries, black-brown (119-119A) with brownish-grey (79–119D) wedges on inner webs and, when fresh, faint buff-white spots at tips. Tertials, light grey-brown (119C) with dark-brown (121) subterminal bands and buff-white to pale pink-buff (pale 121D) fringes. Underwing Coverts, off-white, except for mottled grey (84) leading-edge to primary coverts. Remiges, grey (84) with offwhite (white 54) shafts and broad silvery-grey (86) inner edges about half as broad as inner webs; silvery areas broadest and palest at bases of feathers and grading to grey at tip of inner web. P10 has dull-white outer web, grading to grey (84) distally. Tertials and inner secondaries have dull-white fringes. VARI-ANTS: Some uniform grey above, with poorly defined dull-buff fringes to feathers of upperparts; others, uniform sooty grey above, with no paler fringes but with blackish subterminal bars. Head darker, without white streaks on forecrown but still with obscure white forehead and dull-white supercilium.

First immature non-breeding (First basic). Based on one specimen (SAM-B9483), completing moult of wings in Feb. Similar to juvenile. Head and neck Forehead, white. Crown, dark brown (pale 119) finely streaked with white. Nape, dark brown (119) with small white striations. Lores, white, finely speckled dark brown. Upperparts Grey (85) generally greyer than juvenile, and with only a tinge of brown. Fresh feathers of upperparts and upperwings have narrower fringes of pale grey (pale 86), not buff, at tips. Underparts Like juvenile, but less grey (83). Sides of neck and upper breast lack buff fringes. Tail Grey (84) without fringes; to has white basal third of inner web. Shafts, grey-black, with cream bases. Wings Upperwingcoverts, like upperparts. Primaries have broad white wedges in centre of inner webs, as adult. Tertials, thinly edged white.

BARE PARTS Based on photos (Pringle 1987; Olsen & Larsson 1995) and museum labels. Adult Bill, glossy greyblack (82). Iris, black-brown(-). Legs and feet, dark grey (84-83). Downy young Iris, black; no other information for Aust. Extralimitally, bill, legs and feet, black with slight blue tinge (BWP). Juvenile Like adult, but bill, legs and feet sometimes have paler-grey tinge.

Based on 41 specimens (AM, ANWC, HLW, MV, QM, SAM, WAM) and BWP. Adult post-breeding (Pre-basic). Complete. Primaries outwards. Duration 6-7 months. Timing depends on timing of breeding. In populations with 12-month cycle, moult starts while feeding chicks or when young fledged. Usually starts with p1, but moult sometimes starts on face, crown or mantle. After c. 2 months, when PMS c. 20, moult of head and body almost finished, except for some tertials, back, rump and uppertail-coverts. Tail starts soon after primaries, usually fully replaced when PMS c. 40: sequence of replacement: t1-t6-t3-t2-t4-t5; occasionally t6 before t1, or t2 before t3. Moult complete when p10 fully grown; duration of primary-moult, 6-7 months. For information on moult of Seychelles population, with 7.7-8 month breeding cycle, see Diamond (1976) and BWP. Adult prebreeding (Pre-alternate). Partial. Birds that breed annually moult head, neck, mantle, underparts, tail (not always all rectrices, but usually at least t6), some but unknown number of scapulars, back to uppertail-coverts, and upperwing-coverts. Begins when adult post-breeding moult finished, with moult of p10. In populations with cycle shorter than 12 months, probably moult only a few feathers of head, body, t6 and wingcoverts. In WA, usually finish moult of crown on breeding grounds in Nov. Post-juvenile (First pre-basic). Complete. Begins between 3 and 6 months after fledging. Moult crown, face, mantle and t1, then replace rest of head, body and tail. Moult of primaries begins 4-7 months after fledging and finished c. 1 year after fledging. One specimen (SAM B9483) from Feb. had PMS of 46 and was finishing moult of tail and body. Subsequent moults Not known.

MEASUREMENTS (1-2) Aust., adult breeding; sexed using specimen labels; T6 = length of outer rectrix (tailstreamer); T1 = length of central rectrix; Bill D(N) = depth of bill at basal corner of nostril; Bill D(G) = depth of bill at widest point of gonys (AM, ANWC, HLW, MV, QM, SAM, WAM): (1) Aust. except WA; (2) WA.

Walker	IA	MALE	FEMALE	WU]
WING	(1)	268, 270, 271	263.8 (4.54; 258–271; 6)	
	(2)	261.8 (4.66; 256–269; 10)	258.6 (7.5; 250–267; 5)	ns
T6	(1)	175, 186	178, 181, 223	
	(2)	200.5 (11.73; 185–211; 4)	188, 195	
T1	(1)	73, 73, 75	74.7 (3.01; 71–78; 6)	
	(2)	75.1 (4.11; 68–80; 9)	75.4 (4.51; 70–79; 5)	ns
BILL	(1)	40.2, 41.4, 42.6	39.9 (1.49; 37.7–41.4; 6)	
	(2)	40.9 (1.39; 39.2–42.9; 7)	37.6 (0.94; 36.0–38.4; 5)	**
BILL D(N)(1)	9.1, 9.1	8.3 (0.3; 7.8–8.4; 4)	
	(2)	8.7 (0.37; 8.3–9.2; 5)	8.0 (0.5; 7.5–8.5; 4)	ns
BILL D(G	(1)	7.4, 7.6, 7.7	7.4 (0.54; 6.8–8.4; 6)	
	(2)	7.4 (0.39; 7.1–8.0; 5)	6.7, 7.2, 7.4	
TARSUS	(1)	21, 21, 21.5	22.0 (0.51; 21.3–22.6; 6)	
	(2)	21.6 (0.74; 20.2–22.8; 10)	20.7 (0.62; 20.0–21.5: 5)	ns
TOE C	(1)	29.7, 29.8, 30.7	29.4 (2.06; 27.0–32.7; 6)	
	(2)	28.4 (1.16; 26.3–30.0; 9)	27.5 (1.33; 25.7–29.3; 5)	ns

Populations from WA smaller than rest of Aust. (especially in length of tarsus and bill of female), but samples small. In non-breeding plumage, to about 30-40 mm shorter than in adult breeding (BWP).

(3-4) Aust., adults (AM, ANWC, HLW, MV, QM, SAM, WAM): (3) Aust. except WA; (4) WA.

		UNSEXED AND SEXES COMBINED	
WING	(3)	266.4 (6.34; 256–278; 17)	(Previous
	(4)	260.9 (5.57; 250–269; 16)	
T6	(3)	190.4 (15.34; 175–223; 8)	
	(4)	194.0 (13.29; 173–211; 7)	
T1	(3)	75.1 (2.38; 71–80; 17)	
	(4)	75.3 (3.96; 68–80; 15)	
BILL	(3)	40.3 (1.78; 37.7–43.4; 18)	
	(4)	39.6 (2.03; 36.1–42.9; 13)	
BILL D(N)	(3)	8.4 (0.43; 7.7–9.1; 14)	
	(4)	8.4 (0.54; 7.5–9.2; 9)	
BILL D(G)	(3)	7.4 (0.43; 6.8–8.4; 18)	
	(4)	7.3 (0.39; 6.7–8.0; 8)	
TARSUS	(3)	21.8 (0.86; 20.2–23.4; 18)	
	(4)	21.3 (0.78; 20.0–22.8; 16)	
TOEC	(3)	29.4 (1.56; 27.0–32.7; 18)	
	(4)	28.2 (1.31; 25.7–30.0; 15)	

WA birds have significantly shorter wing and middle toe. (5) Aust., subadults: unsexed juvenile (QM) and first immature non-breeding female (SAM).

gailizerd w	loan	UNSEXED JUVENILE	IMMATURE FEMALE
WING	(5)	261	Segons between Brand on
T6	(5)	139	140
T1	(5)	75	Mult of primaines harms
BILL	(5)	35.1	40.4
BILL D(N)	(5)	8.5	8.2
BILL D(G)	(5)	7.1	7.8
TARSUS	(5)	22.1	20.7
TOEC	(5)	28.8	28.7

The juvenile had measurements similar to adult, except for shorter bill and short outer rectrix. The first immature had bill-length like adult but still has short tail-streamers.

WEIGHTS Little Aust. data. Aust., sexes combined, museum labels (AM, ANWC, QM, WAM): Aust. excluding WA, 149.8 (24.8; 128–177; 5); WA, 127.3 (12.42; 112–142; 4). Juvenile, from Brisbane (QM), weighed 75 g.

STRUCTURE Wing, long, slender, pointed. Eleven primaries: p10 longest, p9 4-8 mm shorter, p8 19-28, p7 37-48, p6 59-70, p5 79-94, p4 102-117, p3 122-135, p2 139-154, p1 150–168; p11 pointed, c. 35 mm long, concealed by greater primary coverts; no emarginations. Eighteen secondaries, including five poorly defined tertials; longest tertials extend to p3 or p4 on folded wing. Tail, deeply forked; adults have elongated outer rectrices, forming long tail-streamers; juveniles lack elongated tail-streamers but still have deeply forked tail; 12 rectrices; in adults: t1 shortest, t6 147–101 mm longer, t5 74-56, t4 53-35, t3 24-15, t2 12-5; in one juvenile: t1 shortest, t6 65 mm longer, t5 49, t4 33, t3 19, t2 8. Bill, stout for Sterna, but slender compared with Sooty Tern. Tarsus, similar to that of Sooty Tern but toes proportionately longer (same length as those of larger Sooty Tern). Tarsus, long, slender and rounded; scutellate. Toes, long; webs between front toes, deeply incised; outer toe c. 84% of middle, inner c. 68%, hind c. 31%.

GEOGRAPHICAL VARIATION Slight; four subspecies usually recognized. Small samples suggest WA birds slightly smaller than populations elsewhere in Aust. (see Measure-

ments). Subspecies antarctica of w. Indian Ocean differs from anaethetus by slightly smaller size; smaller black cap; white collar (though worn Aust. birds can have white collar; see Plumages); and paler upperparts and whiter underparts. Outer web of t6 often all-white but outer rectrices similar to nominate anaethetus. Subspecies melanoptera of Atlantic Ocean, paler and smaller still, but otherwise similar to Indian Ocean birds, except for all-white tail-streamers and larger white bases to t4 and t5. Subspecies nelsoni of e. Pacific Ocean, similar to anaethetus, but with paler upperparts, and tail-pattern like that of melanoptera. For further details, see BWP, Olsen & Larsson (1995).

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Bridled Tern *Sterna anaethetus* (page 738) 1 Adult breeding; 2 Juvenile; 3 Adult breeding; 4 Adult non-breeding; 5 Juvenile

Sooty Tern *Sterna fuscata* (page 752) 6 Adult breeding; 7 Adult non-breeding; 8 Juvenile; 9 Adult breeding; 10 Juvenile; 11 Older immature