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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.
Dromadidae	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 (Fjeldså 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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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 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 (prealternate) 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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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 <i>P. albivitta</i> 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

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sumatrana), primaries replaced in staffelmauser, which is interrupted only when breeding; pre-alternate moults possibly lost in these species. Breeding and moult seldom overlap, except for some pre-basic moult of feathers of head when raising chicks (usually in larger or migratory species); in migratory species, most or all moult of remiges occurs in non-breeding areas and post-breeding moult (if started) is suspended during migration. In several species of oceanic terns nesting in Tropics, annual cycles last for less than 1 year, with duration between breeding events possibly dependent on time needed to complete moult (e.g. Ashmole 1962, 1963, 1968).

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.J. 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.¹ 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 *Stema*, distances between nests can be a body-length. 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, DREADS, 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 bergii Crested Tern

Sterna Bergii Lichtenstein, 1823, Verz. Doubl. Zool. Mus. Berlin: 80 - Cape of Good Hope.

Named in honour of Carl Heinrich Bergius (died 1818) Prussian pharmacist and botanist who collected the first specimen of this tern near Cape Town.

OTHER ENGLISH NAMES Swift Tern, Greater or Great Crested Tern, Torres Straits, Yellow-billed and Bass Straits Tern, Diver.

POLYTYPIC Subspecies *cristata* Stephens, 1826, breeds se. Asia, Indonesia, Aust. and central and w. Pacific Ocean, N to Ryukyu and Marcus Is, and E to Tuamotu Arch. Extralimitally, nominate *bergii* breeds Namibia and s. Africa; subspecies *thalassina* Stresemann, 1914, breeds Tanzania; subspecies *velox* Cretzschmar, 1827, breeds Red Sea, Persian Gulf and Indian Ocean, E to n. Sumatra and w. Malay Pen.

FIELD IDENTIFICATION Length 40–50 cm; wingspan 90–115 cm; weight c. 310 g. Large slender sea-tern, with long narrow strongly angled wings, long deeply forked tail, long often decurved bill, and long legs. Very similar in shape and proportions to Lesser Crested Tern Sterna bengalensis but big-

ger and bulkier, with more rakish silhouette in flight. Grey above and white below, with black cap and shaggy crest. At all ages, combination of large size, shaggy crest and yellow bill, diagnostic. Sexes alike. Slight seasonal variation. Juvenile and immatures separable.

Description Adult breeding Upper forehead, crown and nape form black cap, separated from bill by narrow white band across lower forehead; elongated feathers of nape form shagey crest, variously held flattened and slightly drooping or ragged or erect in display. Moult of head starts during breeding season, showing first as white spotting on upper forehead; some acquire extensive white forehead and crown, as non-breeding, while still feeding young. Rest of head and neck, and underparts, white. Upperparts, grey; rump and tail can be slightly paler. Upperwing, grey, as saddle, with narrow white trailingedge and white fringes to tertials; primaries either uniform silvery grey (and slightly paler than rest of upperwing) or outer primaries appear slightly darker, forming faint dusky wedge; can have slightly darker-grey narrow subterminal secondary bar. With wear, dusky-grey wedge on outerwing and dusky secondary bar darken and contrast more, and tertials become darker and browner. Underwing, white, with narrow dusky trailing-edge to outer 5-6 primaries. Bill, yellow to greenish vellow. Iris, dark brown. Legs and feet, black. Adult nonbreeding Differences from adult breeding. Lores and forehead, white, merging to black-spotted crown; on some, much white on forehead and crown, with only sparse dark streaking or mottling. Black mask extends from nape to eye, with varying patch in front of eye and incomplete narrow white eye-ring; grey-black streaks and spots run from lower edge of mask onto rear ear-coverts and, in some, onto sides of neck as half-collar. Upperwing, grey, with dull black secondary bar and wedge on outerwing; during moult, three generations of primaries may be seen; when moult complete, remiges appear almost uniform silvery grey (as fresh adult breeding). Outer few tail-feathers may appear darker than rest during moult. Bill, slightly duller. Juvenile Differ from adult by: Pattern of head much as adult non-breeding but black mask extends to just below eye and, at first, forehead and lores heavily streaked darker, appearing as dark cap streaked with white. Typically have dark spotting on sides of neck and band of dusky streaks and spots running from ear-coverts, often forming half-collar or complete band on foreneck. Upperparts variegated but varying; some very pale, others darker and greyer. Palest birds: Upperparts, white, with varying black marks on saddle and grey-black mottling through centre of rump and uppertail-coverts. Tail less deeply forked than adult; dark grey, with narrow white tip and edges, and with prominent diffuse black subterminal band. Upperwing strongly patterned: innerwing, grey-black, with paler whitish panel across central coverts from scapulars to carpal (marked with varying dark streaks and spots), and broad white tips to greater coverts; inner few primaries and their coverts, light grey, grading to grey-black on outerwing; narrow white trailing-edge to secondaries and inner primaries. Darkest birds: Saddle and secondary coverts, grey to brown-grey, with less contrasting dark marks and narrow white fringes; pale central panel to upperwing dappled with grey and less contrasting. Underparts, as adult. Bill, shorter and weaker at first; from straw-yellow to much duller greyish- or greenish-yellow. Legs and feet, black; sometimes greyish yellow with black spots. Transition to first immature Post-juvenile moult protracted and gradually attain non-breeding appearance. In early stages, as juvenile except: head-pattern, saddle and rump as adult non-breeding; upperwing generally darker, dull black or blackbrown; pale central panel on secondary coverts may become white, contrasting with rest of wing. Later, much as adult nonbreeding but retain dark worn juvenile plumage: outer few rectrices; secondary and cubital bars; and some outer primaries and primary coverts, forming longer blackish wedge on

outerwing. Bill, similar to adult. At first, legs and feet as juvenile; later, black or with some dull yellow. **First immature** (non-breeding and breeding) Much as adult non-breeding. May be separable by: new tertials as adult but with more contrasting dark centres; and new lesser secondary coverts usually darker, forming narrow dusky cubital bar.

Similar species Often confused with Lesser Crested Tern, which differs by: IN ALL PLUMAGES: (1) smaller and slimmer, with shorter legs, and slightly shorter crest; in flight, appear slimmer and more delicate, with proportionately shorter wings giving more compact jizz; (2) shorter, slightly finer and typically straighter, dagger-shaped bill; (3) bill, bright orange or yellow-orange (though bill of adult Crested can appear more yellow-orange when seen in strong light). From FIRST IMMATURE NON-BREEDING: upperparts, slightly paler grey, obvious only in direct comparison. In ADULT BREEDING PLUMAGES: also distinguished by black cap extending to base of bill (separated from bill by narrow white band in Crested). In NON-BREEDING PLUMAGES: best distinguished by colour of bill and differences in size, shape and colour of upperparts. Lesser Crested typically has more and cleaner white on crown, with sharp border with black nape, giving neater, more black-andwhite head-pattern; and no dark spotting on lower ear-coverts or neck. JUVENILES also distinguished by: (1) typically more and cleaner white on forehead and crown; (2) upperparts generally paler, with less contrasting pattern on secondary coverts (cf. more strongly contrasting black-and-white appearance of Crested); and (3) bright-orange feet and tarsi.

Gregarious; seen singly, in small flocks and in large flocks at favoured roosting sites. Coastal; normally inshore, except round offshore breeding islands, though in s. Aust. regularly in shelf-break and slope-waters. Common and familiar large tern of bays and harbours; often seen roosting on pylons, jetties and boats. Often feed and roost with other terns and gulls, especially Lesser Crested Terns in n. Aust., but also forage alone; join mixed flocks of other terns, boobies and shearwaters when feeding. Forage by plunging steeply from several metres above water, often submerging completely; also dip to snatch prey from surface of water; rest on water. Juveniles often seen begging for food from adults well away from colonies, all the time uttering distinctive high-pitched begging call. At rest, carriage horizontal and rather hunched; wing-tips project well beyond tip of tail; gait a high-stepping trotting walk and run. Flight, swift and powerful, with easy deep beats of flexed wings; wings, long and narrow, with outerwing strongly angled, giving rakish appearance. Usual flight call, loud guttural or rasping kerrak or ke-eck; juveniles utter high-pitched see-see notes.

HABITAT Mostly coastal, on exposed ocean beaches or in sheltered embayments, such as bays, harbours, inlets, estuaries and lagoons (Keast 1943; Morris 1975; Gibson 1977; Harris & Last 1982; Pegler 1983; Storr & Johnstone 1988; Peter 1990). Often on offshore islands (Serventy 1935; Norris 1967). Regularly in pelagic waters; off Wollongong, NSW, ratios in inshore, offshore and pelagic waters 1.18:1.61:1.5, though preferences changed seasonally, with more birds in pelagic than neritic zones Apr.–Sept., and more in neritic than pelagic zone for rest of year (Wood 1991). Rarely far inland (Keast 1943), but may move up rivers and creeks (Storr 1980; Gosper 1986); occasionally on coastal saline lakes (Storr 1964b; Morris 1975) and saltponds (Storr 1984).

Feed from surface of sea to ≤ 1 m deep, mainly in inshore waters, and often close to beaches and shores of islands (Wheeler 1947; D'Ombrain 1954; Storr 1964b; Hornsby 1978;

Langham & Hulsman 1986; Smith & Ogilvie 1989; Walker 1992). Also in estuaries and sheltered inlets, sometimes in shallow waters over submerged beds of seagrass (Harris & Last 1982; Peter 1990). Occasionally forage well out to sea (Storr 1964b), and may feed behind boats beyond continental shelf (Wood 1991; Brandis *et al.* 1992). On One Tree I., Qld, mostly forage at sea beyond edge of reef (>50% frequency); less often over reef-flats and in lagoon waters; least often on reef-crest or in reef-breaks; during low tide, mainly feed on seaward edge of reef and in lagoon (Domm & Recher 1973; Hulsman *et al.* 1989). On Eagle I., Qld, most forage in open sea, with smaller numbers on reef-crests; few forage over reef-flats, and virtually none feed inshore (Smith 1993). Dive from heights of 5–8 m, but only penetrate a few centimetres below surface of water (Bossley & Boord 1992). Rarely feed on land (HASB).

Usually roost or loaf on bare flat sandy areas, either near edge of water in exposed intertidal zones, or above high-water mark; on beaches, banks, spits, shoals, islets and cays (Wheeler 1947; Hindwood et al. 1963; Storr 1964b; Hulsman 1977b; Hornsby 1978; Pegler 1983; Peter 1990); also in estuaries and tidal lagoons (Pegler 1983), and, on Rottnest I., WA, on sandy spits in near-coastal salt-lakes (Storr 1964b). Also on rock stacks, exposed reefs (coral or rocky) or wave-cut platforms; among coral or rocky rubble (Storr 1964a,b; Domm & Recher 1973; Hulsman 1974, 1977b; Pegler 1983; Halse & Halse 1988; Morris 1989). Occasionally on artificial structures, such as pylons, jetties and boats, either in harbours or at sea (D'Ombrain 1954; Storr 1964a; Wood 1991). During breeding season roost at colonies (Hulsman 1977b). During calm weather, may rest on surface of sea (Brandis et al. 1992), but during cyclones and storms recorded sheltering on beach, behind coastal sand-dunes and behind rocks and vegetation (Hulsman 1977b; Langham 1986; Dale 1988).

Breed on islands, cays and banks of sand, shells, coral or rock (*Corella Seabird Is Ser.*). Rarely on reefs or in dunes (van Tets 1977; van Tets & Marlow 1977; Bowker 1980; King *et al.* 1985). May be at periphery of island, on beach above highwater mark, or well away from water on higher ground at centre of island (D'Ombrain 1954; Ford 1965; Domm & Recher 1973; Johnstone 1978; King *et al.* 1983). May be located on bare sand or bedrock; among rocks or coral rubble; or on the edge of, or among, low sparse vegetation, including grasses, dicot-herbs and succulents (Campbell 1907; Gillham 1963; Storr 1964b; Hulsman 1977b; Langham & Hulsman 1986; Walker 1992; Corella Seabird Is Ser.); vegetation usually <25% ground-cover (Limpus & Lyon 1981). On Rabbit I., off Eyre Pen., SA, breeding thought to have stopped because vegetation became too dense (Gill 1985). Occasionally on artificial sites, including islands of dredge-spoil (Vincent 1988) or dilapidated jetty (Webster 1947).

Occasionally killed by collisions with wires (HASB) or light-towers (Abbot 1979).

DISTRIBUTION AND POPULATION Widespread round coasts of Indian Ocean and w.-central Pacific Ocean. In Africa, from Walvis Bay, Namibia, in SW, E to s. and e. coasts, Madagascar and islands of w. Indian Ocean, and N to Red Sea and Arabian Pen. From Persian Gulf and Pakistan to India, Sri Lanka, Maldives, Chagos Arch., Malay Pen., Indonesia and Aust. Extend N through Philippines and Indochina, to se. China, Taiwan and s. Japanese islands. Widespread on islands of w. and central Pacific Ocean, from Micronesia, S to New Caledonia, Fiji and Tonga, and E to Tuamotu Arch. (Ali & Ripley 1969; de Schauensee 1984; Urban *et al.* 1986; Pratt *et al.* 1987; Cooper *et al.* 1990; BWP).

Aust. Widespread in all coastal regions of mainland and Tas. (Aust. Atlas). Rarely, up to 150 km inland, usually after gales, e.g. Edenhope, Vic. (Vic. Atlas); Waikerie, SA (Sonter et al. 1984); Mannum, SA (Cox 1973); Northam, WA (Masters & Milhinch 1974); record from Nowingi, nw. Vic. (Hobbs 1968; Sonter et al. 1984) remarkable.

NZ Vagrant. Most records in Wellington region; isolated records from Far North, Firth of Thames and Hawke's Bay (all singles). NI Beachcast, Spirits Bay, Mar. 1951 (CSN 4); mouth of Piako R., Firth of Thames, 30 Mar. 1974 (Habraken 1975); between Westshore and Bay View, 23 Apr. 1981 (Todd 1981); Scorching Bay, Seatoun, 19 Dec. 1981, mid-Nov. 1982 (CSN 30, 31); Petone Beach, 8 Nov. 1982 (CSN 31); Pauatahanui, 20 Mar. 1983 (CSN 31); Paraparaumu Beach, early Apr. 1983 (CSN 31); Waikanae R. estuary, 20 Oct.





1982–13 Mar. 1983, 10 Oct. 1985, 11 Oct. 1987 (CSN 31, 35, 36), Jan. 1995 (J. Hawkins); Pukerua Bay, 19 Nov. 1985, 29 Sept. 1990, 15 Sept.–6 Oct. 1991, 12–14 Sept. 1992 (CSN 35, 39, 41). SI Single, Farewell Spit, 17 Jan. 1960 (Bell 1960).

Lord Howe I. Single, specimen, 13 Feb. 1915 (during severe gale) (Hindwood 1940).

Kermadec Is Single, specimen, Denham Bay, Raoul I., 1 Apr. 1910 (Oliver 1911, 1912; Sorensen 1964).

Breeding Widespread and scattered on islands off e. and s. coasts, from Torres Str. to w. Eyre Pen.; n. and e. coasts Tas., including islands of Bass Str.; coasts of WA, from Daw I., w. Great Aust. Bight, to Bedout I.; off Kimberley coast, from Buccaneer Arch., N to Ashmore Reef and E to Lesueur I.; in Top End from Sandy I. No. 2, off Port Essington, to Round Haul I. and Boucat Bay; and Gulf of Carpentaria, at Low Rock (near Groote Eylandt), Sir Edward Pellew Grp, North Bountiful and Rocky Is. Larger breeding colonies (>1000 nests or pairs) include: QLD: North Bountiful I., Wellesley Is, 13,000-15,000 pairs (Walker 1992); Bramble Cay, 1800 pairs (Elvish & Walker 1991); Eagle I., 1561 eggs (Smith & Buckley 1986); Michaelmas Cay, three colonies containing 3960 nests (King 1985); Lady Elliott I., 3900 pairs (Walker 1986; King 1993); Eshelby I., c. 2560 nests (Walker & Hegerl 1986); One Tree I., 1000 pairs (Langham 1986). NSW: North Solitary I., 7000-8000 pairs (Lane 1974, 1979); Montagu I., c. 1000 pairs (Fullagar 1973; Lane 1979). VIC.: Mud Is, up to 1000 pairs (Menkhorst et al. 1988). TAS.: Georges I., Georges Rocks, c. 2000 pairs (Napier 1979; Napier & Singline 1979); Governor I., c. 2000 pairs (Tas. Bird Rep. 20). sA: South Neptune Is, c. 6000 nests (Stirling et al. 1970); Troubridge I., 2100 pairs in two colonies (1900; 200) (Lashmar 1987); Penguin I., 2000 young, plus eggs, 1966 (SA Bird Rep. 1966–67); West I., 1500 pairs (Aust. NRS); Stonywell I., The Coorong, >1200 chicks (SA Bird Rep. 1970–71); Lipson Cove I., >1000 nests (Aust. NRS). wa: Pelsaert I., Houtman Abrolhos, 1159 nests (Fuller & Burbidge 1992); Six Mile I., c. 1000 pairs (Storr 1987); Gull

Rock, King George Sound, up to 1000 pairs (Kolichis & Abbott 1978).

Populations No estimates of abundance.

Attracted to fishing activities (Wood 1991; Brandis *et al.* 1992; Martin 1992; Walker 1992). Eggs collected on Bramble Cay, Torres Str. (Draffan *et al.* 1983; Walker 1988a, 1992). People disturb Terns at breeding colonies, birds taking flight when people within 20 m, exposing eggs and chicks to predation by gulls (Langham & Hulsman 1986); thought to have been cause of high mortality at Baudin Rocks, SA, in 1978 (Bonnin 1982). Often attacked or killed by cats and dogs

Plate 37

White-fronted Tern Sterna striata (page 632)

1 Adult breeding; 2 Adult non-breeding; 3 Downy young; 4 Juvenile, black-and-white morph (=typical birds); 5 First immature non-breeding, first austral winter; 6 First immature non-breeding in late stage of moult to second immature nonbreeding, first austral spring to second austral summer

Common Tern Sterna hirundo (page 655)

Subspecies longipennis unless stated

7 Adult breeding; 8 Adult breeding, subspecies *hirundo*;
9 Adult non-breeding; 10 Juvenile, moderately worn plumage;
11 Early stage of moult from juvenile to first immature non-breeding, first austral spring; 12 Mid-way through moult from juvenile to first immature non-breeding, late Jan. of first austral summer

Roseate Tern Sterna dougallii (page 621)

13 Adult breeding, while feeding chicks;
14 Adult breeding, developing red bill during incubation period;
15 Adult non-breeding;
16 Downy young;
17 Juvenile;
18 Late stage of moult from juvenile to first immature non-breeding

Black-naped Tern Sterna sumatrana (page 645)

19 Adult; **20** Downy young; **21** Juvenile; **22** Early stages of moult from juvenile to first immature non-breeding; **23** Late stage of moult from juvenile to first immature non-breeding

(Webster 1947; Carrick et al. 1957; ABBBS 1981a; Walker 1988b). Occasionally hit by cars (ABBBS 1971) or bullets (Carrick et al. 1957).

MOVEMENTS Poorly known; throughout range, considered resident, dispersive and partly migratory (Urban *et al.* 1986; BWP). Five subspecies; one, *cristata*, recorded HANZAB region (discussed below). Not known if much movement in or out of Aust. or if seasonal trends in n. Aust. are movements of local or extralimital populations; young from n. Qld colonies recorded New Guinea (Crawford 1980; McKean 1981; see Dispersal of young).

In Aust., considered sedentary, resident, dispersive and partly migratory. In WA, breeding season extended and populations considered sedentary (see Dunlop 1985a) or resident (Storr 1964a,b; Johnstone & Storr 1994), though birds in first and second years recorded moving long distances, e.g. runner banded Rottnest I. recovered 500 km NNW in second year (ABBBS 1982b); some movements evidently dispersive and related to availability of food, e.g. at Bunbury, numbers increase when small fish apparently move into area (Whitlock 1939). In many parts of e. Aust. breeding seasons shorter, with most of population dispersing from colonies after breeding (see Smith 1993), e.g. Lizard and One Tree Is, Qld (Domm & Recher 1973; Domm 1977; Hulsman 1983). Banding at colonies in Vic. suggests partial migration or dispersion from colonies, with some birds staying near colony and others moving long distances (Minton 1992). Despite banding evidence. reporting rates in Vic. do not suggest any regular long-distance movements (Vic. Atlas). In Aust., accidental away from coast (see Distribution); some inland records associated with bad weather (Watson 1955; Masters & Milhinch 1974).

Departure In e. Aust., at least some move from colonies after breeding: on Montagu I., NSW, chicks fledge late Dec. and early Jan., and birds present at colonies till Jan. (Fullagar 1973); present on Big. I., NSW, till Feb. (Gibson 1976); on One Tree I., Qld, most adults and their young have left by end Feb. (Hulsman 1979). Near Lizard I., Qld, numbers gradually decrease from Jan., after breeding (Domm 1977). Parents accompany and feed flying young for several weeks after leaving colonies (Carrick *et al.* 1957; Langham & Hulsman 1986). Some disperse rapidly: in NSW, adults recorded moving up to

Plate 38

Common Tern Sterna Hirundo (page 655) subspecies longipennis unless stated

Adult breeding, fresh plumage, austral autumn;
 Adult breeding, subspecies *hirundo*, worn plumage, boreal summer;
 Adult non-breeding, early Jan.;
 Juvenile, moderately worn plumage;
 Mid-way through moult from juvenile to first immature non-breeding, late Jan. of first austral summer

White-fronted Tern Sterna striata (page 632)

6 Adult non-breeding; 7 First immature non-breeding, first austral winter; 8 First immature non-breeding in late stage of moult to second immature non-breeding, first austral spring to second austral summer

Roseate Tern Sterna dougallii (page 621)

9 Adult breeding; 10 Early stage of moult from juvenile to first immature non-breeding; 11 Late stage of moult from juvenile to first immature non-breeding

Black-naped Tern Sterna sumatrana (page 645)

12 Adult breeding; 13 Early stage of moult from juvenile to first immature non-breeding; 14 Late stage of moult from juvenlie to first immature non-breeding

c. 230 km within a few weeks of banding; one adult banded Five Is sighted Melbourne, Vic., by May (Carrick *et al.* 1957). Subsequent movement into non-breeding areas: fledged young being fed by adults at Richmond R. estuary, NSW, from late Feb.; near Ballina, NSW, from mid-Jan. (Gosper 1981, 1983). At some non-breeding areas maximum numbers recorded after dispersal from breeding colonies (e.g. at Laverton, Vic., Mar.– Apr., Watson 1955).

Non-breeding Adults and young from different colonies mix during non-breeding season (Carrick *et al.* 1957). In e. Aust., some adults occur far from breeding areas in non-breeding season, e.g. adult breeding SA found dead 830 km SE in Vic. in Apr. (ABBBS 1982a) and adult breeding SA recovered 840 km away in Vic. in Mar. (ABBBS 1982c). Chicks banded Vic., 1979–92 recovered in second or subsequent years during non-breeding period (Mar.–Sept.) in Vic., NSW, s. Qld and SA (Minton 1992).

In some areas where breeding not recorded, present throughout year (e.g. off Sydney, and estuaries of Hunter and Richmond Rs; Milledge 1977; Gosper 1981), though greatest numbers may occur in non-breeding season (e.g. Richmond R. estuary, Mar.–Sept.; Gosper 1981). In some areas, no obvious seasonal patterns of abundance (e.g. off Wollongong, NSW; Wood 1991). On some islands where seasonal breeding occurs, present all year, though numbers lower during non-breeding season (e.g. Lizard I., One Tree I., Michaelmas Cay; Domm & Recher 1973; Domm 1977; King 1985).

Return At non-breeding sites, numbers drop as birds return to breeding colonies, e.g. at Laverton, Vic., after early Nov. (Watson 1955), in Geelong district, Vic., about Oct., though some remain throughout year (Belcher 1914). Aug. influx to Long Reef, Sydney, NSW, possibly flocking before s. movement to breeding grounds; numbers at Long Reef and Botany Bay, Sydney, high into Nov. when already breeding at nearest colony (Hindwood 1942; Carrick et al. 1957). Before breeding, first return to pre-breeding gathering sites, which may be up to 40 km from breeding sites (Dunlop 1985a), though often much less (e.g. only 200 m, Langham & Hulsman 1986). Numbers increase at colonies before breeding: on Eagle I., Qld, numbers increase Nov.-Dec. (Smith & Buckley 1986; Smith 1989); near Lizard I., Old, sharp increase in numbers. Nov. (Domm 1977); on One Tree I., Qld, begin to arrive Sept., occurrence sporadic till 19 Nov., and maximum numbers, early Dec. (Langham & Hulsman 1986). On Montagu I., NSW, normally arrive from beginning July till end Aug. (North); at Montagu and Big Is, NSW, present in colonies from Sept. (Fullagar 1973; Gibson 1976).

Breeding In waters of se. Aust., most records inshore near breeding sites (Aust. Seabird Atlas). Of birds banded as chicks, 1979–92, three recovered during breeding period (Oct.– Feb.) when 2+ years old, all within 100 km of natal area (Minton 1992). Some adults occur away from breeding colonies during breeding season, e.g. adults have been recorded *c*. 175 km from breeding site of previous season (Carrick *et al.* 1957). Some banded as chicks on Penguin I., SA, recovered as adults on e. coast, N of 30°S, Nov. (Purchase 1973).

In at least some areas, faithful to local area rather than specific colony. Off Fremantle, WA, use a number of traditional breeding sites within area; colour-marked birds, including successful and unsuccessful breeders in previous season, switched colonies from year to year. However, high fidelity to local area, with 94–95% of birds marked at nests sighted following year (Dunlop 1985a). Tendency for main colony sites to at least sometimes change between years (e.g. Carrick et al. 1957; Liddy 1964, 1968), and so sometimes absent from breeding sites for 1 or more years (Lane 1979). On Egg I., Tas., apparently bred in alternate years (van Tets 1977). On some islands, breeding considered irregular, e.g. South Solitary I., NSW; Korffs I., NSW; Carnac I., WA (Lane 1975, 1976; Dunlop & Storr 1981). Breed annually at some colonies, e.g. Mud Is, Vic. (Menkhorst et al. 1988), though position of colonies, number breeding and peak period of laving can vary (e.g. Big I., NSW, Gibson 1976; ne. Tas., Liddy 1964, 1968). Variation in numbers breeding and locations of breeding leads to claims of nomadic breeding populations (e.g. King 1993); banding suggests strong fidelity to natal area of breeding adults (e.g. Dunlop 1985a). Liddy (1968) suggests nomadic breeding groups from NSW and Vic. might occasionally augment and breed with more sedentary Tas. breeding population, but without good evidence (see Thomas 1969).

At least some birds return to natal colonies (e.g. ABBBS 1970b), sometimes years after banding (e.g. ABBBS 1980). Also recorded breeding short distances (mostly <110 km) from natal colonies (e.g. ABBBS 1968, 1970a, 1972a, 1980), though some banded adults breeding Vic. came from SA (Vic. Atlas). At least some adults breed at same colony in consecutive years (Carrick et al. 1957) and some banded as breeding adults recovered years later breeding at same site (e.g. 12 years after banding, ABBBS 1980). Some adults breed in different colonies in consecutive years, e.g. in NSW, two adults bred at Five Is colony in 1955 and c. 125 km away at Montagu I. colony in 1956 (Carrick et al. 1957); colour-marked breeders changed breeding sites from Carnac I. to Rottnest I., WA (Dunlop & Storr 1981); one banded as a breeding adult in 1959-60 season recaptured breeding 80 km away in 1971-72 season (ABBBS 1972a).

At some colonies, numbers vary during breeding season, e.g. at Rottnest I., WA, marked seasonal pattern of numbers present, with both annual maximum and minimum occurring during breeding season (Saunders & de Rebeira 1993). In WA, breeding areas sometimes occupied by different breeding subpopulations within a breeding season, e.g. on Carnac, Rottnest and Seal Is, autumn, winter and spring nesting groups in population (Dunlop & Storr 1981; Dunlop 1985a, 1987). Foraging range of breeding adults, not known (Carrick *et al.* 1957); on Great Barrier Reef, most forage within 3 km of colony but some venture up to 11 km away (Hulsman 1983, 1988).

Dispersal of young Some remain near natal colony in first and second years (e.g. Carrick et al. 1957). Others disperse, some moving long distances soon after fledging, e.g. nestling banded SA recovered 19 days later in Vic., 575 km away (ABBBS 1983) and chick banded Vic. recovered 1062 km NE 7 weeks after banding (Minton 1992). Dispersal of first-year birds from NSW island colonies well studied: recorded on coast in Jan.; had dispersed c. 400 km from colony by Feb.; to c. 960 km by about May (Carrick et al. 1957). Maximum movements of SA chicks: 512 km within 2 months of banding (ABBBS 1987), c. 1570 km within 3 months (ABBBS 1970c), 1815 km within 4 months (ABBBS 1972b), 1840 km within 6 months (ABBBS 1962, 1966). Young apparently disperse in all directions along coasts (Carrick et al. 1957; ABBBS 1977; Minton 1992); some Vic. and SA birds cross Bass Str. in first year (Purchase 1973; Minton 1992). Of chicks banded at Vic. colonies 1979-92 and recovered within 3 months, 76% (n=25) were recovered ≤ 100 km from natal colony; some dispersed W up to 211 km (n=3), one moved 284 km S to Tas. and two moved >1000 km to NE (Minton 1992).

In WA, many young appear to remain near colony (e.g. Carrick et al. 1957), but some disperse, e.g. recovery of nestling banded Rottnest I., 1150 km N within 5 months of banding (ABBBS) 1985). Some nestlings banded n. Qld recovered within 2.5 months in PNG (ABBBS 1981b, 1986, 1990). In Vic., 1979-92, at least some young spent first non-breeding season (Apr.-Sept.) close to natal colony; others recovered from as far away as s. Old (Minton 1992). Some young also remain away from colonies in breeding season after they hatched (e.g. ABBBS 1964, 1965); chicks banded Penguin I., SA, recovered up e. coast, even N of 30°S, in breeding period after hatching (Purchase 1973). Of birds banded as chicks in Vic. 1979-92 and recovered during following breeding season (Oct.-Feb.), some remained in non-breeding range, with recoveries as far away as NSW coast, but birds tended to move closer to natal area in first summer (Minton 1992); some even recovered breeding at natal colony in breeding season after being banded as chick (ABBBS 1968).

Banding Substantial; see details above. Longest movement: nestling banded Tas. recovered 1939 km N in Qld within 8 months (ABBBS 1987).

FOOD Carnivorous; mainly fish; occasionally prawns and squid. Behaviour Diurnal (Domm & Recher 1973). Mainly forage inshore; on Great Barrier Reef, most forage within 3 km of colony but some venture up to 11 km (Hulsman 1983, 1988). On One Tree I., use all identified foraging zones, though mostly in open sea, reef-flats and lagoons (Hulsman et al. 1989). On Eagle I., Qld, 47% of foraging time spent on reefflats and edges, 53% on open sea (Smith 1989). Mainly feed by PLUNGING from 7-10 m, diving head or feet first; submerge completely (SHALLOW PLUNGING), diving up to 50 cm below surface (Hulsman 1977a). Shiver in flight after re-emerging (Wheeler 1947). Sometimes feed opportunistically, following schools of small fish forced to surface by feeding gamefish (Domm & Recher 1973) and dolphins (Bossley & Boord 1992). Observed skimming, often with fish in bill, possibly cleaning it (Hulsman 1974). Take large fish from nets (HASB). Take offal thrown from boats (Wood 1991) and, in Moreton Bay, large proportion of diet comes from trawl bi-catch, especially those species that float after death (Blaber & Wassenberg 1989; Wassenberg & Hill 1990). Commonly steal food from other Crested Terns, especially at colonies; also, often have food stolen by gulls, herons and other species of terns (Domm & Recher 1973; Hulsman 1974, 1976, 1984, 1986; Smith 1989, 1991). Tend to forage on rising tides, especially in early morning or late afternoon (Hulsman 1977a). Recorded scavenging food discarded from prawn trawlers at night (Wassenberg & Hill 1990). Composition of diet changes with tidal cycle, and with season as different prey become available (see Hulsman et al. 1989). Overall foraging success 16.5%; birds made 79 dives in 103 min, catching 13 fish at a rate of 0.8 dive/min and 0.13 fish/min (Hulsman 1977a).

Adults In Moreton Bay, Qld (68 pellets, 130 items; Blaber & Wassenberg 1989): Plants: macrophytes 0.1% wt, 0.8% no. Animals: Molluscs: cephalopods: Sepiidae: Sepia 0.6, 1.5. Fish: Apogoniidae: Apogon fasciatus 15.0, 34.6; A. poecilopterus 1.1, 1.5; Ariidae: Arius 1.1, 1.5; Atherinidae: Atherinomorus lacunosus 0.8, 2.3; Callionymidae: Callionymus 0.1, 0.8; Clupeidae: Herklotsichthys 1.4, 0.8; Engraulididae: Stolephorus carpentariae 0.1, 1.5; Gerridae: Gerres ovatus 1.7, 0.8; Leiognathidae: Leiognathus moretoniensis 5.4, 24.6; Platycephalidae: Inegocia harrisii 0.2, 0.8; Plotosidae: Plotosus anguillaris 4.4, 0.8; Sciaenidae: Johnius australis 21.2, 9.2; Sillaginidae: Sillago maculata 46.5, 16.1; Terapontidae: Pelates quadralineatus 0.4, 2.3.

On Lizard I., Qld (1400 food items collected Jan. 1992-Aug. 1993; S. Blaber): Molluscs: cephalopods: Ommastrephidae: Stenoteuthis tr.; unident. 0.2% freq. Crustaceans: decapods: crabs 0.1; Alphaeidae tr.; Penaeidae: Penaeus latisucatus 0.1; P. plebejus 0.1; Metapenaeus endevouri tr.; unident. tr.; Callianassidae: Callianassa 3.0; isopods tr.; stomatopods tr. Fish: Apogonidae 7.0; Atherinidae: Atherinomorus lacunosus 0.7; Carangidae: Caranx 0.5; Herklotsichthys quadrimaculatus tr.; Megalaspis cordyla tr.; Clupeidae: Amblygaster sirm 63%; Spratelloides delicatulus 0.2; unident. 0.2; Gerreidae 0.5; Gobiidae 14.0; Hemiramphidae 0.1; Labridae: Choerodon 0.7; Halichoeres tr.: Stethojulis strigiventer tr.; Pomacentridae: Pristotis jerdoni 0.5; unident. 2.0; Pseudochromidae: Pseudochromis tr.; Sillaginidae: Sillago 0.6; Terapontidae tr.; Tetraodontidae: Anchisomus mullistriatus tr.; unident. teleosts 4.0. Reptiles: Agamidae lizard tr.; Green Turtle Chelonia midas hatchlings 0.4.

On **One Tree I., Qld** (obs., regurgitations and items dropped, Dec. 1974, Jan. 1975; Hulsman *et al.* 1989): Molluscs: cephalopods (including squid) 10.4% freq. Dec. 1974, 10.1% freq. Jan. 1975; Fish: silver species (Atherinidae, Clupeidae, Engraulididae, Hemirhamphidae and Scombridae) 52.0, 37.9; Blenniidae: Atrosalarias fuscus 2.6, 0.7; Carangidae 2.2, 1.95; Exocoetidae 5.4, 5.55; Gobiidae 3.0, 1.35; Labridae 6.2, 2.5; Monocanthidae: Monacanthus filicauda 5.3, 10.9; Pomacentridae: Abudefduf coelestinus 2.3, 2.7; Scaridae: Scarus niger 0.9, 1.7; Tetraodontidae Arthron stellatus (pre-juvenile) 9.7, 24.7. Further details of size of prey in Hulsman (1977a) and Hulsman *et al.* (1989).

On islands off Fremantle, WA (337 obs.; Dunlop 1986): Fish: Clupeidae: Sardinops neopilchardus 40.9% freq.; Hyperlophus vittatus 1.2; Spratelloides robustus 19.9; Kyphosidae: Kyphosus imm. 15.4; Hemiramphidae: Hyporhamphus melanochir 0.6; Carangidae: Pseudocaranx imm. 0.3; Seriola hippos imm. 0.3; Gerreidae: Gerres subfasciatus 0.3; Atherinidae: Pranesus ogilbyi tr.; Isonidae: Iso rhothophilus tr.; Labridae: Halichoeres brownfieldi 1.8; Monocanthidae: Acanthaluteres spilomelanurus 0.6; Clinidae: Heteroclinus roseus 0.3; Pemphiridae Parapriacanthus elongatus tr.; Veliferidae: Velifer multiradiatus larv. tr.; unident. fish 18.1.

Other records CRUSTACEANS: euphausids (Le Souëf 1926). INSECTS: Coleoptera: Scarabaeidae: Onthophagus; Diptera: Coelopidae larv.; Hymenoptera: Formicidae: Camponotus (McKeown 1944; Jenkins 1969). FISH: Acanthuridae; Anguillididae; Arripidae: Arripis geogianus (11.4 cm); Clupeidae: Hyperlophus vittatus; Sardinops neopilchardus; Spratelloides robustus (5.1–6.4 cm); Diodontidae; Lutjanidae; Mugilidae; Scombridae: Pneumatophorus australasicus young; Sphyraenidae; Terapontidae; Anguilliformes (MacGillivray 1914, 1917; Le Souëf 1926; Serventy 1939; Keast 1943; Wheeler 1947; D'Ombrain 1954; Watson 1955; Bedggood 1970; Milledge 1977; Hulsman 1977a; HASB; FAB). REPTILES: turtle eggs, young (MacGillivray 1917; HASB). Trawl spill, offal, fat (Milledge 1977; Wood 1991).

Young Adults feed young by regurgitation, or carry fish (usually one, up to five) to young in bill; remove long spines before swallowing fish to be fed to young (Domm & Recher 1973; Hulsman 1977a). Smaller fish fed to younger chicks (Hulsman *et al.* 1989; Smith 1989). On Eagle I., length of fish given to young \leq 7 days old, 50–100 mm; \geq 7 days old, 75–100 mm (Smith 1993). Young still fed after able to fly. Juvenile birds feeding with parents tend not to submerge completely when diving (Feare 1975).

On One Tree I., Qld (153 regurgitations and dropped items; * = specimens measured without heads; Domm & Recher 1973): Molluscs: cephalopods: squid 0.7% no. Crustaceans: prawns: Penaeidae: Penaeus caesius 1.3% no. (6-10 cm long). Fish: unident. 1.3; Carangidae: Caranx sexfasciatus 0.7 (8 cm); Eleotridae: Eleotriodes strigatus 0.7 (6 cm*); E. longipinnis 0.7 (>10 cm); Engraulididae: Engraulis 13.1 (2-10 cm^{*}); E. australis 24.8 (2-10 cm*), 20.2 (2-8 cm); Exocoetidae: Parexocoetus brachypterus 4.6 (8–10 cm*); Carangoides 0.7 (8 cm*); Labridae: unident. 0.7 (8-10 cm^{*}); Stethojulis axillaris 2.0 (8-10 cm); S. strigiventer 0.7 (8 cm); Monocanthidae: Arotrolepis filicauda 7.8 (6-10 cm); Cantherines fronticinctus 0.7 (6-8 cm); Pomacentridae: unident. 0.7 (8 cm); Pomacentrus 0.7 (>10 cm^{*}); Scaridae: unident. 0.7 (>10 cm); Scarus 0.7 (>10 cm); Scombridae: Euthynnus affinus 15.0 (6->10 cm); Tetraodontidae: Arothron hispidus 0.7 (10 cm); Lagocephalus 0.7 (6 cm*); L. sceratus or luvase 0.7 (6-8 cm). On Lachlan I., Tas. (24 regurgitated items; Harris & Last 1982): Molluscs: cephalopods: squid 4.2; Crustaceans: parasitic isopod 4.2; Atherinidae: Atherinosoma microstoma 4.2; A. presbyteroides 12.5; Atherinason hepsetoides 8.3; Engraulididae: Engraulis australis 4.2% no.; Monacanthidae: Acanthaluteres spilomelanurus 25.0; Mugilidae: Aldrichetta forsteri juv. 4.2; Odacidae: Neodax attenuatus 4.2; N. balteatus 16.7; Pencipelta vittiger 12.5. Items ranged from 80 to 130 mm in length. On Eagle I., Qld (53 regurgitated items; Smith 1989, 1993): Crustaceans: decapods: prawns 6% freq.; Fish: Clupeidae 58. Also (% freq. estimated from graph): Fish: Carangidae 9% freq.; Pomacentridae 8; Exocoetidae 5; Mugillidae 6; Labridae 4; Tetraodontidae 4.

Intake Average length of food, 98.5 mm (Hulsman 1981). However, size of prey varies daily, seasonally and annually (Hulsman 1977a). In Moreton Bay, Qld, mean length of fish 83 mm (21; 33–226; 130), weight 19 g (12; 0.4–84.6; 130) (Blaber & Wassenberg 1989). At Fremantle, WA, length of fish, 20–180 mm, modal size 100–120 mm (Dunlop 1986).

SOCIAL ORGANIZATION Account based mainly on studies by K. Hulsman in Aust. and published in BWP (references to BWP below refer to these studies); for extralimital information, also see BWP. Solitary or gregarious; generally seen singly, in pairs or small groups; occasionally larger groups (1000s) (e.g. Warham 1962; Stirling et al. 1970; Lane 1984). Flocks and gatherings of various sizes recorded feeding or roosting, e.g. up to 1200 (Gosper 1981), 1400+ (M. Walker), <700, up to 1600+ (Gosper 1983). Some evidence of segregation of ages: at Laverton, immatures up to 80% of maximum autumn numbers (Watson 1955). In Qld, arrive at breeding islands in small groups (Hulsman 1977a). Before laying, gather in Clubs (see Roosting, Sexual behaviour). Associate with other terns, gulls and, sometimes, cormorants (Wheeler 1946; Watson 1955; CSN 30, 31; Aust. NRS); seen roosting with Roseate Sterna dougallii, Black-naped S. sumatrana and, especially, Lesser Crested Terns (Hulsman 1977a). Also seen feeding in mixed flocks (Domm & Recher 1976) with shearwaters Puffinus (Dunlop 1986), Black Noddies Anous minutus, and Roseate and Bridled S. anaethetus Terns (Hulsman 1977a); often seen following Bottle-nosed Dolphins Tursiops truncatus herding mullet (Bossley & Boord 1992).

Bonds Monogamous; pair-bond sometimes lasts from year to year, and maintained during year (Dunlop 1985a). Birds from same nesting group may pair, possibly to match their reproductive cycles (see Dunlop 1985a). Age of first breeding usually 2 years old (BWP), or 3 years or more

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(Langham & Hulsman 1986; Dunlop & Wooller 1990), but recorded breeding when 1 year old (ABBBS 1968; Purchase 1973). In breeding condition for 11-13 weeks each season (Dunlop 1987). Parental care Both sexes select site, incubate, and brood, feed and care for young (Hulsman 1977a; Smith 1989; BWP). Young ready to leave nest when 2-5 days old (Davies & Carrick 1962; Hulsman 1977a; Dunlop 1986), but may stay in nest till 3 weeks old (Domm & Recher 1973); after this, leave nesting area (Dunlop 1986) escorted by adults (Hulsman 1977a). Young sometimes form crèches till old enough to fly; otherwise, chicks scatter through colony, with one parent looking after each chick (Reithmüller 1931; Domm 1977; BWP). Crèches of up to c. 300 young recorded (Domm & Recher 1973); chaperoned by several adults, though chicks fed only by own parents (BWP). Loose groups attended by single adults also observed (Hulsman 1977a). About 1 week after able to fly, juveniles accompany parents to foraging areas. On One Tree I., some juveniles, with their parents, left colony 13-19 days after fledging (Hulsman 1977a). Parents continue to feed young for varying time after fledging; probably for at least 4 months (Dunlop 1985a, 1986).

Breeding dispersion Nest in dense colonies (Smith 1989); rarely as isolated pairs (Aust. NRS). Colonies range from small groups, such as three pairs with four pairs of Lesser Crested Terns, to many thousands of pairs, sometimes consisting of many small sub-colonies close together (e.g. seven colonies, each of c. 100 pairs, c. 50 m apart) (Cooper 1948; Stirling et al. 1970; King & Buckley 1985; Walker 1992; Aust. NRS); largest recorded colony 13,000-15,000 nesting pairs (Gulf of Carpentaria) (Walker 1992). Pairs and single birds preferred to nest near other incubating Crested Terns, but large flocks preferred to settle in other areas (Dunlop 1986, 1987). Within large colonies, older nests found at centre, with progression of nesting stages radiating outward; small colonies often have spatially distinct groups of synchronous nests (Dunlop 1986; see Flock behaviour). Sites of colonies to some extent traditional, though breeding at some colonies may be irregular. Show high fidelity to local area and at least some return to natal colonies. However, individuals have no permanent attachment to site or colony and birds re-laying within season may move (Domm 1977; Hulsman 1977a; Dunlop & Storr 1981; Dunlop 1985a, 1986, 1987; see Movements: Breeding for more details). When associated with other nesting seabirds (see Breeding), usually form one or more distinct and compact groups (e.g. Keast 1943; Skira & Brothers 1987; Aust. NRS). Nesting density varies with locality and year and within colonies. Distance between nests at least partly determined by behaviour: if neighbours face each other while making scrape, distance at least 30 cm, but closer if orient themselves at right angles (BWP). On One Tree I. in some years, neighbouring birds can touch bills; in others, density only 0.97-1.04 nests/ m² (Hulsman 1977c); on Eagle I., 6.3 nests/m² and some birds able to touch bills of neighbours (Smith 1989); in sw. Aust., nests closely packed (0.3-0.5 m apart) (Dunlop 1986; also see Dunlop 1987); on Lancelin I., WA, in 1975, >115 nests in 36 m², 30-43 cm apart where density highest, and, in 1976, 99 nests in 50 m² (Aust. NRS); on Five Is, WA, average 1.3 m between nests (Keast 1943); on Rottnest I., WA, average 35.6 cm (n=6) between nests (Campbell); at Pt Cloates, nw. WA, 14 nests within radius of c. 1 m (North). On South Neptune I... SA, average distance between nests in centre of colony, 31 cm (4.9; 59), and at edge of colony, 33 cm (5.0; 43) (Stirling et al. 1970); on One Tree I., same trend observed, with average distance between nests 33-36 cm in centre of sub-colonies and

39–44 mm on perimeter (Langham & Hulsman 1986). Territories Defend small, roughly circular territory round nest; generally 0.03–0.13 m². Off-duty bird usually loafs outside, though near, its territory, especially if territory small (i.e. distance to nearest neighbour <30 cm) (BWP). A few birds defend feeding territories against other Crested Terns, chasing some of those that caught fish (Hulsman 1977a). Home-range Most said to hunt within 3 km of colonies but may venture up to 11 km away (Keast 1943). During breeding season in sw. WA, feed inshore (Dunlop 1986); in Qld, forage at sea or near reef (Hulsman 1977a; Smith 1989); tend to feed farther offshore than Black-naped Terns, though feeding ranges overlap considerably (Smith 1993).

Roosting Foraging and resting routines possibly vary individually (Hulsman 1977a). Throughout day, especially early evening (from 16:30), sometimes before 07:00 (Buchanan 1991); tend to loaf in early afternoon (Smith 1989); by day, loaf on shore between foraging bouts, especially at times less suitable for fishing (Hulsman 1977b). On One Tree I., maximum number of Terns present just before high tide (Hulsman 1977a). Roost at night (Limpus 1980) but forage or active for 2 h after dark (Dunlop 1986; Smith 1989). Roost in tight flocks of up to at least 1600 (Gosper 1983) but often fewer; with other terns, specially Lesser Crested Terns, and gulls (Warham 1962; Storr 1964a,b; Child 1982; BWP). If nesting, most congregate in nesting area (Hulsman 1977a). At sea, rest on water (Brandis et al. 1992). At start of breeding season, roost at traditional pre-breeding site, Club, near colony; Club becomes centre of interactive behaviour, with displays by whole group and between prospective mates, including start of aerial and ground courtship, and copulation (Dunlop 1986. 1987; BWP). Chicks sometimes lie in parents' shadow or near coral boulder (Hulsman 1977a).

SOCIAL BEHAVIOUR Reasonably well known. Account based mainly on observations from One Tree I. (Hulsman 1977a; BWP); for extralimital details see BWP. Flock behaviour First bird in colony to detect danger gives Alarm Call (if on ground, accompanied by Aggressive Upright) and flies up; alerted neighbours then take flight and wheel overhead (Alarm). DREADS, PANICS OF MASS FLIGHTS OCCUF, as in Common Tern Sterna hirundo (see BWP) but only in pre-breeding Clubs (Hulsman 1977a; BWP). In Mass Flights observed by Dunlop (1986), part of flock would fly up and away from Club, calling noisily. At first, birds return to area after flight (Hulsman 1977a). Later in season, some pairs, trios or groups of 4-5 break away to participate in courtship flights and return gradually to Club in pairs or small groups; often followed by ground displays and copulation. Maximum number of Mass Flights recorded 12-16 days before start of laying; stop when colonies established (Dunlop 1986) (also see Sexual behaviour). Settlement of colony observed at L. Baghdad Isl., on Rottnest I., WA (Dunlop 1987): 12 days before laying, flock of 50 hovered over site in tight group but left without landing; next day, behaviour repeated, but birds landed then left after 45 min; pattern repeated on successive days, birds settling in same area each time; birds did not reoccupy island at any other time on these days; at site, some pairs could be identified and some nest-building displays (STOOPING, FIXATING and SCRAPING; Veen 1977), brooding movements and threat displays observed. One record of colony moving at start of laying, with 6–7 pairs abandoning eggs (see Dunlop 1987). Breeding within some colonies highly synchronous; others have greater synchrony within sub-colonies (Noske 1974; Hulsman 1977a; Dunlop

1986; Langham & Hulsman 1986); see Breeding. Comfort behaviour At Bremer Bay, WA, always bathe in shallows next to roost after arrival. Vigorously duck head under water, at least 20 times, splashing wings and preening between duckings. After this, birds join roost to preen, then settle. Usually only two bathe at same time, newly arrived birds waiting till one bathing bird leaves. At times, two groups have formed separate roosts, each with adjacent bathing spot (Buchanan 1991).

Agonistic behaviour Ground behaviours well developed but, as in related 'crested' terns (e.g. Sandwich Tern Sterna sandvicensis), aerial attack poorly developed compared with other Sterna (see Cullen 1960). Much bickering occurs in dense colonies, especially between neighbours with minimum distance between nests (Hulsman 1977c); often two Terns fight with bills while on nests. Steal food from other Crested Terns; more often later in season when young present (Smith 1989). Food also often stolen by Silver Gulls and, occasionally, Roseate Terns (Hulsman 1977a; see Food). In WA, often fight with Sooty Terns with which they nest (Serventy 1959). Adults aggressive to strange chicks, vigorously pecking any that stray too close to own young, so often scatter other chicks in crèche before feeding their own. Chick that does not escape often grabbed by nape (BWP). Threat While incoming birds hover overhead looking for a place to land, birds below point bills up at them and raise crests in threat (Warham 1956). Aggressive bird adopts intimidating AGGRESSIVE UPRIGHT posture (Fig. 1) (Tinbergen & Broekhuysen 1954) in which plumage on stretched neck ruffled, bill pointed down, and carpal



Figure 1 Aggressive Upright posture

joints and crest raised; maintaining posture, may charge opponent (BWP). HEAD-BOBBING: head and neck bobbed up and down; indicates heightened threat (BWP). Fighting Incubating birds duel with bills, and give Gakkering Call (Hulsman 1977c). Standing birds may fight in Aggressive Upright, giving Gakkering Call (BWP). Appeasement Adults challenged or attacked on ground may appease by sidling away in ERECT POSTURE (Fig. 2): neck stretched, bill pointed vertically upwards, crest and plumage of body sleeked, wings held out, and wing-tips sometimes held below tail, touching ground; this indicates high tendency to escape (Tinbergen & Broekhuysen 1954). Alarm See Flock behaviour and Parental anti-predator strategies.



Figure 2 Erect Posture

Sexual behaviour Courtship similar to that of Sandwich Tern (Smith 1989). Birds in breeding plumage begin to gather up to 2 months before laying (Dunlop 1986). Pair-formation, courtship and copulation concentrated in pre-breeding Club

usually 80 m to 8 km from prospective breeding colony (Gibson 1956; BWP) but up to 20-40 km (Dunlop 1986). Flocks observed visiting future colony site up to 12 days before laying (Dunlop 1987), though pairs said not to frequent nesting area until clutch about to be laid, and that birds may enter colony. establish nest-site and lay within 1 day (BWP; see Flock behaviour). Courtship Occurs in air and on ground. Aerial courtship Courtship flights become more common just before nesting; frequency of courtship flights decreases as more Terns nest, but increases after first chicks fledge; display still occurs after many adults with young have left (Hulsman 1977a). Usually elicited by unpaired male arriving at pre-breeding roost, uttering Advertising Call (with or without fish in bill); bird often uses BUTTERFLY FLIGHT: slow and emphatic flight, with unusually deep wing-beats (BWP). Bird's arrival often precipitates Dread; thereafter, bird with fish either attracts no further attention, or is chased, sometimes by several birds, which it tries to evade by twisting, turning and swooping; when pursuer overtakes bird with fish (PASS CEREMONY), pursuer extends neck (aerial version of Erect Posture) and sways from side to side in front of bird with fish, which may give Karr Call. As pre-breeding period progresses, Dreads increasingly lead to High Flights and to courtship displays on ground (see below); High Flights may originate directly from Dread, without intervening courtship on ground, or from courtship on ground. HIGH FLIGHT: one bird (usually male) generally carries fish; if initiated from ground, male, without noticeable inviting posture, takes off, followed by female (or sometimes two birds); birds spiral upwards, c. 20 m apart, accelerating till 100-130 m above ground, when wing-beats at three times normal rate; call often during ascent, calling subsiding as gap between birds closes, often at great height (BWP); then, with one slightly ahead of other and appearing almost to touch, two birds bank and glide swiftly down, with wings half-open and weaving from side to side, sometimes rising till they almost halt, then falling again, in perfect synchrony (Gibson 1956). During glide, leader and pursuer may swap positions (Pass Ceremony) one or more times; give rapid Kek Calls. Aerial version of Bent Posture, which occurs during Pass Ceremony of Sandwich Tern, not recorded (BWP). Pair eventually return to flock, go fishing or engage in a paired flight. Paired flight involves Butterfly Flight, which generally starts straight after a glide, and aerial version of Erect Posture, with Pass Ceremony occuring a few times before landing; as leader overtaken, occasionally gives Karr Call. As pre-laying period progresses, High Flights increasingly initiated without prior collective upflight. Frequency of upflights and High Flights decreases rapidly when most birds have started nesting (BWP). Mass Flights do not take place if incubating or brooding Terns present (Dunlop 1987). Resurgence of courtship noted when first chicks fledge; mostly advertising males being chased by other birds with Pass Ceremonies and, less commonly, High Flights (participants mostly unpaired adults, immatures and failed breeders) (BWP); pre-breeding pairs often display among crèches of young (Dunlop 1987). Courtship on ground Usually performed before or after High Flight. If before, male carrying fish flies into social roost and walks among Terns, uttering Advertising Call and adopting FORWARD-ERECT (Fig. 3): wings and plumage as in Erect Posture, body and neck more or less upright, and bill held slightly below horizontal but raised with each call; on encountering co-operative female, both adopt Forward-Erect, and STRUT round each other, headto-tail, in tight circle, with short mincing steps. When after High Flight, pair return to flock, stand quietly and display to



Figure 3 Forward-erect

one another, at first adopting Erect Posture and HEAD-TURN-ING: turning upraised head jerkily from side to side; then both relax to Forward-Erect (BWP). Courtship feeding Occurs from pre-breeding period at Club to early incubation. Male feeds several females before feeding one particular female often; in earlier stages, female sometimes accompanies male to foraging area or remains close by, where he feeds her. Female sometimes begs for food (see Copulation) and occasionally pecks at bill or snatches at fish (Warham 1956; Hulsman 1976, 1977a). If fed, female usually eats fish immediately; sometimes struts with it in bill while giving Advertising Call; rarely, returns fish to male, who eats it or returns it again, which may lead to fish changing custody several times before one bird, usually female, eats it. Fish may eventually be eaten by male if he fails to find recipient (Hulsman 1977a; BWP). Greeting Especially during first few days of incubation, incoming bird sometimes brings fish and gives Advertising Call on approach: lands near nest, adopts Forward-Erect (Warham 1956), and gives version of Advertising Call, sometimes changing to Kuk Call when very close to nest. Sitting bird recognizes call of mate, stands and adopts Forward-Erect, and usually leaves nest just before, or as, mate arrives; similar to Lesser Crested Tern (Hulsman 1977a; BWP). Both birds circle round in strut posture, as in courtship display (Langham & Hulsman 1986). Copulation Often stimulated by female begging: adopts crouching HUNCHED POSTURE with crest half-raised, uttering Begging Calls while pointing at male and trying to keep in front of him; male adopts Forward-Erect or DOWN-ERECT (bill lowered) and tries to approach from side or rear and mount; many attempts fail because female often mainly interested in begging for food. Most copulation occurs in pre-breeding Clubs (BWP).

Relations within family group Both sexes incubate: parents may shade eggs during day, only partly settling on eggs, with wings lowered almost to ground. Parents do not recognize own eggs or newly hatched young, but mutual recognition, apparently by voice, established by time young ready to leave nest when 2 days old (see Voice). Chicks are induced to leave nest by parental calls (Stirling et al. 1970) and scatter or form crèches (see Bonds). Parents seek own chicks in crèche, forcibly rejecting others. At first, chicks passive when pecked by strange adults but begin to retaliate from c. 1 week old (BWP). Crested Terns and Silver Gulls may try to steal food from parents returning with food, though such behaviour in unmated Terns may be related to pairing. Some incoming parents call once and go straight to chicks; others call on approaching colony and chicks answer, allowing birds trying to steal food to gather round chicks; rarely, unmated birds are attracted by call of incoming parent and give chase. When chased, parent flies fast, zigzagging, climbing and diving; arriving parent may threaten birds trying to steal food. Silver Gulls, apparently attempting to force regurgitation, sometimes peck and may kill chicks (Hulsman 1977a). Both chicks and juveniles beg by calling and may later be fed by parent hovering above; chicks take food from bills of parents, rarely from ground; large chicks can take several fish at once. Fish that are not eaten by chicks usually eaten by adult, especially when theft imminent

(Hulsman 1977a; Smith 1989). At first, young not aggressive. but 2-3-week-old chicks aggressive to other chicks, strange adults and other birds, including Silver Gulls (Hulsman 1977a). In first week after fledging, juveniles, awaiting return of parents with food, often practise fishing, dipping to pick up floating objects (BWP). Anti-predator responses of young In response to Alarm Call of parent or other adults, small chicks crouch or lie prone; when a few days older, scramble for cover. May regularly gather under vegetation for shade and safety (Hulsman 1977a; BWP). Sometimes form crèches: when disturbed, chicks in crèche may scatter and hide in vegetation (Hulsman 1977a) or bunch together and run, even over edge of cliff into water and drown (Keast 1943). Parental antipredator strategies Nests often more effectively defended if colony crowded. If not in crèche, chicks up to 2 weeks old attended by one parent while other forages, though some left for up to 3-4 h while both parents forage (Hulsman 1977a). At approach of danger, adults give Alarm Calls. Raise crest at any provocation (Iredale 1928), though Cooper (1948) said crest always raised when incubating and lowered only when outside colony. Do not defend nesting areas aggressively; sit on nest when confronted by intruder (Dunlop 1986). Little co-operation to mob avian predators in air, and individuals rarely fly from nest to challenge them. Birds on One Tree I. took flight but only three chased approaching White-bellied Sea-eagle Haliaeetus leucogaster, which took one chick. Do not mob Silver Gulls (Hulsman 1977a); adults drive Gulls from their own chicks, but not from chicks of others unless their own close by; sitting birds lunge, peck, and give Gakkering Call at Gulls passing within 0.75 m. If nests close enough, birds can effectively ward off groups of Gulls (Hulsman 1977a); excited birds may fly up and dive on nearby Gull but this is generally a less effective defence, as it leaves clutch exposed (Hulsman 1974, 1977c); often relieving bird chases nearby Gulls away before change-over (Hulsman 1977a; Langham & Hulsman 1986). Bird may pass fish quickly to young and then shield it with own body if threatening aggressor hovering overhead (Hulsman 1976). When person approaches within 30 m of colony, birds raise wings and some give Alarm Calls; when c. 20 m away, fly overhead and swoop (not closer than c. 1 m to head of intruder), sometimes defecating (Hulsman 1977a).

VOICE Well known from study in Aust. by K. Hulsman (in BWP). Highly vocal, especially on breeding grounds (BWP). Can also be noisy at night (Campbell & White 1910), and particularly so in flight about dawn (Hogan 1925). When fishing, give querulous whistle or wail, harsher guttural cry or short sharp cries (North). Call noisily during Mass Flights (Dunlop 1986; see Social Behaviour). When intruders near nest or chicks, adults fly overhead, calling or screeching (Langham & Hulsman 1986). During incubation, relieving bird calls after landing; relieved bird calls after moving off eggs (Hulsman 1977a). Adults feeding young call as they approach colony, and are often chased by conspecifics; when chick answers, before or while being fed, other birds gather about it, calling and displaying to one another (Hulsman 1977a). In confusion caused by human intrusion, adults returning with food called to locate chicks (Keast 1943). Calls similar to those of Lesser Crested Tern but of lower pitch (Hulsman 1977a). Mates recognize each other and chicks recognize parents by means of Advertising Call, a pulsed call in which the number of pulses per unit time declines during middle of call; in analysis of 17 parameters, segment duration (of the beginning, middle, and end of call) and number of pulses varied

most and are most likely characters used in individual recognition (Veen 1985). Parents do not recognize eggs or own newly hatched chicks, but do so by time chicks 2 days old; some 2and 3-day-old chicks recognize their parents (Davies & Carrick 1962); most adults returning with food recognize chicks by call (Langham & Hulsman 1986). NON-VOCAL SOUNDS: In gliding phase of High Flight (see Social Behaviour) wings of birds said to hum like 'distant deep-toned siren of steamer' (Campbell & White 1910).

Adult Based on Aust. study by K. Hulsman (in BWP) unless stated. ALARM CALL: a hard wep-wep (Warham 1956). GAKKERING CALL: throaty cawing korrkorrkorr (Warham 1956) (see sonagram A). Expresses threat or alarm; given by birds on nests, duelling with neighbours, in standing fights with wings partly spread, while sitting and lunging at Silver Gulls, or in response to aerial predators. Harsh krow-krow a related call.



Croak, given when people enter colonies (Iredale 1928), probably one of these calls. ADVERTISING CALL: raucous *kirrak*, *kirrik*, or *kirrah* (see sonagram B). Uttered more often by male: when flying, advertising for female to follow; and when arriving at colony with fish or for nest-relief. Uttered by female, while strutting about, after receiving fish from male. Often given by both birds during ascent phase of High Flight (Gibson 1956; see Social Behaviour) with calling often alternating between birds and subsiding as gap between pair closes. KARR





CALL: often uttered after an interaction complete: after billing fight between sitting birds; after ground courtship parade; from both birds on ground after male has swallowed fish instead of presenting it to female; sometimes from both birds during nestrelief just before departure of relieved bird; occasionally given during Pass Ceremony (see Social Behaviour) by leader when overtaken. KEK CALL: rapid *kekekekeker*, last syllable dropping in pitch; given when leader and pursuer swap positions during gliding phase of High Flight. KUK CALL: soft call, uttered once, or slowly repeated, inviting close approach; given by incoming bird at nest-relief, or when summoning young to be brooded or to follow. Deep *kré-kré* by male during copulation apparently related. BEGGING CALL: persistent, penetrating *quee-quee-quee*; by female only; to beg fish from male or to solicit copulation. Young In 3 days after chipping of egg, *peep* of chick becomes shorter, clearer and sharper (Davies & Carrick 1962, with sonagrams).

BREEDING Well known; detailed studies on One Tree I. (Hulsman 1977), Eagle I. (Smith 1989) and in sw. WA (Dunlop 1986); 61 records in Aust. NRS till Nov. 1993.

Season N. QLD: N. Great Barrier Reef: at different colonies and islands, eggs and young present in most months, suggesting asynchronous timing and duration of laying throughout region (Smith 1993); nesting, early July and Oct.-Dec. (MacGillivray 1914; Gill 1970), Dec.-July, with maximum Jan. and Feb. (King et al. 1992); laving, Dec.-Feb. (Smith 1993), Nov.-Jan.; clutches laid after mid-Dec. probably replacements (Langham & Hulsman 1986; Smith 1993). Gulf of Carpentaria: nesting, Apr.-June (Walker 1992); eggs, Dec. and Apr. (MacGillivray 1914; Hogan 1925); addled eggs in early July (Garnett & Crowley 1987). ONE TREE I., QLD: First arrive Sept. and Oct.; sporadic till mid-Nov., then numbers increase rapidly, with maximum early Dec. (Langham & Hulsman 1986). N. WA: Nesting, early May to mid-July (Aust. Atlas); laying Apr.-May, and eggs, Aug.-Sept. (Dunlop et al. 1994). s. wa: Laying, late Mar. or early Apr. to early Nov., mostly mid-Apr. to late Oct., with maximum late Apr. and late Sept. and minimum in July (Dunlop 1986). Laying, early Apr. to late Nov., with two distinct peaks in late Mar. to early Apr. (autumn) and late Sept. to early Oct. (spring); no marked individuals bred in both periods in same year (n=65 birds); laying interval between seasons (n=88 marked birds) 305-385 days for autumn nesters and 315-405 days for spring nesters (Dunlop 1985a). Eggs, late Apr. and early Sept. to mid-Dec. (Carter 1902; Warham 1956; Storr 1964b; Ford 1965). SA: Nesting, Nov.-Feb. on Troubridge I. (Lashmar 1987); eggs, late Oct. to early Jan. (Aust. NRS); laying began, 2 Dec.; hatching, 31 Dec. (Stirling et al. 1970); eggs and fledged young in early Jan., suggests second laying (Brummitt 1935). NSW: Eggs, late Sept. to early Jan. (Basset Hull 1908, 1912; Holmes 1977; Aust. NRS). VIC.: Eggs, early Oct. to late Dec. (Aust. NRS); at Kilarney Reef, started nesting after Silver Gulls had finished (Wheeler & Watson 1963). TAS.: Nesting, Nov.-Mar. (Napier & Singline 1979; Aust. Atlas).

Site On islands, reefs and cays, sand-spits, rocky points, any area of rather level ground above high water, without tall vegetation; on bare sandy mound, highest part of island, between rocky outcrops, in grass or bare patches among grass, sand at edge of vegetation, in pigface, iceplant, Sea Purslane Sesuvium portulacastrum, Melanthera biflora; one colony in grass in shade of casuarinas (Carter 1902; Iredale 1928; Reithmüller 1931; Cooper 1948; Hulsman 1984; Langham & Hulsman 1986; Aust. NRS). In sw. WA, autumn and spring nesting occurs at same sites (though different birds) (Dunlop 1985a). High fidelity to colony-site (see Movements: Breeding). Change colonies after one or more seasons (Basset Hull 1912: Langham & Hulsman 1986). Some colonies grow from centre, with later arrivals nesting on edge of colony, thus fresh eggs occur at edge of colony, and hatched young in centre (MacGillivray 1917; Storr 1964b); on Eagle I., Great Barrier Reef, colony grows from one edge (G. Smith). Dense colony found in centre of Silver Gull colony (Keast 1943), and Silver Gulls sometimes nest on edges of Tern colony. Nests close to Sooty Terns (Hogan 1925; Iredale 1928), and Bridled Terns nest round colony (Aust. NRS); can also nest in association with Lesser Crested Terns (G. Smith).

Nest, Materials Depression in sand, usually unlined;

sometimes lined with a little grass, guano or shells. Occasionally, a well-formed bowl of grass; in some colonies, lay eggs on trampled grass or other vegetation (Carter 1902; Cooper 1948; Napier & Singline 1979; Aust. NRS). On One Tree I., birds made nests by pulling out vegetation *Sesuvium portulacastrum* to leave a depression (Hulsman 1977a). MEASUREMENTS: Diameter of scrape, 15–30 cm (Aust. NRS).

Eggs Oval to very pointed at smaller end; rather closegrained, smooth, slightly lustrous. Eggs vary greatly in colour and markings: ground-colour, white to dark brown; faint yellowish-stone to creamy buff, light reddish-buff and pale brown, rarely dull white; marked with heavy blotches, spots, speckles or scrolling; with scattered angular lines, streaks and blurs of black or brownish black, intermingled with similar but fewer underlying markings of brownish black, inky or bluish grey, others with irregular angular streaks and broader lines; many penumbral, umber-brown at sides and black in centre, often with intermingled irregular shapes, spots and small blotches; marked with shades of blue, pink, green, red, brown, black and other dark colours, some lightly spotted, others almost solid (Cooper 1948; Tarr 1949; North). Eggs from tropical Aust. said to be pinkish white or roseate, blotched or streaked dark or rich reddish-brown and purplish brown (Campbell). MEAS-UREMENTS: 61.2 (56.3-65.6; 15) x 41.1 (39.6-42.8) (Storr 1964b); 58.7 (2.87; 55.4-63.5; 20) x 40.9 (1.60; 38.1-43.9) (North). WEIGHT: Eggs 12-17% female weight (Dunlop 1986). VOLUME: SW. WA, 1982: Apr., 54.5 (3.4; 74); July, 53.8 (4.3; 64); Oct., 52.4 (4.8; 43); Oct.-Nov., 49.7 (3.4; 31); eggs in Oct. significantly smaller than those in Apr. (Dunlop 1986). Size of eggs gradually decreases through season; Terns induced to nest among decoys at beginning of season lay eggs smaller than average (Dunlop 1986).

Clutch-size Usually one, occasionally two; in some colonies, all clutches one (Aust. NRS); *c*. 6000 nests, each C/1 (Stirling *et al.* 1970); C/1 x 47, C/2 x 1 (Storr 1964b). One clutch of three (Basset Hull 1912).

Laying In colonies, highly synchronous, more so within sub-colonies (Dunlop 1986; Langham & Hulsman 1986). On One Tree I., within sub-colonies, birds nested within 5 days of the first pair to nest in that sub-colony and laying highly synchronized; birds in different sub-colonies nested more than 1 week apart (Hulsman 1977a). Laying more prolonged in subcolonies that form first than in those that form later. On One Tree I., average duration of laying within sub-colonies, 11.5 days (2–18; 11) for sub-colonies of 9–267 nests; laying in whole colony spread over longer period, 29–53 days (Langham & Hulsman 1986); On Eagle I., laying in sub-colonies spread over a period of 6 to >20 days (Smith 1993). Three replacement clutches laid at 10, 11 and<20 days after loss (Dunlop 1985a). In sw. WA, Terns do not breed twice in single year (see Season).

Incubation Both sexes incubate. On One Tree I.: duration of stints, 41±14 to 213±26 min; shifts tend to be longer as incubation progresses, e.g. between 08:30 and 15:30 on four separate days (12 Dec., 15–17 Dec.), average duration of shifts 41, 109, 114 and 135 min. Number of change-overs per hour greater between 07:00 and 08:00, and between 11:00 and 12:00; change-overs more frequent during ebb and flow of tides (rather than at slack water) (Langham & Hulsman 1986). Average incubation spell, 184 min (n=73) (BWP). During heat of day, incubate with wings lowered almost to ground, shading eggs (Cooper 1948). Incubating bird fed on nest by mate (Warham 1956). INCUBATION PERIOD: 21-24 days (Hulsman 1977a), 28±1 days (Langham & Hulsman 1986). probably c. 29 days (Stirling et al. 1970). Do not sit on broken eggs or remove them from nest. Incubating adult raises tail and squirts faeces outside nest or over rim (Hulsman 1977a). On One Tree I., most left egg-shells near nests; some remove broken egg-shells from nest and drop them in vegetation round pond (Hulsman 1977a).

Young Precocial, semi-nidifugous. Growth WEIGHT: See Table 1. Reach 95% asymptotic weight 1-3 days before fledging (Langham & Hulsman 1986). WING, CULMEN: See Table 1: based on regression formulae in Smith (1989); regression of length of wing and age significantly different in two seasons (Smith 1989). Parental care, Role of sexes Chicks brooded and fed by both parents; fed in nest for at least first 3 days after hatching; fed very little on first day (Hulsman 1977a). Taken to edge of water when a few days old; generally kept in groups, returning to cover if disturbed (Reithmüller 1931); young escorted from nest by parents 3-5 days after hatching and moved away from colony; protected and brooded by parents until crèche formed; chicks sometimes stay in loose groups instead of forming crèches (Hulsman 1977a,c; Langham & Hulsman 1986). Chicks formed loose crèche in saltmarsh c. 30 m from colony (Aust. NRS). On One Tree I., in a season where chicks stayed in loose groups, one parent stayed with chick, even when chicks 2 weeks old; chicks could be left alone for 4 h or more; some lone chicks formed loose groups of 2-15 birds. Chicks fed bill to bill; do not usually pick up fish dropped on ground by adults, but will eat it if adult picks it up and offers it to chick. Large chicks take one fish at a time or several simultaneously from parents that carried more than one; chicks grabbed elongated hemirhamphids in middle and these were bent double as chicks swallowed them; chicks defecate wherever they are standing (Hulsman 1977a).

Fledging to maturity FLEDGING PERIOD: On One Tree I., 38–40 days. Bad weather may delay fledging. On One Tree I., some young accompany parents to foraging areas within 7 days of fledging, others waited on reef to be fed; some young left island with parents 13–19 days after fledging. Two chicks with

Table 1

andganaka terti tiriy.e	LOCATION	AT HATCHING	10	20	30	35	40	REFERENCE
WEIGHT	One Tree I.	45	97	163	220	adala <u>niy</u> lagi	233	the store las
	Eagle I.	41.8	109.5	177.2	244.9	278.8	ansleader a	2
WING	One Tree I.	asel-rusine-r	NUTSDA SE	76	129	195	ald (<u>Agid-ir</u>)	9480d Citlibile
	Eagle I.	4.3	38.4	103.8	155.6	172.8	dent beren for	3
CULMEN	One Tree I.	8.9	20.6	30.0	35.7	hief: (44.3	1
	Eagle I.	14.7	21.6	28.5	35.4	38.9	-	4

(1) From growth curves in Langham & Hulsman (1986); n=75 chicks in a sub-colony; (2) From linear regression formula in Smith (1989); (3) From logistic regression formula in Smith (1989); (4) From linear regression formula in Smith (1989).

deformed wings fed by parents for 4 months (from 11 Dec.) then abandoned. In some areas, usually start to breed when 3+ years old (Hulsman 1977a; Langham & Hulsman 1986), but elsewhere sometimes earlier (see Social Organization).

Success On One Tree I., for 615 eggs in two seasons, 222 (36.1%) hatched and 211 (34.3%) fledged; fledging success per season, 0.5% and 34%; hatching success was higher in larger sub-colonies (Hulsman 1977c). On One Tree I., for 1737 eggs in four seasons, 935 (53.8%) hatched and 818 (47.1%) fledged; annual hatching rate, 0.5-69%; annual fledging rate, 0.5-59%; of eggs that failed, 404 (23%) depredated, 386 (22%) deserted or addled and 12 (0.7%) lost through flooding; in one season, hatching success per sub-colony ranged from 0 to 91%; mortality of chicks highest in first 10 days, with >70% in first 5 days (Langham & Hulsman 1986). On Eagle I., for 2080 eggs in two seasons, 867 (41.7%) fledged; annual success rate, 31.3% and 63.9% (Smith 1989). On One Tree L. a cyclone caused much mortality of chicks through starvation and chilling. No instances of a pair raising two chicks (Langham & Hulsman 1986). A disturbed colony had all eggs destroyed by Silver Gulls (Cooper 1948), which take many eggs and can totally annihilate small sub-colonies; numbers in one colony on One Tree I. fell from 181 to no nests in 18 days, with daily rate of decrease up to 36% eggs per day; few chicks taken by Gulls, which cannot swallow chicks older than 3 weeks; chicks taken by White-bellied Sea-Eagle; some young trampled by adults (Hulsman 1977a; Langham & Hulsman 1986). Eggs and young taken by Ruddy Turnstones Arenaria interpres. Silver Gulls, Eastern Reef Egrets Egretta sacra, White-bellied Sea-Eagles and Ghost Crabs (Smith 1986); on Eagle I. most chicks lost through predation by White-bellied Sea-Eagles (Smith 1991). Some young, disturbed by observer, jumped off island and drowned (Keast 1943). Twice, nests washed off reef during storms (Wheeler & Watson 1963). Turtles can break many eggs (MacGillivray 1917).

PLUMAGES Prepared by A.M. Dunn. Timing of breeding varies round Aust., so all plumages can be seen at any time of the year, depending on timing of local breeding. Probably begin post-natal moult to juvenile plumage a few days after hatching. Begin complete post-juvenile moult to first immature non-breeding (first basic) plumage 5-6 months after hatching. Undergo restricted partial pre-breeding moult to first immature breeding (first alternate) plumage but with little or no change in appearance. Thereafter, undergo complete postbreeding (pre-basic) and partial pre-breeding (pre-alternate) moults each cycle, producing non-breeding and breeding plumages, which differ mainly in extent of black cap. Sexes similar. Usually first breed when 2 years old (BWP) or 3 or more years old (Langham & Hulsman 1986; Dunlop & Wooller 1990) though some first breed when 1 year old. Five subspecies. Subspecies cristata occurs Aust., and described below.

Adult breeding (Second and subsequent alternate). Head and neck Upper forehead, crown, nape and feathers in front of and behind eye, black (89); feathers of hindcrown and nape elongated; combine to form neat black cap with prominent shaggy black crest at back of head. White band extends from mid-forehead to base of bill, continuing across anterior lores to join white of rest of head and neck below eye; border between black and white very sharply defined (cf. adult non-breeding). Upperparts Uppermost mantle, white. Lower mantle, scapulars, back, rump and uppertail-coverts grade from grey (84–85) on mantle to light grey (85) on coverts, with concealed white bases to feathers. Underparts White. Tail Grey (c84) to light grey (c85), grading to white toward bases of feathers. Upperwing Coverts, tertials and alula, grey (84-85); tertials grade to white at base of inner webs. When fresh, primaries and secondaries, grey (84–85), sometimes slightly darker on outer primaries; white tips to secondaries and inner primaries form narrow trailing-edge. Outer primaries have very narrow white inner edges at tips, quickly lost with wear. Broad concealed white inner edges to remiges sharply defined on outer primaries, more diffusely elsewhere; shafts, white. Primaries and secondaries darken with wear, as overlying silvery sheen gradually lost to expose grey-black (82) ground-colour; outer primaries darken faster than other remiges, especially at tips and where feathers overlap on folded wings. When worn, outer primaries form dark wedge, contrasting with paler inner primaries, and secondaries develop dark subterminal band, boldest on inner feathers. Underwing White except for primaries. Outer primaries, grey (84) with broad white edge to inner web; innermost primaries, light grey (85) with narrow white edge to inner web. Most grey areas of primaries concealed; only tips of outer 4-5 primaries and leading-edge of p10 appear dark in flight. Secondaries have concealed lightgrey (c85) edges; appear white in flight.

Adult non-breeding (Second and subsequent basic). Differences from adult breeding: Head and neck Upper forehead, crown and nape, mostly black (89) with varying white fringes or tips to feathers; feathers of forehead often have distinct white fringes, though fringe sometimes merges into grey-black (82) centres of feathers; feathers of forecrown narrowly fringed white; feathers of hindcrown and nape, elongated, forming crest at back of head, with narrow white tips, which are lost with wear. Lower forehead, most of lores, lower cheeks, chin and throat, white. Narrow band in front of and below eye, black (89) with white speckling; varies in extent. Sides of neck and hindneck, white, often with large grey (c85) spots or streaks. Upperwing Before they are moulted, outer primaries and secondary bar more worn and darker than in adult breeding.

Downy young Down has spiny texture. Much variation in colour and pattern. **Head and neck** Forehead, crown, nape, lores and ear-coverts, off-white to cream (c92) with varying black (89) shafts or centres to many feathers; some have orange-buff (c118) wash. Chin and throat, off-white to buff (c124). **Upperparts, Wing-pads** Ground-colour varies from off-white to buff (c123D) to orange-buff (118). Evenly spotted with black-brown (119) in paler birds; others more heavily blotched black-brown (119) above; dark spots often meet to form irregular lines. **Underparts** Off-white.

Juvenile Head and neck Upper forehead and crown, black-brown (119) with white edges to feathers, giving streaked appearance. Lower forehead and lores, evenly speckled blackbrown (119) and white. Ear-coverts and nape, black (89) to black-brown (119) with fine white tips to feathers. Chin and throat, white. Cheeks and sides of neck, white, with black (89) streaks or spots, sometimes extending across throat as partial or complete collar. The amount of spotting on the neck and white in the cap varies individually and with wear. Upperparts Mantle usually white, with large black (89) to black-brown (119) subterminal spots; extent of spotting varies individually and some birds appear much darker than others. Smaller scapulars, dark greyish-brown (greyish 121) with dark-brown (c219) subterminal bar and narrow white tips to feathers; in some, dark greyish-brown ground-colour extends over most of mantle and on larger scapulars. Larger scapulars, white, with two dark-brown (c219) subterminal bars and brownish-grey

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(brownish 84) bases; scapulars appear barred. Back and rump, grey (84) with white tips and concealed white bases to feathers. Uppertail-coverts, white, with large light-grey (c85) subterminal streak on inner webs. Underparts White, occasionally with some grey-black (c82) spots or streaks to feathers at sides of breast. Tail Dark grevish-brown (c121), darkest subterminally, with white tips and white base to inner webs; outer webs grade to light grey (c85) near base. Upperwing Lesser primary and secondary coverts, grey-black (82) with narrow white fringes. Most median secondary coverts, dark greyish-brown (greyish 121) with white tips and white bases; dark areas of feathers eventually bleach or wear away leaving contrasting white wing-bar. Longest median secondary coverts and greater secondary coverts, dark brownish-grey (brownish 83) with white fringes. Alula, grey-black (82) with narrow white inner edge. Median and greater primary coverts, greyblack (82) with narrow white terminal fringe. In fresh plumage, the amount of white in wing-coverts, especially median secondary coverts, varies, and some juveniles appear much darker than others. Outer primaries similar to those of adult but with little silvery sheen, appearing grey-black (c82) when fresh. Inner primaries and outer secondaries, dark grey (83), grading to grey-black (82) on inner secondaries; all have white tips and white inner webs. Shafts of primaries and secondaries, dark brown (c121), which bleach to brownish white with wear (but never as white as in adult). Tertials, black-brown (c119) with broad white fringes and small black-brown (c119) subterminal blotches. Underwing As adult.

First immature non-breeding (First basic). Similar to adult non-breeding; can be distinguished before completion of prolonged post-juvenile moult (see Moults) by retained juvenile wing-coverts and primaries, which often retained for almost 1 year; dark juvenile outer primaries and their coverts often form a dark wedge on outer edge of spread wing. Before replacement of upperwing-coverts, cubital bar very dark, contrasting with surrounding coverts, which are often worn and very pale because white bases to feathers exposed. Old juvenile plumage usually rather brown, showing considerable wear. particularly on wings. New plumage similar to that of adult, but new tertials differ from those of juvenile and adult: outer webs mainly grey-black (82) (paler near tip and along outer edge) and white on most of inner webs; and lesser secondary coverts usually have darker grey centres, forming subdued dark cubital bar.

Subsequent immature plumages (First alternate and, possibly, second basic). Recognition difficult. Very similar to adult non-breeding but some have darker cubital bar and timing of moult of primaries can differ from adults in the same region. Many probably indistinguishable, especially if moult of primaries of adult population varies in timing.

BARE PARTS Based on photos (Pringle 1987; unpubl.: D.W. Eades) and published descriptions (Mathews & Iredale 1921; Lane 1994; Olsen & Larsson 1995; BWP). Adult Bill, straw-yellow (c56) to orange-yellow (18); often brighter just before breeding. Iris, dark brown (c121). Legs and feet, grey-black (82) with yellow or partly yellow soles; occasionally, yellow blotches extend up legs. Downy young Bill, pink (c108D) to pale greyish-green (greyish 162D); also described as dirty white or dull grey. Iris, pale brown. Legs and feet, brownish white (Mathews & Iredale 1921). Juvenile, First immature non-breeding Bill, lime green (59) to straw-yellow (c57). Iris, dark brown (c121). Legs and feet, similar to adult

but sometimes greyish yellow with black spots; black spreads gradually with age.

MOULTS Based on examination of 109 museum skins (AM, ANWC, HLW, MV, WAM), 323 live birds (AWSG) and published material (Dwight 1901; Dunlop 1985b).

Adult post-breeding (Third and subsequent pre-basic). Complete; primaries outwards. Timing of moult dependent on timing of breeding and so varies round Aust. and within areas with sub-populations that breed at different times. In all locations, moult of primaries begins soon after young fledge and proceeds slowly, growing only one feather at a time. Replacement of feathers of cap sometimes begins during incubation but often later in breeding; occasionally some attain a complete non-breeding cap before incubation finished (Dunlop 1985b). Body-moult begins at base of neck, front of head, sides of breast, flanks and back, and spreads backwards, but timing of onset of moult not known. In WA, breeding season extended, with two main peaks in breeding activity, one in spring and another in autumn, but nesting may begin throughout Apr.-Nov. and individual adults can be found in most stages of moult throughout year (Dunlop 1985b). In Vic., a single peak in breeding between Nov. and Jan., though considerable variation in timing of moult of primaries. Most probably begin primary-moult in Dec.-Jan.; PMS in Jan. 18.2 (12.98; 0-44; 40) (AWSG). Primary-moult proceeds slowly and probably finishes Aug.-Sept. Average PMS between Feb. and June: Feb., 23.5 (8.46; 5-45; 37); Mar., 21.1 (11.2; 1-44; 49); June, 41.4 (9.87; 10-50; 22) (AWSG). Timing in other e. States similar to Vic. Adult pre-breeding (Second and subsequent pre-alternate). Partial; involves feathers of head and neck, tail and, often, inner primaries. Extent of primary-moult can vary between locations. Replacement of feathers of head and neck begins just before laying, and coincides with completion of post-breeding moult and replacement of p10. Most adults have complete black caps during peak of laying (Dunlop 1985b). In Vic., moult of head and neck begins late Aug. to early Sept. and finished by Oct. In WA, onset of moult of head and neck varies with timing of breeding and may occur in many months of year. Pre-breeding moult of primaries begins with p1 before finish of post-breeding (pre-basic) primary-moult, but is arrested after inner 1-4 primaries have been replaced; extent of moult appears to vary with location. In Vic., not all adults moult inner primaries; only 13 of 127 adults caught between Jan. and June showed indications of having replaced inner primaries in a pre-breeding moult (AWSG). In WA, most birds begin a pre-breeding primary-moult, replacing innermost two or three primaries when the preceding wave of postbreeding (pre-basic) primary-moult reaches p7-p9 (Dunlop 1985b); this may occur in a number of months because the timing of breeding varies. Post-juvenile (First pre-basic). Complete, beginning in about May in Vic. Starts with some feathers of mantle and scapulars. Most of head, body and wingcoverts replaced by Aug.-Sept. In Vic., primary-moult begins July-Aug.; PMS in Jan., 27.9 (5.38; 19-36; 10), in Feb. 32.0 (3.81; 27-37; 5) (AWSG); probably finished in June-July of second calendar year. Other e. States similar to Vic. Very little information from WA but probably show considerable variation in timing because breeding season extended. First immature pre-breeding (First pre-alternate). Extent uncertain. Possibly replace feathers of head and neck but appearance of new plumage similar to non-breeding plumage. In Jan.-Feb. in Vic., two of 24 immatures had begun replacing primaries from p1 before completion of post-juvenile moult of primaries; this

moult appears to be homologous with adult pre-breeding primary-moult but occurs much later. No information on timing elsewhere in Aust. **First immature post-breeding** (Second pre-basic). Complete. Poorly known in Aust. as few data from Aug. to Oct. In Palaearctic populations (BWP), may begin moult earlier than adults begin post-breeding moult (1–2 months before breeding season) but moult more slowly and finish at same time adults finish post-breeding moult.

MEASUREMENTS (1–8) Aust., skins (AM, ANWC, HLW, MV, TMAG, QM, QVM, WAM): (1) Qld, adults; (2) NSW, adults; (3) Vic., adults; (4) Vic., juveniles and immatures; (5) Tas., adults; (6) SA, adults; (7) WA, adults; (8) NT, adults.

Menkhor	sc, I	MALES	FEMALES	For
WING	(1)	348.5 (9.95; 341–362; 4)	335, 337, 352	
	(2)	351.1 (7.92; 338–368; 18)	344.2 (9.02; 326–360; 17)	*
	(3)	335.4 (10.14; 323-352; 9)	323, 344	
	(4)	329.4 (9.85; 306-345; 12)	315, 342	
	(5)	327.5 (9.37; 315-344; 8)	332.0 (6.69; 320-338; 6)	ns
	(6)	330, 348	_	
	(7)	362.1 (10.24; 347-385; 15)	353.3 (12.47; 337-374; 9)	ns
	(8)		347, 351	
TAIL	(1)	170.0 (4.60; 162–175; 6)	150, 150, 154	
	(2)	171.6 (13.7; 141–194; 20)	162.6 (14.1; 120–180; 19)	*
	(3)	153.2 (14.41; 130–173; 8)	126, 150, 151	
	(4)	127.1 (8.98; 114–142; 13)	117, 151	
	(5)	150.3 (8.04; 136–156; 6)	156.5 (12.66; 142–171; 4)	ns
	(6)	147, 150	1942. Proc. R. mal-S-	
	(7)	165.7 (12.92; 137–192; 19)	156.9 (12.12; 137–179; 14)	ns
	(8)	172, 175	151, 165	
BILL	(2)	61.2 (3.31; 53.3–66.2; 22)	57.7 (3.36; 52.9-63.7; 21)	**
	(1)	62.9 (1.89; 59.3-65.3; 7)	59.3 (2.61; 55.6-62.2; 7)	*
	(3)	59.4 (2.37; 56.4-64.1; 12)	54.3 (2.62; 52.6-58.2; 4)	**
	(4)	53.3 (4.23; 42.1–58.6; 15)	52.2 (6.93; 42.8–59.3; 4)	ns
	(6)	60.2, 62.6	1976. Emu 76: 143-9_	
	(5)	58.6 (2.98; 53.4–61.8; 8)	56.4 (1.90; 54.6–59.9; 6)	ns
	(7)	65.8 (3.54; 60.0–73.2; 21)	62.0 (3.27; 54.1-66.8; 17)	**
	(8)	60.9, 61.3	59.3, 60.9	
TARSUS	(1)	29.5 (0.84; 28.6–30.5; 7)	28.1 (0.59; 27.1–28.7; 7)	**
	(2)	27.7 (1.67; 22.5–30.4; 23)	28.0 (1.29; 25.0–30.1; 21)	ns
	(3)	27.6 (1.02; 26.6–29.5; 12)	26.5 (0.77; 26.0–27.7; 4)	ns
	(4)	26.9 (1.00; 25.1–28.4; 15)	26.5 (1.25; 25.2–27.8; 4)	ns
	(5)	27.6 (1.40; 25.4–29.8; 8)	27.4 (0.84; 26.0–28.6; 7)	ns
	(6)	27.7, 28.1	1094 Conden Sci 130 9	
	(7)	29.5 (0.99; 28.0–31.5; 22)	28.8 (0.82; 27.7–30.1; 17)	*
	(8)	28.4, 28.8	27.7, 29.5	
TOEC	(1)	34.3 (1.70; 32.2–37.6; 7)	32.4 (0.87; 31.2–33.6; 7)	*
	(2)	33.2 (1.40; 30.8–35.7; 23)	32.4 (2.00; 28.0–35.3; 21)	ns
	(3)	31.6 (1.24; 29.4–33.5; 12)	31.8 (1.04; 31.0–33.3; 4)	ns
	(4)	31.0 (0.89; 29.8–32.5; 14)	30.5 (0.66; 29.6–31.0; 4)	ns
	(5)	31.6 (1.46; 30.5–34.4; 8)	30.9 (1.29; 29.1–32.4; 7)	ns
	(6)	32.8, 33.8	4. I.A. 1943, Ema 42: 731	
	(7)	34.2 (1.74; 31.2–37.8; 22)	33.5 (1.36; 31.1–35.7; 17)	ns
	(8)	35.0, 35.8	33.0, 34.5	

Juvenile and immature males have significantly shorter tails and bills than adult males; length of juvenile wing said to be 10 mm shorter than adult wing (BWP) but this not shown in above samples, possibly because length of wing varies with wear of p10. Length of tail (t6) and depth of tail-fork of adult non-breeding and immatures *c*. 12 mm shorter than in adult breeding.

(9–10) Adults, live (AWSG): (9) Vic.; (10) NW. Aust. (11) SE. Tas., adults, live (modified from Woehler *et al.* 1991).

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arron o hills	a measure than those between	nominate hervil seem n
	(11) 113.0 (3.42; 107.5–120.9; 53)	
	(10) 115.0 (6.99; 96.4–125.4; 27)	
THL	(9) 112.6 (3.44; 105.5–120.5; 76)	
TARSUS	(11) 34.9 (1.19; 32.5–37.9; 53)	
	(11) 58.8 (2.73; 54.2–65.3; 53)	
	(10) 62.6 (3.30; 56.2–69.1; 25)	
BILL	(9) 58.5 (2.98; 52.5–67.3; 103)	

WEIGHTS (1) Vic., adults, skins (HLW, MV).

WING

Tinberg	MALES	FEMALES	
1)	305.7 (67.41; 215–365; 6)	241.7 (47.03; 190–290; 4)	ns

(2) Vic., adults, live (AWSG). (3) NW. Aust., adults, live (AWSG).

Vincen	UNSEXED	
Jan.	(2) 327.6 (27.79; 269–400; 50)	
Feb.	(2) 318.0 (19.00; 280–350; 42)	
Mar.	(2) 309.5 (30.39; 250–385; 41)	
	(3) 340.1 (52.92; 245-430; 10)	
Apr.	(3) 313.8 (51.78; 230–376; 22)	
May	(2) 302.5 (12.58; 290–320; 4)	
June	(2) 320.2 (26.94; 275–370; 29)	
Sept.	(3) 317, 340, 360	

STRUCTURE Wing, long, narrow and pointed. Eleven primaries: p10 longest, p9 14–15 mm shorter, p8 36–40, p7 60–68, p6 87–98, p5 115–124, p4 140–153, p3 167–180, p2 187–205, p1 211–227; p11 minute. Twenty-two secondaries, including about five tertials; tips of longest tertials fall between p4 and p5 on folded wing. Tail, deeply forked; 12 rectrices; t6 longest, t1 63–78 mm shorter. Bill, long and rather heavy, gradually tapering to a point; slightly decurved. Tarsus, very short, stout and rounded; scutellate in front and reticulate at rear. Tibia, 10–14 mm exposed. Complete webs between front toes. Outer toe 82–91% of middle, inner 63–67%, hind 26–30%.

RECOGNITION Discussed fully in Field Identification (see Similar species). The shafts of primaries white in juvenile Lesser Crested Terns, brown in juvenile Crested Terns.

GEOGRAPHICAL VARIATION Complex. Four subspecies, differing mainly in size and colour of upperparts. Following summary based largely on BWP and Olsen & Larsson (1995). Aust. subspecies *cristatus* relatively small (especially in length of bill) and pale above (especially on tail and uppertail-coverts); varies geographically. Within Aust., upperparts of adult typically grey (84) on e. coast, slightly lighter grey (84–85) in WA; difference subtle, and only evident with direct comparison in the hand. WA birds also significantly larger (see Measurements); data from e. coast suggest clinal increase in size from S to N, but more information needed. BWP considered *cristatus* from Micronesia, Polynesia, Greater Sundas and e. Malay Pen. to be about the same size and colour as in Aust.,

while those from N of range (Philippines, Taiwan, China) said to be smaller. However, wing (331) and bill (58) from latter regions similar to those from se. Aust.

Subspecies velox from n. Indian Ocean and Middle East is largest (average wing 366, bill 64) and darkest, with slaty grey (c83) upperparts; replaced abrubtly in w. Indian Ocean by smaller subspecies thalassina (wing 340, bill 56), which is also paler, with upperparts resembling WA cristata. Nominate bergii of South Africa and Namibia larger than thalassina (average wing 362, bill 62) with upperparts resembling those of cristata from e. Aust. Differences between subspecies thalassina and nominate bergii seem no greater than those between different populations of cristata in Aust., which suggests that further work on subspeciation is needed.

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Sponsors: Mr D Prest, Mr Al Sinclair



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Crested Tern Sterna bergii (page 605) 1 Adult breeding; 2 Adult non-breeding; 3 Downy young; 4 Juvenile; 5 Early stage of moult from juvenile to first immature non-breeding; 6 Late stage of moult from juvenile to first immature non-breeding; 7, 8 Adult breeding; 9 Adult non-breeding; 10, 11 Juvenile; 12 Late stage of moult from juvenile to first immature non-breeding

Lesser Crested Tern Sterna bengalensis (page 597)
13 Adult breeding; 14 Adult non-breeding; 15 Downy young; 16 Juvenile, dark bird; 17 Early stage of moult from juvenile to first immature non-breeding; 18 Late stage of moult from juvenile to first immature non-breeding; 19, 20 Adult breeding; 21 Adult non-breeding; 22 Juvenile, pale bird; 23 Late stage of moult from juvenile to first immature non-breeding