

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	pratinoles, 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	aucs; 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, Procellariiformes, 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 charadriids and allies (Chionididae, Burhinidae, Haematopodidae, Recurvirostridae, Ibidiorhynchidae, Charadriidae, Pluvianellidae, Dromadidae, Glareolidae, Stercorariidae, 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 charadriids (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, Stercorariidae, Laridae and Sternidae will be dealt with in Volume 3 of HANZAB.

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Order CHARADRIIFORMES

Family SCOLOPACIDAE sandpipers and allies

Small to large shorebirds (12–66 cm) with long bills and legs. Largest family of suborder Charadrii, with some 88 species in c. 24 genera; most species only breed in higher latitudes of Holarctic, but migrate long distances and occur almost worldwide in non-breeding period. In HANZAB area, 51 species in 18 genera: two breeding species, 27 regular non-breeding migrants, 19 accidentals and three doubtfully recorded. All are transequatorial migrants except for the two species of *Coenocorypha* that breed NZ, which are sedentary. The family is usually split into six subfamilies (e.g. Jehl 1968; BWP): Scolopacinae, Gallinagoninae, Tringinae, Arenariinae, Calidridinae and Phalaropodinae; we place the dowitchers *Limnodromus* in a separate subfamily, Limnodrominae (q.v. for details). All except Scolopacinae (woodcocks) represented in HANZAB region. Though they are convenient groupings, these subfamilies may not be wholly monophyletic (e.g. Strauch 1978; Dittman *et al.* 1989; Sibley & Ahlquist 1990; BWP); until phylogeny within the Family is understood, sequence of genera and species followed by different authors is likely to remain unsettled. Sequence and taxonomy used here follows Christidis & Boles (1994). Studies of allozymes (Christian *et al.* 1992), DNA hybridization (Sibley *et al.* 1988; Sibley & Ahlquist 1990), osteology (Strauch 1978) and patterns of downy young (Jehl 1968) generally agree in treating Scolopacidae as monophyletic, with distant links to Jacanidae, Rostratulidae, Thinocoridae and Pedionomidae.

Body-form diverse, from slender to stocky. Females slightly to considerably larger than males, though in a few species males are larger (Jehl & Murray 1986). Wings, long and pointed; p10 longest; 15–22 secondaries, including elongate tertials, which, with scapulars, cover back and rump when at rest. Tail, short; 12 feathers except in *Gallinago*, which have 14–28, and *Coenocorypha*, which have 14. Neck, long. Shape of bill varies considerably, though generally long and slender; usually straight to decurved, but recurved in a few Tringinae; tip of bill, fine or only slightly swollen (cf. Charadriidae) with sensory pits. Compared to Charadriidae, eyes small and head narrow. Unlike Charadriidae, have numerous fine pores in premaxillary bone to accommodate Herbst's corpuscles, which are assumed to be associated with more tactile, less visual, methods of foraging; some species have been shown to be capable of sensing buried prey, either through chemoreception (van Heezik *et al.* 1983) or mechanical detection of vibrations or self-induced pressure signals (Gerritsen *et al.* 1983; Gerritsen 1988; Piersma *et al.* 1994). Skeleton and musculature of jaw distinctive (Burton 1974). In most species, rynchokinesis of skull highly developed, enabling flexible upper mandible to be opened or retracted at tip only (to grasp prey while probing). Tarsi and tibiae, short to long, with transverse scales (except in *Numenius*). Four toes in all species except Sanderling *Calidris alba*; toes fairly long with lateral membrane (webbed in some); hindtoe, small and raised (except in Arenariinae). No crop. Caeca present. Apparently no other waders have spiral sperm cells (similar to those of Passeriformes).

Non-breeding plumage mostly dull and cryptic: mottled greys and browns above, and paler or white below, with or without streaks and spots. Breeding plumage generally much brighter (except in curlews, snipes and woodcocks), with more rufous or black. In HANZAB region, adults seen mainly during austral summer in non-breeding plumage, though breeding plumage can be seen on birds just before n. migration or on arrival after s. migration. Sexes usually similar. Bills, legs and feet variously, sometimes brightly, coloured. Adults generally have two moults per cycle: (1) a partial pre-breeding (pre-alternate) moult of most feathers of body, and, often, some tertials and upperwing-coverts; and (2) a complete post-breeding (pre-basic) moult; both usually performed in non-breeding areas or while staging on migration. Primaries moult outwards, usually after s. migration; some subspecies of Dunlin *Calidris alpina* (q.v.), Purple Sandpiper *C. maritima* and Rock Sandpiper *C. ptilocnemis* moult all primaries on or near breeding grounds before s. migration, a strategy rare in *Calidris*; Bristle-thighed Curlew *Numenius tahitiensis* moult remiges rapidly, inducing flightlessness in 50–70% of birds, apparently uniquely among Charadriiformes. Precocial young nidifugous; most feed themselves. Down varies greatly in structure and pattern; pattern mainly of spotted or striped type (Fjeldså 1977). Juvenile plumage usually distinctive; most like that of non-breeding adults, but often a little brighter, especially in Calidridinae. Moults of subadults complex and vary considerably with species, route of migration and age of first breeding. Adult plumage attained when 3–21 months old; most scolopacids of our region (except snipes) first attain adult plumage through partial first pre-alternate moult when c. 8–11 months old, or through complete second pre-basic moult when c. 12–16 months old (see discussion of Moults in General Introduction). Swift runners; wade expertly and some species swim habitually (Phalaropodinae). Stance often upright. Flight, fast and direct, often in tight flocks.

When breeding, most scolopacids (except some snipes and woodcocks) are birds of open habitats, including tundra. At other times, use a variety of habitats, including forests (woodcocks) and open sea (phalaropes), though most prefer shallow, fresh, brackish or intertidal wetlands. Greatest concentrations occur on intertidal mudflats,

especially estuaries. Feed mainly by touch, and the mandibular skeleton has distinctive features associated with tactile methods of foraging. When feeding, most probe into soft, moist substrata to catch invertebrates; some (e.g. Arenariinae) forage on rocky shores; surface-tension mechanism for feeding on plankton, recently described for Red-necked Phalaropes *Phalaropus lobatus* (Rubega & Obst 1993), may prove to be widespread among scolopacids with fine bills. Mixed-species foraging flocks common.

Migration the most striking feature of scolopacids. All but some Gallinagoninae, Scolopacinae and two aberrant Tringinae migrate (though some Tringinae partly resident in Europe), usually from breeding grounds in higher latitudes of n. hemisphere to lower latitudes of n. or s. hemispheres; many undertake extremely long migration steps, with non-stop flights of several thousand kilometres preceded by dramatic increase in weight. Scolopacids of HANZAB region breed mainly in e. Russia, Mongolia, n. China and Alaska; Latham's Snipe *Gallinago hardwickii* breeds Japan and in small numbers in e. Russia.

Migratory routes vary dramatically depending on the relationship between breeding and non-breeding ranges, and the ability to undertake long-distance non-stop flights. Some species migrate overland, some via coastal routes and others cross oceans; many species use a combination of these routes. Some species return to breeding grounds by the same route used in s. migration while others return by different routes, and make a loop migration (e.g. Curlew Sandpiper *Calidris ferruginea*). Timing of departure from breeding grounds often varies between sexes (e.g. Bar-tailed Godwit *Limosa lapponica*) and between ages; juveniles often leave at slightly different time (e.g. Bar-tailed Godwit *Limosa lapponica*) or migrate via a different route (e.g. Sharp-tailed Sandpiper *Calidris acuminata*). Most regular non-breeding migrants to Aust. migrate via East-Asian–Australasian Flyway; others to Aust. and, especially NZ, cross Pacific Ocean. Generally, in Aust. and NZ, s. migration Aug.–Nov. and n. migration, Feb.–May. Individuals of most species display a high degree of site-fidelity at breeding, non-breeding and even staging areas; others have little fidelity to breeding site and populations mix much (e.g. Curlew Sandpipers; P.S. Tomkovich). In HANZAB region, displays sometimes seen before migration, e.g. Red Knots in tight single-species flocks in nw. Aust. before migration (Lane & Jessop 1985). Pre-migratory flighting observed during Mar. in NZ (McKenzie 1967).

In non-breeding areas, most species undertake regular local movements between feeding and roosting sites or between different feeding sites. Most local movements are in response to tides, which affect exposure of feeding grounds (e.g. Hindwood & Hoskin 1954; Carter *et al.* 1976; Saunders & de Rebeira 1985; Smith 1985; Lane). Some roosting and feeding sites are close together, birds gradually dispersing from or returning to roosting sites as tides fall and rise (e.g. Robertson & Dennison 1979). At other sites, roosting and feeding sites farther apart, with birds even flying between islands or between islands and mainland (Saunders & de Rebeira 1985); in Capricorn Grp, Qld, Ruddy Turnstones and Grey-tailed Tattlers *Heteroscelus brevipes* fly at least 4 km from Tyron I., where roost at high tide, to North West Reef, where thought to feed (Prendergast *et al.* 1985); at Cairns, Qld, Whimbrels *Numenius phaeopus* move to mouth of Barron R. every evening (Amiet 1957) and can travel up to c. 20 km between roosting and feeding sites (McKenzie 1967; Garnett 1989). In poor weather, such as days of high winds or in storms, may move to sheltered areas other than normal roosting sites, such as near-coastal wetlands or pools in dunes (e.g. Crawford 1972; Forest 1982; Aust. Atlas). Some species dispersive, either locally or over longer distances (see accounts), sometimes in response to availability of food or availability of suitable wetland habitat. In NZ, Common Greenshanks *Tringa nebularia* tend to move round within harbours rather than returning to roosting site each day (Sibson 1965) and, in Tas., Common Greenshanks appear to move between coastal sites (Wall 1953); Curlew Sandpipers apparently move from Westport Bay, Vic., in Aug. when daily exposure of intertidal feeding grounds reduced (Loyn 1978; see also Hindwood & Hoskin 1954; Alcorn 1988).

Mainly feed and roost in single-species flocks. All species are strong fliers and those that form flocks often perform spectacular and complex aerial movements, which are performed with remarkable precision. Many species territorial during breeding season, but others lack specific territorial boundaries and are semi-colonial. Courtship displays, elaborate, including spectacular song-flights, often associated with formation of pairs. Distraction displays include repetitive display-flights, rodent-runs, and feigning injury.

Mating systems extraordinarily diverse, including monogamy (some species pair for life), polygyny (in some species, males display on leks, mating with females that visit their territories; in others, males maintain simultaneous pair-bonds with more than one female but provide no parental care) and polyandry (including double-clutching monogamy, where female lays two successive clutches, each of which is incubated by single adult; and classical polyandry, where female maintains pair-bonds with more than one male). Reasons for diversity of mating systems not clear but short breeding seasons and ability of single parent to incubate clutch and brood and raise chicks probably involved; possibly also related to phylogenetic history. For reviews of mating systems, see Ligon (1993) and Pitelka *et al.* (1974).

In CALIDRIDINAE, mating systems remarkably varied, including monogamy, polygyny, polyandry; most species monogamous (e.g. Pitelka *et al.* 1974). Role of sexes in parental care as diverse as mating systems. Apparently solely by female in the four polygynous species; roughly equally shared in some (e.g. Dunlin *C. alpina*), though female tends to leave chicks earlier; in others, male undertakes more of work and females leave before chick-rearing (or even

incubation) complete. Behaviour more complex in successive polyandrous species, with males raising first brood while females may lay and raise another clutch. In GALLINAGONINAE, mating systems poorly known but several species monogamous; Great Snipe *Gallinago media* promiscuous, mating at leks, and apparently unique among snipe in performing courtship display on ground; others have crepuscular or nocturnal display-flights accompanied by distinctive calls and non-vocal sounds (see Gallinagoninae). Mass flights of displaying snipes have been said to be aerial leks in several species, but confirmation needed (could be result of unsettled territorial boundaries early in breeding season) (Byrkjedal 1990). In TRINGINAE, most species monogamous but successive polyandry can occur in Spotted Redshank *Tringa erythropus* and Spotted Sandpiper *Actitis macularia*. Parental care shared about equally or females leave breeding grounds early while males undertake or finish rearing chicks. ARENARIINAE are monogamous; Ruddy Turnstone territorial and aggressive. LIMNODROMINAE, poorly known; apparently monogamous; territorial but *L. semipalmatus* nests in small colonies. Both sexes incubate; males undertake most of chick-rearing. In PHALAROPODINAE, many sex roles reversed when breeding; females almost unique among Scolopacidae in undertaking courtship behaviour, contesting access to mates in 'scramble displays' (Reynolds 1987; Colwell & Oring 1988a). Phalaropes usually monogamous, though polyandry recorded in all three species; incidence of polyandry may vary between populations but reasons not yet clear (e.g. Colwell & Oring 1988b). Males undertake virtually all incubation and raise chicks alone (see Colwell 1986; Colwell & Oring 1988a,b).

Most scolopacids breed first at 2 years old, though some species can breed in their first year and maturity may be delayed for more than 2 years in some large long-distance migrants. Usually nest on ground, often concealed in herbage. The scrape, often made during a scraping ceremony by the male in the presence of female, is often lined, usually after laying the first egg and more lining is added during incubation. Unusually, Solitary *Tringa solitaria*, Green *Tringa ochropus* and some Wood *Tringa glareola* Sandpipers recorded nesting in trees, usually in nests of other birds (see BWP). Usually four eggs per clutch, in some cases two or three. Eggs usually pyriform, with dark-brown and black markings, over paler ground-colour; all are cryptically coloured. Incubation normally starts with laying of last egg and chicks hatch almost simultaneously. Both sexes usually share incubation, though one bird often takes greater share. Downy young leave nest within 1 day of hatching and generally accompanied by brooding adult till able to fly. Social organization, social behaviour and breeding not discussed further in subfamily accounts.

In East-Asian–Australasian Flyway, hunting and destruction of wetland habitats major threats to shorebirds; this Flyway said to be probably the most threatened migration system in world (Lane & Parish 1991). Outside Aust. and NZ, hunting widespread, mainly for food, but little information available on impact on populations (Lane & Parish 1991). For example, in Thailand and n. Vietnam, both Great Knot and Red-necked Stint on passage or overwintering are eaten, and captive birds are kept to act as decoys to catch other waders; band-recoveries of Red-necked Stints in n. Vietnam have come from birds taken for food (Starks 1987; J.R. Starks). Many wetlands destroyed by reclamation for agriculture, aquaculture, salt-production, and urban or industrial development, including wetland habitats in Aust. and NZ (Lane & Parish 1991). Aust. is signatory to the Ramsar Convention and to bilateral treaties with Japan (JAMBA) and China (CAMBA) to protect migratory birds.

In many n. hemisphere breeding areas, breeding success cyclical and thought to be linked to population cycles of lemmings, which in turn influence levels of predation of breeding birds (Underhill *et al.* 1993). For example, in breeding areas of Curlew Sandpipers, decreased populations of lemmings *Lemmus sibiricus* and *Dicrostonyx torquatus*, the regular prey of Arctic Foxes *Alopex lagopus*, results in increased predation of eggs and young of Curlew Sandpipers (Roselaar 1979). Reproductive success in n. hemisphere in preceding breeding season reflected in numbers and proportion of juveniles and immatures in populations in non-breeding areas, such as Aust. and NZ.

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28 Gallinagoninae

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Subfamily CALIDRIDINAE arctic sandpipers and allies

Small to medium-sized (15–29 cm) migratory shorebirds. Twenty-four species in seven genera (see Table 1); six genera monotypic; *Calidris* comprises remaining 18 species (though these were once placed in several different genera). In HANZAB region, 19 species recorded: ten regular non-breeding migrants, eight accidental, one doubtfully recorded (and one problematic hybrid). *Calidris* may contain 2–3 species-groups (BWP): (1) knots (two species), which have much in common with Surf-bird *Aphriza virgata*, especially Great Knot *C. tenuirostris* (Jehl 1968a); (2) sandpipers with partially webbed feet ('*Ereunetes*' group: *C. pusilla* and *C. semipalmatus*); and (3) other sandpipers ('*Erolia*' group). Groups (2) and (3) do not differ greatly, and may be more closely related to *Micropalama*, *Limicola*, *Eurynorhynchus*, *Tryngites* and *Philomachus* than they are to knots and Surf-birds (Jehl 1968a; BWP). Patterns of downy young suggest possible affinities of Calidridinae to Gallinagoninae, Limnodrominae and, possibly, Arenariinae (Jehl 1968a,b; Fjeldså 1977) but precise relationships not clear; allozyme and DNA research so far (e.g. Dittman *et al.* 1989; Dittman & Zink 1991; Christian *et al.* 1992) have not included comparison with all other subfamilies of Scolopacidae.

Table 1

GENUS	NUMBER OF SPECIES	NUMBER OF SPECIES IN HANZAB REGION ¹
<i>Aphriza</i>	1 (Surfbird)	0
<i>Calidris</i>	18	8 NB, 6A, 1D
<i>Eurynorhynchus</i>	1 (Spoon-billed Sandpiper)	0
<i>Micropalama</i>	1 (Stilt Sandpiper)	1 NA
<i>Tryngites</i>	1 (Buff-breasted Sandpiper)	1 NA
<i>Limicola</i>	1 (Broad-billed Sandpiper)	1 NB
<i>Philomachus</i>	1 (Ruff)	1 NB

¹ NB = regular non-breeding migrant; A = accidental; D = unacceptably claimed.

Females generally slightly larger than males, but male is larger in polygynous species: Pectoral *C. melanotos*, Sharp-tailed *C. acuminata*, and Buff-breasted *T. subruficollis* Sandpipers, and Ruff *P. pugnax* (Jehl & Murray 1986). Bill, short and finely pointed in most species, but superficially plover-like in *Tryngites* and broad and flattened in *Eurynorhynchus*. Nostrils in a depression extending anteriorly as a groove that nearly reaches tip of upper mandible. Highly rhyndokinetic except in *Aphriza*; upper jaw typically lightly built and tip of bill sensitive, with many Herbst's corpuscles (associated with tactile foraging). Muscles of jaw and tongue hypertrophied in *Limicola* and *Tryngites*; latter also has hypertrophied salivary glands, in these respects resembling plovers. Internal feeding apparatus of *Calidris* and *Micropalama* very similar (Burton 1974) and further research needed on whether *Micropalama* merits generic recognition. Legs, moderately long and tarsus scutellate. Hindtoe small and raised in most; uniquely among Scolopacidae, it is absent in Sanderling *C. alba*. Anterior toes usually unwebbed but *Calidris* of '*Ereunetes*' group have small basal web between front toes.

Adult breeding plumage finely patterned in rufous, black, grey and buff; white or rufous below, usually with dark spotting, streaking or suffusion on breast. Sexes alike or nearly so, except for strong sexual dimorphism in Ruff, which is also unusual in attaining breeding plumage in pre-supplemental (rather than pre-alternate) moult. Adult non-breeding usually much plainer, grey to brown above and mostly white below; in *Tryngites*, little seasonal change in appearance. Juvenile plumage distinctive, usually with upperparts superficially like that of adult breeding and underparts more like adult non-breeding. All species replace most of juvenile body-plumage early in first pre-basic moult (attaining plumage like non-breeding), typically when in late stages of s. migration or after arrival in non-breeding areas. Thereafter, moult-strategies of subadults complex, but can be separated into three broad categories: (1) Undergo complete moult of all juvenile feathers in first pre-basic when c. 6–8 months old, developing adult breeding plumage in first pre-alternate moult just before first n. migration when c. 9–10 months old (e.g. most Little Stints *C. minuta*, Least *C. minutilla* and Sharp-tailed *C. acuminata* Sandpipers). (2) Retain juvenile remiges, and often much of tail and wing-coverts, through first pre-basic; may replace some outer primaries in partial first pre-supplemental moult; attain plumage very similar to that of adult breeding in first pre-alternate moult before undertaking first n. migration when c. 9–10 months old (e.g. Dunlin *C. alpina* and Purple Sandpiper *C. maritima*). (3) Like second strategy, but first pre-alternate moult produces dull plumage, mostly like non-breeding but often

with varying number of feathers like breeding plumage (colours of these feathers often duller than adult breeding); such birds typically delay first n. migration until at least 2 years old, first attaining adult non-breeding plumage in complete second pre-basic moult when c. 12–15 months old (e.g. Red-necked Stint *C. ruficollis*, Curlew Sandpiper *C. ferruginea* and Great Knot *C. tenuirostris*). Down of precocial young, long and loose, especially on nape. Mainly ochraceous to rich brown above, with complex patterns of black blotches and bands, including characteristic marking shaped like hour-glass on centre of back; white below, often with brown wash on foreneck and breast. As in Gallinagoninae and Limnodrominae, spotted dorsal pattern formed by white powder-puffs attached to tips of black down. In most species, white barbules at each feather-tip densely packed and interlock with those of other feathers as large closely knit puffs (resembling scattering of large snow-flakes). In knots and *Aphriza*, powder-puffs have looser microstructure and do not entangle much, so some areas (especially in older chicks) may appear to have diffuse white mottling rather than distinct spots. Some other variation in colour and pattern of downy young attributed to breeding habitat rather than taxonomy (see Jehl 1968b; Fjeldså 1977; BWP).

Most species breed in tundra, a few in other open habitats S to Temperate regions of n. hemisphere. Highly migratory; those breeding high Arctic breed faster and migrate farther than most other species of waders. In non-breeding season, inhabit wide range of shallow wetlands. Some species almost exclusively coastal (e.g. Red *C. canutus* and Great *C. tenuirostris* Knots and Sanderling *C. alba*); some typically occur on inland wetlands (e.g. Long-toed Stint *C. subminuta*); others rather catholic in choice of habitat. Feeding behaviour varies; include probing and stitching (a rapid series of shallow probes made close to one another). Usually forage by touch and several species known to detect prey by chemoreception or detection of vibrations (e.g. van Heezik *et al.* 1983; Gerritsen 1988).

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Calidris tenuirostris Great Knot

COLOUR PLATE FACING PAGE 257

Totanus tenuirostris Horsfield, 1821, *Trans. Linn. Soc. Lond.* 13: 192 — Java.

Calidris is derived from the specific name *Tringa Calidris* given to the Red Knot *Calidris canutus* by Gmelin (1789, *Syst. Nat.* 1[2]) and comes from the Greek (καλίδρις), a form of σκαλίδρις, an unidentified ash-coloured bird mentioned by Aristotle and taken by subsequent authors to be some sort of sandpiper (perhaps the Common Sandpiper; see Oliver, 1968, *Wildl. Publ.* 106: 176). The specific epithet is Latin for slender (*tenuis*) billed (*-rostris*, from *rostrum*, bill); this Knot was originally considered to be allied to the redshanks and its bill was more slender than that of the European members of that group.

OTHER ENGLISH NAMES Slender-billed, Stripe-crowned or Eastern Knot; Large or Great Sandpiper.

MONOTYPIC

FIELD IDENTIFICATION Length 26–28 cm; wingspan c. 58 cm; weight c. 155 g. The largest *Calidris*. Medium-sized, bulky but attenuated wader with medium-length, fairly slender bill, straight or faintly decurved at tip; long wings that project beyond tip of tail at rest; and short dark legs. Between Curlew Sandpiper *Calidris ferruginea* and Grey Plover *Pluvialis squatarola* in size, though closer to latter. Similar in size, shape and proportions to Red Knot *Calidris canutus* but larger and bulkier, with proportionately longer and heavier bill, slightly deeper at base and tapering to finer, often drooping, tip; proportionately smaller head; longer neck; flatter back and

belly profile and deeper chest, which combine with longer wings to give more attenuated shape. In all plumages, head and neck heavily streaked, with diffuse dusky loreal patch and off-white supercilium, narrow white wing-bar, and obvious white patch on rump and uppertail-coverts. Sexes alike, though female slightly larger and tends to have less chestnut in scapulars in breeding plumage. Marked seasonal variation. Juvenile distinctive. Immatures separable when close.

Description Adult breeding Chin and throat, white; rest of head and neck, white, heavily streaked black, with indistinct off-white supercilium (clearest above and just

behind eye but often almost obscured by dark streaking) and diffuse dusky triangular loreal patch. Feathers of mantle and upper few rows of scapulars, black, broadly fringed white or pale grey or, occasionally, rufous; rest of scapulars vary: most are black with broad greyish tip, narrow white fringe and, on larger feathers of central few rows, large, paired subterminal chestnut spots; others show pattern intermediate between breeding and non-breeding, appearing grey with black shaft and varying black centres, and narrow white fringe; a few worn, plainer brownish-grey feathers often retained from non-breeding. Tertials often plain brownish-grey with diffuse dark centres and narrow white fringes, retained from non-breeding; or fresh, darker, with black centres and narrow white fringes, sometimes with broad wavy chestnut fringes and narrow white tip; often a mixture of both. Back and upper rump, dark grey, broadly streaked white. Innerwing-coverts, dark brownish-grey with black shafts, narrowly fringed white. Underbody, white, with heavy black streaking on foreneck and upper breast, bold black spots and bars on lower breast and upper belly, and large black spots and arrowheads along flanks and sides of belly to lateral undertail-coverts. In flight: show brownish-grey upperwing with contrasting blackish primary coverts and narrow white wing-bar (white shafts of primaries and narrow white tips of greater secondary and inner primary coverts); white patch on lower rump and uppertail-coverts, sparsely marked with black streaks and spots and contrasting with plain dark-grey tail; mostly white underwing, with slightly darker, greyish greater primary coverts and trailing-edge, narrow dark leading-edge to coverts, and fine dark markings on axillaries. In worn plumage, pale fringes and tips of feathers wear away: mantle and back become almost black; a striking chestnut band formed on central scapulars above folded wing; and black streaking on neck and spotting on breast forms almost solid area of black. Bill, black, tinged green towards base. Iris, dark brown. Legs and feet, dark slate-grey or greenish-grey. **Adult non-breeding** Like breeding, but: head and neck, brownish grey streaked black; chin and throat, white; has somewhat grey-faced, expressionless appearance. Mantle, back, scapulars and innerwing-coverts, brownish grey, and all feathers with diffuse darker centres, blackish shaft-streaks and contrasting narrow white fringes giving upperparts streaked or variegated appearance. Underbody, white, with faint grey suffusion on breast and heavy grey streaking on foreneck, grading to spots on breast; and with grey triangular streaks or rounded spots along flanks to lateral undertail-coverts. In flight, white patch on lower rump and uppertail-coverts less streaked and spotted. Upperparts become browner with wear. **Juvenile** Like adult non-breeding but darker and more boldly patterned. Head and neck more coarsely streaked; sides of head and neck paler and more finely streaked than rest, giving dark-capped appearance; some show longer, clearer supercilium. Feathers of mantle and scapulars, blackish grading to dull grey on bases, former with crisp narrow off-white fringes, latter, narrow off-white spots on fringes; tertials and innerwing-coverts, paler, brownish grey, with clear blackish shaft-streaks, blackish subterminal bands and narrow white fringes, though distal parts of tertials and inner few greater coverts usually show off-white spots on fringes, as scapulars. Underbody, white, with similar pattern of streaking and spotting to adult non-breeding, though markings are larger, bolder and darker, blackish brown, often coalescing to form dark band on breast similar to that of adult breeding; often show fairly sharp demarcation between dark breast and more sparsely spotted upper belly and flanks; in very fresh plumage, ground-colour of breast suffused

pale buff. With wear, mantle, back and scapulars become more uniform, black; pale fringes to tertials and innerwing-coverts somewhat reduced; and dark markings on foreneck and breast merge to form more uniform blackish breast-band. Legs and feet, dull green, paler and greener than adult. **First immature non-breeding** Like adult non-breeding but retain some (usually many) pale-fringed juvenile innerwing-coverts and tertials, which contrast with fresh plumage of upperparts (all plumage uniformly patterned and fresh in adult); also distinguished by differences in wear and moult of remiges (see Ageing). **First immature breeding** Many as first immature non-breeding (though may replace scattered feathers on head, upperparts and underbody with feathers intermediate between those of adult breeding and non-breeding), others similar to adult breeding; both separable from adult by active differences in moult of remiges (see Ageing).

Similar species Adult in breeding plumage readily distinguished from other calidrids by large size, heavy black streaking on head and neck, blackish upperparts with contrasting chestnut blaze through scapulars, white underbody with distinctive black spots on breast and flanks, and no red on underbody (cf. Red Knot). In non-breeding and juvenile plumages, can be confused with **Red Knot** (q.v.). In distant flight views, may be confused with other basically grey waders, particularly **Bar-tailed Godwit** *Limosa lapponica*, **Asian Dowitcher** *Limnodromus semipalmatus* and **Grey Plover** in non-breeding and juvenile plumages. Bar-tailed Godwit and Asian Dowitcher have longer necks, much longer bills, and feet project beyond tip of tail; Godwit is also larger. Grey Plover is bigger, with more conspicuous wing-bar, distinctly paler, white-tailed appearance, and diagnostic black axillaries contrasting strongly with white underwing.

Highly gregarious, in small to large flocks on sandy or muddy estuaries and coasts with large tidal mudflats; often in dense flocks of hundreds or thousands at favoured sites. Form dense flocks at roost; associate freely with other waders, especially Red Knots, godwits, sand plovers and Red-necked Stints. Gait and feeding actions similar to those of Red Knot, but walk more slowly, and work more steadily across mud or through shallows, probing one spot at a time with several deep jabs and immersing entire bill and face. Flight typical of genus; similar to that of Red Knot, but action often looser, with slow beats of long wings; appear longer-winged and less compact than Red Knot; flying flocks often less dense than those of Red Knot, in looser lines, like those of Bar-tailed Godwit. Quiet in non-breeding season, rarely calling when flushed; usual flight call similar to that of Red Knot: low disyllabic *nyut nyut*.

HABITAT In Asia: sheltered coastal habitats, with large intertidal mudflats or sandflats, including inlets, bays, harbours, estuaries and lagoons; also ocean beaches. Often on sandy beaches with mudflats nearby, sandy spits and islets, and sometimes on exposed reefs or rock platforms (Sedgwick 1949; Morris 1989; Bamford 1988). Sometimes on shorelines with mangroves, but not flats and banks with seagrass (Boekel 1976; Lane; Garnett 1989). Occasionally on ponds in saltworks, swamps near coast, saltlakes and non-tidal lagoons (Smith 1964; Smith *et al.* 1971; Crawford 1972; Storr 1977). Rarely, on inland lakes and swamps (McKean 1963; Wheeler 1963).

Forage on intertidal flats, in soft mud or sand; usually in shallow water, often at edge of water as tide recedes (Garnett 1989; Lane; Vic. Atlas). Occasionally forage on ocean beaches (Pegler 1983). Once seen foraging, well out from shore, in small shallow unvegetated swamp (Smith *et al.* 1971). Roost

in sheltered sites on spits, banks, islets or beaches, often at edge of water or in shallow water; also in coastal dunes and saltflats among mangroves (Wheeler 1963; Smith *et al.* 1971; Ewart 1973; Brown 1980; Garnett 1989; Lane).

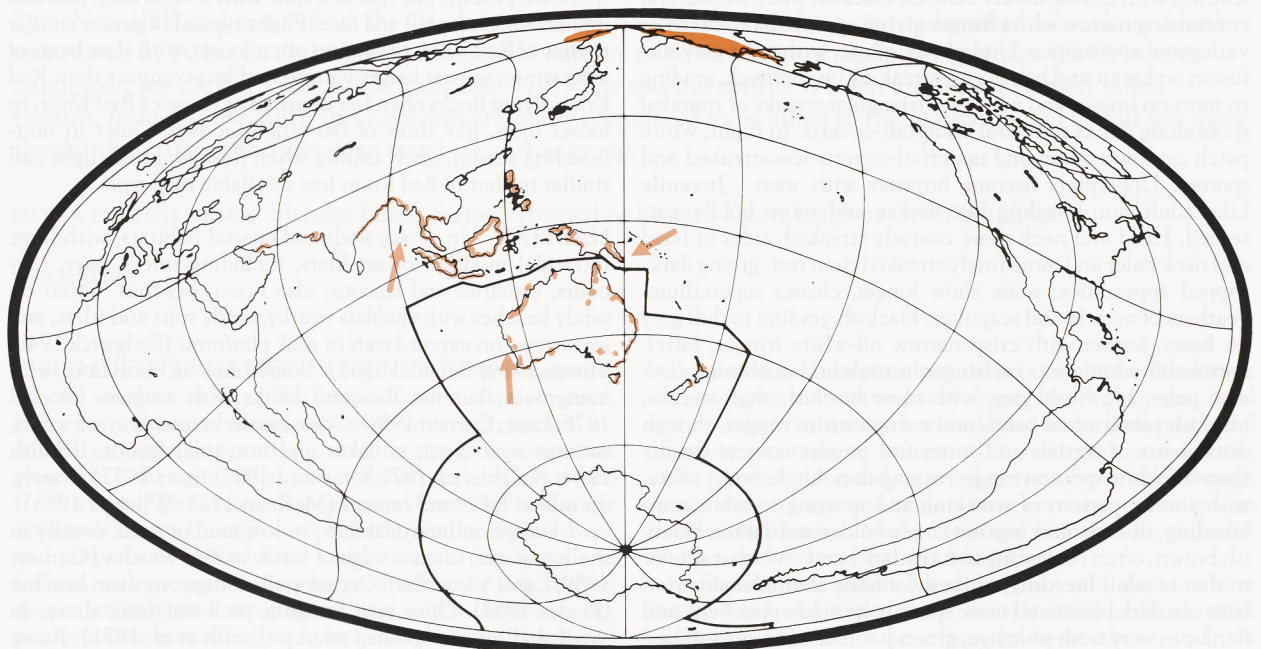
DISTRIBUTION AND POPULATION Breed ne. Siberia but distribution poorly known: from mouth of Kolyma R. and Gorelovy Mts (possibly from Verkhoyanskii Ras), E to Anadyr and Koryatsky Ras. Common passage migrant e. China and Japan; uncommon to rare on passage in Korea, Philippines, Vietnam, Thailand, Malaysia and Indonesia; rare New Guinea. Most spend non-breeding season in Aust. Winter in small numbers from Burma and Bangladesh, W to Bay of Bengal, and occasionally to Persian Gulf. Vagrant to NZ, Arabia, islands of Indian Ocean, Morocco, nw. Europe and Alaska (Dement'ev & Gladkov 1951; Hindwood & Hoskin 1954; Ali & Ripley 1980; Myers *et al.* 1982; Marchant 1986; Anon. 1991; Safford 1992; Lane; BWP).

Aust. Common in N, from Dampier Arch., WA, to Moreton Bay, Qld; less common in S. In s. Aust., first recorded only recently; now recorded regularly. **Qld** Passage migrant from se. Gulf of Carpentaria to islands of Torres Str. and on Qld coast S to Moreton Bay. Mostly se. Gulf of Carpentaria, Broad Sound–Shoalwater Bay, Mackay region and Moreton Bay (Lane; Aust. Atlas); scattered records inland (Storr 1984; Qld Bird Rep. 1986). **NSW** Scarce on coast S to about Narooma (Morris *et al.* 1981; Whiter 1991). Rarely inland, including Armidale, Gilgandra and Griffith (Morris *et al.* 1981; Lane). **Vic.** First confirmed record, 29 Jan. 1961 (Wheeler 1963). Mostly round Port Phillip Bay, especially Mud I., and e. Corner Inlet; also recorded Mallacoota, Gippsland Ls, Westernport Bay and Port Fairy (Vic. Bird Reps 1981–86; Vic. Atlas). Inland at Woorinen and Mildura (Wheeler 1963; Thomas 1970; Aust. Atlas). **Tas.** First record, Nov. 1965 (Thomas 1968). Irregular, in small numbers: Bird Pt (60, 28 Feb. 1987; Tas. Bird Rep. 17); Robbins and Perkins Is; Sorrell; C. Portland and Little Mulletroe Bay. In SE, from Marion Bay, Orielton, Derwent Estuary, Ralph's Bay and S. Arm (Thomas 1968, 1970; Smith *et al.* 1971; Ashby 1987; Tas.

Bird Reps). **SA** First record, Gulf St Vincent, 6 May 1957 (McPherson 1957). Recorded from SE to Streaky Bay, with most in Spencer Gulf, Gulf St Vincent and on Kangaroo I. (Close & McCrie 1986; Lane; Aust. Atlas). **WA** Scattered, on s. coast from Eyre to Perth, and from Murchison R. to Carnarvon; very common coasts of Pilbara and Kimberley, from Dampier Arch. to NT border (Davies & Chapman 1975; Johnstone 1983; Storr 1985; Lane; Aust. Atlas). **NT** Common on coast from Darwin and Melville I., through Arnhem Land to se. Gulf of Carpentaria (Lane; H.A.F. Thompson & D.K. Goodfellow).

NZ Rare visitor (singles unless stated): **NI** Karaka, Manukau: 16 Apr. 1972, 18 Mar.–1 Apr. 1979 (Brown 1980; CSN 19, 26); Miranda, Firth of Thames: two, 7–8 Feb. 1970; Feb.–Mar. 1972 (Brown 1970; CSN 19); Mar. 1971, 30 Sept. 1972, Feb.–11 Mar. 1973, 1981 (CSN 19,20; NZCL); Wanganui R. estuary: 1 Feb. 1986 (CSN 34), three: 24 Oct. 1992, 27 Dec. 1992–20 Mar. 1993 (CSN 41); Manawatu Estuary: three, 15 Oct. 1967 (Andrew 1968); 1 Jan.–3 Mar. 1980, 1983, 27–28 Dec. 1987 (CSN 28, 36; NZCL). **SI** Farewell Spit, Nelson: 1981, Nov. 1984 (Sagar 1985; NZCL); Port Waikato, 8 Nov. 1992 (CSN 41).

Status One of the most abundant shorebirds in Aust. though considered rare, endangered or uncommon till 1970s (Johnsgard 1981; Myers *et al.* 1982; Barter 1986; Tulp & de Goeij 1991; Lane). **Population Aust.** Estimated 270,000 (Watkins 1993); till late 1970s, world population thought to be 10,000–20,000 individuals (Barter 1986). Totals for summer and winter counts, 1986–89, summarized in Table 1 (Hewish 1986, 1987a,b, 1988, 1989a,b, 1990a,b). Sites of significance and maximum or average counts from summer and winter surveys round Aust., 1981–85, were: Eighty Mile Beach, WA, 160,000; se. Gulf of Carpentaria, Qld, 68,000; ne. Arnhem Land, NT, 65,200; Roebuck Bay, WA, 22,600; sw. corner Gulf of Carpentaria, NT, 21,400 (Lane). Other sites of international importance and maximum counts (Watkins 1993) include: Roper R. area, NT, 21,400; Darwin area, NT, 14,800; Boucat Bay, NT, 4895; Broad Sound–Shoalwater Bay, Qld, 4200; Mackay area, Qld, 4000.



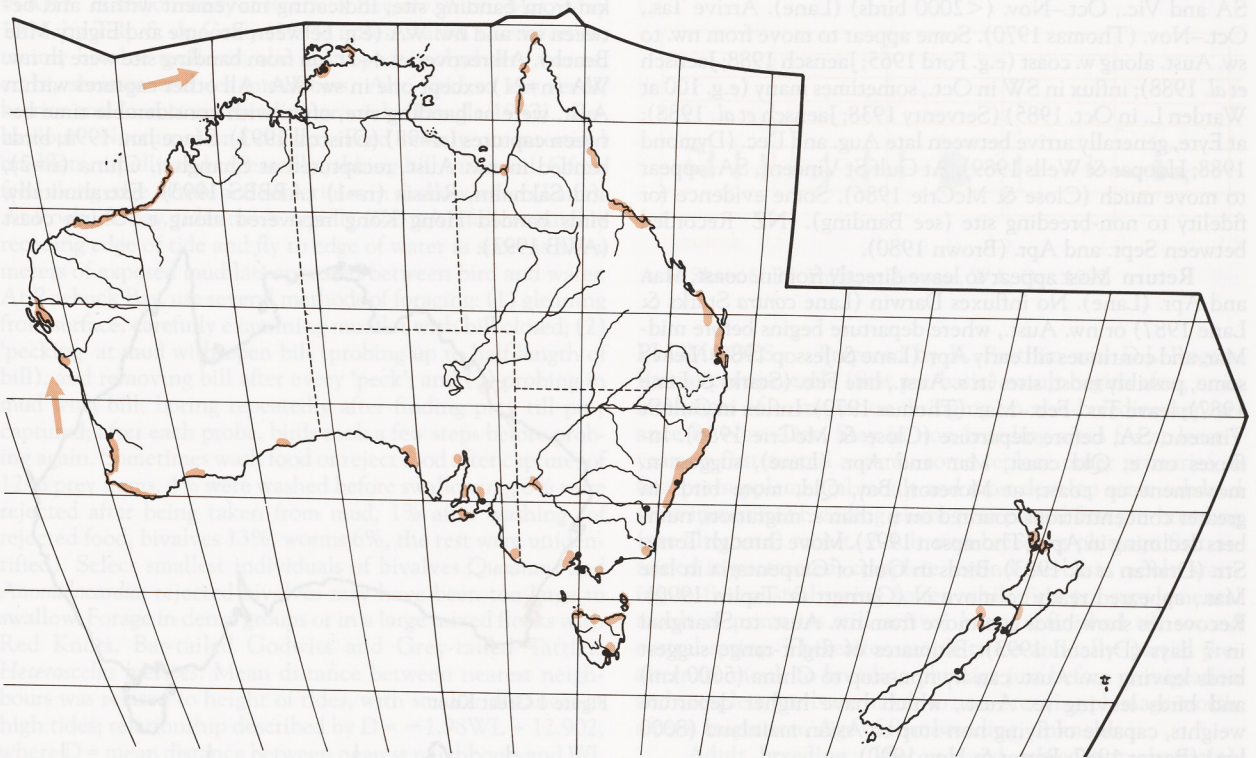


Table 1

Year	Summer Total	No. Sites	Winter Total	No. Sites
1986	4,658	23	1,181	23
1987	10,850	22	822	23
1988	6,415	23	489	23
1989	2,575	22	620	21

MOVEMENTS Migratory. Move S to non-breeding areas in Aust. or Persian Gulf. Mainly migrate along coasts (Dement’ev & Gladkov 1951), though some visit inland wetlands on passage (Beehler *et al.* 1987). Probably make long flights between a few staging sites (Barter & Hou 1990; Lane). Some long-distance vagrancy (Hayman *et al.* 1986; Marchant 1986; Anon. 1991; Safford 1992).

Departure Move to coast soon after breeding, though recorded in inland Ussuriland, Russia (Dement’ev & Gladkov 1951). Females leave before males (Myers *et al.* 1982). Pass through se. Siberia, and along coasts of Sea of Okhotsk, Sea of Japan and East China Sea (BWP). Move through: s. Ussuriland from beginning of Aug., but mainly first half Sept. (Dement’ev & Gladkov 1951); e. China, late July to late Oct., with most Aug.–Sept. (when birds banded in Aust. have been recovered) (la Touche 1931–34; Hemmingsen & Guildal 1968; Driscoll 1993; Lane); in e. China birds appear to use different routes or staging sites on s. and n. migrations (AWB 1993). Considered uncommon passage migrant Korea (Gore & Won 1971), though recently many counted on passage, Sept. (Piersma 1985; AWB 1993). Move through Japan, Sept. (Dement’ev & Gladkov 1951). Some move through Taiwan, Sept.–Oct. (AWB 1993), and Hong Kong, late Aug.–Nov. (Chalmers 1986). Uncommon on passage in Burma and Thailand, though w. coast Thailand may be an important route (Smythies 1981; Lekagul

& Round 1991). Rare in Philippines (Delacour & Mayr 1946), though recorded moving through Olango I., Aug. to at least Oct. 1989 (Magsalay *et al.* 1990). Some passage in w. Micronesia, with a few passing Pulau, Sept. (Baker 1951); rare in Truk (Pratt *et al.* 1987). Recorded Cambodia (AWB 1993); generally uncommon Vietnam (Cheng 1976), Malaysia (Glenister 1971) and Indonesia (Driscoll 1993). Apparently pass through Sumatra, Oct.–Dec. (van Marle & Voous 1988). Move through Borneo in small numbers; at Sabah, 1984, maximum numbers on passage, late Sept. and early Oct. (Beadle & Whittaker 1984; Smythies 1986); move through Wallacea, from Oct. (White & Bruce 1986). Small numbers Bali, Aug.–Sept. 1982 (Ash 1984) and Timor, Oct. 1973 (McKean *et al.* 1975). Locally common se. Irian Jaya from Sept., with flocks of thousands in Nov.; probably regular in small numbers along s. coast of PNG, E to Central Province, early Sept. to early Dec. (Hoogerwerf 1964; Coates 1985; Hicks 1990). **Aust.** Large numbers arrive in NW, late Aug. and early Sept. (Lane); juveniles and many males may not arrive till Oct.–Nov. (Barter 1986). Some move through Torres Str. (Draffan *et al.* 1983). Most stay in N (Lane). **NZ** Rare visitor, mainly to NI.

Non-breeding Aust. Most common in N (Aust. Atlas). After arriving in NW, some move on by Nov., appearing to move E along n. coast; influx at Darwin, Nov.; arrive Gulf of Carpentaria, Sept.–Dec. (Garnett 1989; Lane); some may move SE from Gulf of Carpentaria to e. coast, where hundreds appear S of Townsville, Sept.–Nov. (Lane); later in year may occur as far N as Cairns (e.g. Hewish 1992). Some move down e. coast: arrive Moreton Bay, se. Qld, first weeks of Oct. (Thompson 1992). Some move through inland Qld, NSW and Vic., with dated records between Sept. and Feb. (McKean 1963; Wheeler 1963; Thomas 1970; Morris *et al.* 1981; Storr 1984; Qld Bird Rep. 1986; Lane; Aust. Atlas). Usually arrive

SA and Vic., Oct.–Nov. (<2000 birds) (Lane). Arrive Tas., Oct.–Nov. (Thomas 1970). Some appear to move from nw. to sw. Aust. along w. coast (e.g. Ford 1965; Jaensch 1988; Jaensch *et al.* 1988); influx in SW in Oct., sometimes many (e.g. 100 at Warden L. in Oct. 1985) (Serventy 1938; Jaensch *et al.* 1988); at Eyre, generally arrive between late Aug. and Dec. (Dymond 1988; Hooper & Wells 1989). At Gulf St Vincent, SA, appear to move much (Close & McCrie 1986). Some evidence for fidelity to non-breeding site (see Banding). **NZ** Recorded between Sept. and Apr. (Brown 1980).

Return Most appear to leave directly from n. coast, Mar. and Apr. (Lane). No influxes Darwin (Lane *contra* Starks & Lane 1987) or nw. Aust., where departure begins before mid-Mar. and continues till early Apr. (Lane & Jessop 1985). Leave some, possibly most, sites in s. Aust., late Feb. (Starks & Lane 1987); leave Tas., Feb.–Mar. (Thomas 1970). Influx in Gulf St Vincent, SA, before departure (Close & McCrie 1986). Influxes on e. Qld coast, Mar. and Apr. (Lane), suggest n. movement up coast; at Moreton Bay, Qld, more birds in greater concentrations counted on n. than s. migration, numbers declining in Apr. (Thompson 1992). Move through Torres Str. (Draffan *et al.* 1983). Birds in Gulf of Carpentaria in late Mar., appeared ready to move N (Garnett & Taplin 1990). Recoveries show birds can move from nw. Aust. to Shanghai in 7 days (Driscoll 1993). Estimates of flight-range suggest birds leaving nw. Aust. can fly non-stop to China (5000 km) and birds leaving se. Aust., which have higher departure weights, capable of flying non-stop to Asian mainland (8000 km) (Barter 1987; Barter & Hou 1990).

Extralimitally, thousands se. Irian Jaya, Feb.–Apr. (Hoogerwerf 1964). Small numbers in Bali, Mar. 1982 (Ash 1984). Not recorded after Jan. in Wallacea (White & Bruce 1986). Record in Sumatra, Mar.–Apr. 1986 (van Marle & Voous 1988). Move through Olango I., Philippines, Feb.–Mar. but as late as May (Magsalay *et al.* 1990; Magsalay 1991). Some move through Vietnam (AWB 1993). Small numbers Hong Kong, Apr.–June, with some large flocks, late Apr. and mid-May (Chalmers 1986). Move through Taiwan, Mar.–Apr., once in large numbers (AWB 1993). Move along e. China coast, early Apr. to early June (of birds banded Aust., most recovered Apr.) (la Touche 1931–34; Driscoll 1993). Move through Japan, mainly first half May (Dement'ev & Gladkov 1951). Recent counts suggest more numerous in South Korea on n. migration (AWB 1993). Up to 20,000 seen Kamchatka Pen., e. Siberia, on n. migration. Arrive breeding grounds late May or early June (see Myers *et al.* 1982).

Breeding First-year birds said to stay in tropical parts of non-breeding range (Hayman *et al.* 1986). Extralimitally, recorded Borneo (Smythies 1986), Java (BWP), and New Guinea (Coates 1985). **Aust.** Reporting rates 0.57% in summer, and 0.16% in winter (Aust. Atlas). Mainly winter in N (Aust. Atlas), e.g. Darwin, Gulf of Carpentaria, coastal Qld (Garnett 1989; Hewish 1989b; Lane); some in s. Aust. (e.g. Serventy 1938; Close & McCrie 1986; Hewish 1989b; Vic. Atlas). At Gulf St Vincent, SA, proportion of summer population that remains over winter varies; in some years, influx of birds in Mar.–Apr. that remains for several months (Close & McCrie 1986). **NZ** No winter records.

Banding Of 185 recaptures up to 1991, 59 were international recoveries; birds banded Vic. recovered Shanghai (n=2); birds banded WA recovered from near Shanghai (n=49), Vietnam (n=2) and Sea of Okhotsk, e. Siberia (n=6). No birds banded overseas have been recovered in Aust. and no interstate recoveries, though six recoveries within WA were >100

km from banding site, indicating movement within and between sw. and nw. WA (e.g. between Broome and Eighty Mile Beach). All recoveries 4–11 km from banding site were in nw. WA (n=21) except one in sw. WA. All other captures within Aust. were at banding site, often with considerable time between captures (n=98) (Driscoll 1993). Since Jan. 1991, birds banded in nw. Aust. recaptured at Shanghai, China (n=2), and Sakhalin, Russia (n=1) (ABBBS 1993). Extralimitally, birds banded Hong Kong recovered along e. China coast (AWB 1993).



Figure 1 Great Knot

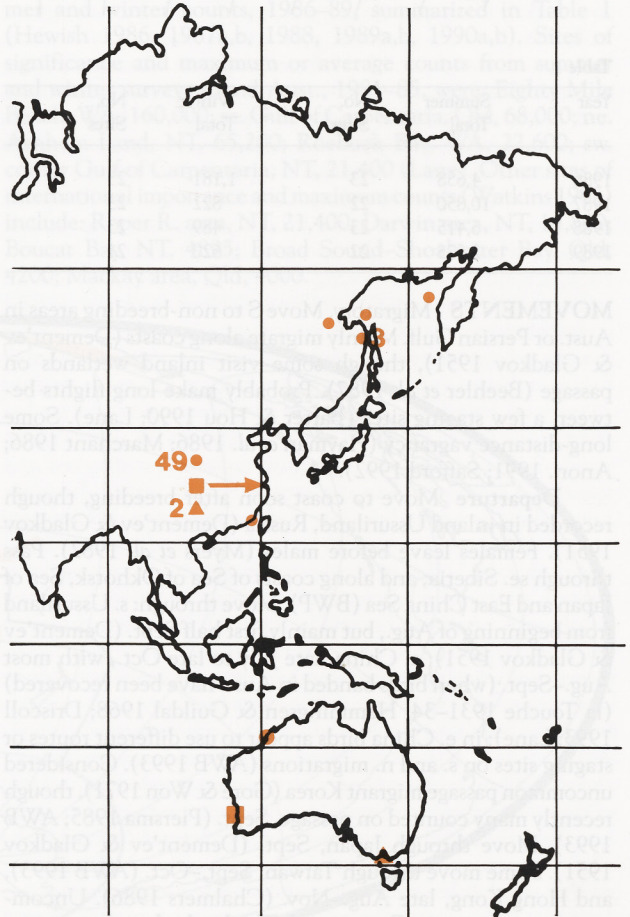


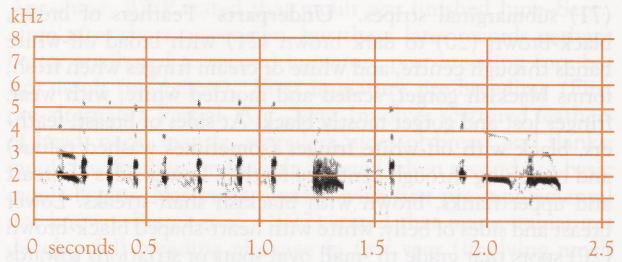
Figure 2 Great Knot

FOOD Based on study at Roebuck Bay, nw. Aust., Mar.–May 1991, by Tulp & de Goeij (1994) unless stated. Carnivorous; mainly bivalve molluscs; also gastropods, polychaete worms, crabs, shrimps and sea-cucumbers. Also said to eat seeds, berries and insects on breeding grounds (Pringle 1987). **Behaviour** Nocturnal and diurnal. Feed mainly on intertidal mudflats, rapidly and repeatedly jabbing bill into mud. Often feed along edge of tide and sometimes in shallow water (Lane). At Roebuck Bay, tides move rapidly (0.2 m/s); follow quickly receding edge of tide and fly to edge of water as soon as a few meters of exposed mudflats appeared between bird and water. At Roebuck Bay, use several methods of foraging: (1) gleaning from surface, carefully examining mudflat with bill closed; (2) 'pecking' at mud with open bill (probing up to half length of bill), and removing bill after every 'peck'; and (3) probing in mud with bill, boring repeatedly after finding prey till prey captured; after each probe, birds took a few steps before probing again. Sometimes wash food or reject food after capture; of 1246 prey items, 4% were washed before swallowing; 8% were rejected after being taken from mud, 1% after washing (of rejected food, bivalves 13%, worms 6%, the rest were unidentified). Select smallest individuals of bivalves *Quadrans* and *Anomalocardia*; rejected bivalves may have been too large to swallow. Forage in dense groups or in a large mixed flocks with Red Knots, Bar-tailed Godwits and Grey-tailed Tattlers *Heteroscelus brevipes*. Mean distance between nearest neighbours was related to height of tides, with smaller distances at high tides; relationship described by $D = -1.98WL + 12.902$, where D = mean distance between nearest neighbours and WL = water level ($r=0.58$; $P<0.01$; $n=75$); these data suggest that birds do not seek alternative feeding areas at high water levels.

Adult At Roebuck Bay (1180 min obs.): Annelids: polychaetes 11.0% of total items taken; Molluscs: bivalves 69.5; gastropods 1.5; Crustaceans: decapods crabs and shrimps 11.5; Echinoderms: Holothuroidea sea-cucumbers 6.5. From analysis of droppings (15 samples containing 241 droppings and a total of 931 recognizable items; remains of shells unless stated): Sarcodina: Foraminifera 4.6% of total remains; Molluscs: gastropods: Pyramidellidae 7.1; Eulimidae 1.6; Neritidae 5.9; Bullidae 0.3; unident. 2.3; bivalves: *Nucula* 3.0; *Modiolus micropterus* 19.2 (average length of shell, 8.2 mm [2–17]); *Anomalocardia aquamosa* 5.9 (6.1 [2–9]); *Macoma* 0.1; *Siliqua* cf. *winteriana* 0.1; *Quadrans pristin* 2.5 (12.9 [9–19]); unident. 1.5; Crustaceans: decapods: *Brachyura dactylus* 8.3, prodopus 7.3, carapace remains 7.8; ostracod carapace remains 19.1; Fish: Gobiidae spinal remains 3.4. Polychaete worms and echinoderms were digested completely and were not recorded. For more details on estimation of composition of diet and availability of prey, see Tulp & de Goeij (1994). **Other records** Gastronomy recorded in three stomachs (Serventy 1932).

Intake At Roebuck Bay, using two different methods, intake estimated at 0.24 mg/s and 0.33 mg/s. Maximum daily net energy intake 221. kJ/day, with 22 kJ/day available for storage.

VOICE No detailed studies (Miller 1992). Very quiet (Hayman *et al.* 1986; BWP). Usual call in flight a low *nyutnyut* (BWP), first syllable longer with rising inflexion, second shorter and lower pitched (Hayman *et al.* 1986). Sonagram A depicts two kinds of soft calls from captive birds, which are shorter and higher pitched than those of Red Knot (q.v.) with a tinkling quality in the short call and less gruffness in the long call.



A E. Slater & P.J. Fullagar; Broome, WA, Oct. 1992

PLUMAGES Prepared by K. Bartram and D.I. Rogers. Partial post-juvenile (first pre-basic) moult begins after, or in late stages of, s. migration, bringing on non-breeding appearance by Nov.–Dec. Stay in non-breeding areas for at least 1 year; in first austral autumn some replace outer primaries in first pre-supplemental moult and most develop some subdued (first immature) breeding plumage in partial first pre-breeding (pre-alternate) moult. Adult non-breeding plumage first attained in protracted, complete second pre-basic moult, starting in first austral spring (often while first pre-supplemental moult of primaries still active) but not finished till second austral spring. Thereafter, moult twice annually: partial pre-alternate moult to breeding plumage just before n. migration and complete pre-basic moult to non-breeding plumage mostly after s. migration. Age of first breeding, unknown.

Adult breeding (Second and subsequent alternate). Sexes similar, though females often slightly duller. **Head and neck** Top of head and nape, streaked; feathers, dark brown (21) with pale pink-buff (c121D) edges that fade to off-white and are reduced with wear. Hindneck, like cap but finely streaked brown. Supercilium, dull white, finely streaked dark brown, contrasting slightly with crown when worn. Eye-ring, small, off-white, contrasting slightly with supercilium. Loes slightly darker than supercilium: off-white, lightly speckled by dark-brown centres to feathers. Ear-coverts, off-white or pale buff, sometimes with light rufous-brown wash and always streaked dark brown. Lower face, paler, mostly white, finely streaked dark brown. Chin, white. Throat and lower neck, white, coarsely marked by small rounded dark-brown (21) to black-brown (20) shaft-streaks at tip of feathers. **Upperparts** Feathers of mantle and inner (upper) scapulars, dark brown (21) to black-brown (20), grading to light grey at base; shafts, black-brown (20); sides of feathers either: (1) narrowly fringed pale brown-grey (pale 80) or cream, with pale-rufous wash towards tip; or (2) with white or off-white fringes adjoining large rufous-tinged spot on each web. When very worn, feathers of mantle lose pale tip, leaving cream or pale-rufous oval spots on side of feather, and centres of feathers become darker, almost black; overall appearance of mantle then blotched black, spotted with cream or rufous. Scapulars vary; on some birds, bright rufous-brown and black-brown (20); some birds have no rufous-brown and are cream and dark brown (BWP). Scapulars usually have varying oval rufous-brown (38) to light-brown (reddish 39) spots on sides of feathers; tip, fringed brownish white; central rows of scapulars strikingly rufous and black in full breeding plumage, especially after fringes have worn. Feathers of back and rump, dark brown (21) with greyish-white fringes, which are broader and whiter on rump. Uppertail-coverts, white with black-brown blotches, striations and shafts; longest pair of central coverts has three black-brown blotches; lateral coverts have elongated dark-brown

(71) submarginal stripes. **Underparts** Feathers of breast, black-brown (20) to dark brown (21) with broad off-white bands through centre, and white or cream fringes when fresh; forms blackish gorget, scaled and mottled white; with wear, fringes lost and gorget mostly black. At sides of breast, feathers, black with off-white fringes (sometimes washed rufous) and blotching through centre of feather. Lower sides of breast and upper flanks, brown with blackish shaft-streaks. Lower breast and sides of belly, white with heart-shaped black-brown (20) spots that grade to small oval spots or striations towards upper belly and lower sides of belly; centre of belly to vent, white. Rear flanks have long brown (121C) striations. Axillaries, pale grey-brown (119D), edged white, with light grey-brown variegated submarginal stripes, patterned inside with grey-brown shaft-streaks and wavy markings. Undertail-coverts, white, with small black-brown striations on lateral coverts. **Tail** Outer feathers, light grey-brown (119D); central feathers, darker grey (85–86) when fresh, grey-brown (119C) when worn, with brownish wash through centre; all narrowly fringed off-white when fresh; shafts, white, grading to brown (dark 23) at tips. **Upperwing** Mostly retained from adult non-breeding (q.v.); attain some breeding plumage on coverts and tertials; these are much more pointed (especially tertials), dark brown with light grey-brown (119D) edges (grey in adult non-breeding). Some said to attain a few black tertials with wavy cinnamon patterning round edges (BWP). **Underwing** As adult non-breeding (q.v.)

Adult non-breeding (Second and subsequent basic).

Head and neck Crown, hindneck, sides of neck and ear-coverts, pale brownish-grey (c86) with fine black (119) shaft-streaks, coarsest on crown; grading to greyish white on forehead, supercilium and cheeks, and white on chin and throat, all of which faintly streaked by dusky shafts to feathers. Supercilium, indistinct, contrasting only weakly with broad diffuse dark-brown loreal stripe that tapers towards bill. **Upperparts** Mantle, back and scapulars appear variegated: feathers, dull brownish-grey, grading to diffuse darker-brown (c27) centres (especially on mantle) with black-brown (119) shaft-streaks and, when fresh, narrow white fringes (broadest on scapulars). Rump and uppertail-coverts, like those of adult breeding but with broader white tips to feathers of rump and sparser black blotches on uppertail-coverts. **Underparts** Mostly white, with greyish suffusion on breast when fresh. Breast and foreneck speckled or streaked by small, elongate dark-brown (21) to black-brown (20) spots, occasionally interspersed with a few larger black-brown (c20) blotches, especially on sides of breast. Speckling continues on flanks as sparser but larger streaks (or roughly triangular spots), mixed with a few fine greyish streaks that may extend onto lateral undertail-coverts. **Upperwing** Outer webs and tip of primaries, dark brown (221); shafts, horn-white; inner webs grade from dark brown at tip to light grey-brown at the base of each web; primaries fringed white when fresh, more broadly so towards inner primaries. Greater primary coverts, dark brown (221) with white fringes that become broader towards innerwing. Alula and rest of primary coverts, dark brown, narrowly fringed white; marginal coverts have broader white fringes, forming thin off-white leading-edge. Secondaries, light grey-brown (27) with slightly broader white fringe than primaries; inner secondaries have darker elongated submarginal lines. Greater secondary coverts slightly darker, with white tip (2–3 mm wide) which, with white tips of inner greater primary coverts, forms narrow white wing-bar. Rest of secondary coverts, brown-grey (27–85) in centre, with off-white edges that give uneven scaly

effect. Tertials, grey (84) with darker grey (83) centres, paler grey (brownish 85) edges and white tips. **Underwing** Outer web, tip and stripe along shaft of inner web of outer primaries, dark brown (119A–121); rest of primaries and secondaries, light grey (c85–86) with brown tone and off-white bases to inner webs. Greater coverts, light grey (c86) with slightly darker-grey (85–84) submarginal lines meeting as thorn-shaped point on distal shaft; narrow white edges of feathers merge to broad white tips. Inner greater coverts variegated grey inside submarginal lines. Median and larger lesser coverts, white with light-brown (dull 27) bases, broken by white shaft-streaks. Marginal coverts, brown (28) with white fringes; leading-edge appears brown mottled with white.

Juvenile Differences from adult non-breeding. **Head and neck** Forehead and crown, dark brown (119A–219A), streaked by dull off-white edges to feathers that are reduced (even lost) with wear, which then accentuates appearance of distinct dark cap. Rest of head generally patterned like adult non-breeding, but with coarser dark streaking on neck and ear-coverts; often also differ in bolder white supercilium, with few grey streaks. **Upperparts** Mantle, blotchy dark brown, scalloped with white; feathers, dark brown (119A–219A) with concealed, greyer bases and off-white fringes at tips. Smaller scapulars, like mantle but with white variegated fringes. Larger scapulars have partly exposed grey-brown (grey 119B) bases that contrast with dark-brown (119A–219A) shaft-streaks and submarginal lines, and cream (c92) to white fringes of uneven width; submarginal lines broken along edges but broad at tips of feathers, where they often contrast with diffuse pair of pale buff oval patches. **Underparts** White with mottled brown gorget; feathers of gorget, brown (239) with thin dull pink-buff (121D) edges. Brown (239) blotches on upper flanks grade to long brown (239) striations on lower flanks. **Upperwing** Generally browner than in other plumages, each feather fringed off-white to pale buff (c92). Most tertials, grey-brown (grey 119B) with broad white fringes enclosing elongated, slightly variegated dark-brown (121A–121) submarginal lines. Inner tertials, brown (grey 119B) with white tips and pale buff spots along edges, fringed with small diffuse pale-buff patch inside submarginal fringe at each spot. Greater, median and larger lesser secondary coverts, brown (119B) with darker brown shaft-streaks and submarginal line, and neat white fringes, slightly notched on middle of each side of feather; greater coverts have broad white tips (c. 5 mm wide) forming slightly broader wing-bar than on adult.

First immature non-breeding (First basic). Distinguished from adult non-breeding by retained juvenile plumage: remiges, all upperwing-coverts, back to tail, and outer or all tertials. By end of first austral summer some only retain juvenile remiges, some smaller wing-coverts and a few heavily worn tertials and rectrices. Fresh first-basic plumage differs from adult non-breeding in more heavily streaked and blotched foreneck and sides of breast (BWP). Small series of Aust. skins also differed in brown, rather than greyish, upperparts; centres of feathers, brown (119B) to light grey-brown (119C) with less distinct white fringes.

First immature breeding (First alternate). Most reliably separated from adults by moult of primaries (see Ageing). Retain much non-breeding (first-basic) body-plumage but usually have scattered new breeding feathers on head, mantle, scapulars, uppertail-coverts and underparts, usually intermediate in character between adult breeding and non-breeding. Feathers of upperparts, black with grey fringes and, sometimes, grey subterminal spots, but usually no rufous; on breast and

foreneck, feathers mostly white with some large black spots or short rounded bars. Claims that some develop much breeding plumage (e.g. Hayman *et al.* 1986; Lewington *et al.* 1993) have not been adequately described and no such individuals noted in BWP or found in Aust. museums.

BARE PARTS From photographs (Marchant 1986; Pringle 1987; Paulson 1993) and unpublished notes and photographs (AWSG; H.M. Gibbs). **Adult** Bill, grey-black (82); base of lower mandible, black to olive-grey (42); basal half, sometimes olive-grey. Iris, black-brown (20–22). Legs and feet, blackish olive (blackish 49), olive-grey (42–43), to greenish yellow, often with slightly darker joints. Paulson (1993) said legs were grey when in breeding plumage, greener in non-breeding; published photos consistent with this claim but confirmation needed. **Juvenile** Legs and feet often paler than in adult (BWP; Hayman *et al.* 1986), usually olive-green (50) or pale green (dull 162D), to dark olive (49). Paulson (1993) said legs like adult non-breeding.

MOULTS From Barter (1986, 1987), BWP and Aust. skins (AM, ANWC, HLW, MV, SAM, WAM). **Adult post-breeding** (Third and subsequent pre-basic). Complete; primaries outwards. May moult scattered feathers on crown, mantle, scapulars and upper breast before arrival in HANZAB region, but most moult (including moult of all primaries) occurs in non-breeding areas; non-breeding appearance attained Sept.–Oct., with traces of breeding plumage retained longest on breast. In Vic., moult of primaries begins late Sept., and finished (with replacement of p10) by late Dec. in some, perhaps as late as Feb. in others; duration roughly estimated at 141 days (Barter 1987). Moult of primaries begins earlier in nw. WA; at Broome, 58% had begun moult by 30 Aug.–2 Sept., and median PMS c. 30 by late Oct.; at Port Hedland, timing apparently similar, but at Anna Plains, moult starts slightly later: none in moult by 7–8 Oct. (n=14) and median PMS only 22 at end Oct. **Adult pre-breeding** (Second and subsequent pre-alternate). Partial, beginning late Feb. to mid-Apr. before n. migration. Involves most of body, including many or all scapulars, outer and larger tertials, some inner median or greater upperwing-coverts and, sometimes, uppertail-coverts. At Broome from 24 to 26 Mar. 1985, average amount of breeding plumage was 52%; at Anna Plains, 13 Apr. (when most advanced adults had probably left), average was 29%. **Post-juvenile** (First pre-basic). Partial, involving most feathers of body and some wing-coverts and rectrices. Often starts on s. migration; most feathers moulted and immature non-breeding appearance attained by Nov.–Dec. Moult apparently continues slowly through rest of austral summer; by Mar.–Apr., only juvenile plumage remaining are all primaries and secondaries, a few feathers on back and rump, some rectrices (especially t4 and t5), many shorter lesser coverts and outer greater secondary coverts. **Post-juvenile moult of primaries** (First pre-supplemental). Partial; involves varying number of outer primaries, replaced in outwards wave that usually starts at p7 or p8 in HANZAB region, but between p4 and p7 in Indonesia (BWP). In our region, begins about Mar.; date of completion not known, though some have finished moult by late Mar.–Apr. Not all birds moult; in late Mar. to mid-Apr., pre-supplemental moult seen in 13 of 14 moulting immatures trapped at Anna Plains, but in only three of 14 trapped at Broome; pre-supplemental moult probably also rare in Vic., as four immatures caught June had not moulted outer primaries. In Indonesian specimens, pre-supplemental moult recorded

Apr.–June; BWP stated that moult was finished June–Sept., often after short suspension, but these later records perhaps better attributed to second immature post-breeding (pre-basic) moult (see below). **First immature pre-breeding** (First pre-alternate). Partial, Apr.–May. Involves scattered feathers of head, neck, mantle, scapulars, sides of breast and flanks; moult few feathers and moult arrested when second pre-basic moult begins. Nature of overlap with first pre-supplemental not known. Prater *et al.* (1977) stated that many immatures develop full breeding plumage in first year (implying much first pre-alternate moult) but confirmation needed. **Second immature post-breeding** (Second pre-basic). Complete, except perhaps for outer primaries of some birds (see below). Primaries moult outwards; sequences in other tracts unknown. Usually begins in first austral autumn, much earlier than adult post-breeding (and earlier than second pre-basic of most other waders); can begin in late Mar. and seven of 13 caught in Broome in mid-Apr. had started moult; latest starting date not known but one in NT had all juvenile primaries in mid-June. Apparently begins earlier in those birds that have not replaced juvenile outer primaries in a first pre-supplemental moult. Often begin second pre-basic moult of primaries before first pre-supplemental moult of juvenile outer primaries finished, thus showing two active moult-centres in wing; this condition recorded in seven of 20 Indonesian immatures between May and Oct. (BWP); in two of 14 at Broome (24–26 Mar.); and one of 14 at Anna Plains (5–13 Mar.) (Barter 1986). Few data available May–July, so not known if all first-supplemental primaries replaced in second pre-basic. Judging by surprisingly low moult-scores in nw. WA from Aug. to Sept., many immatures probably suspend second pre-basic moult of primaries during austral winter; this confirmed in Vic., where four caught June had suspended moult after moulting inner 4–9 primaries. Despite slow progress over winter, moult of primaries more advanced than in adults during return in Aug.–Sept.; median PMS at Broome 38 between 30 Aug. and 2 Sept. (n=44; seven had finished moult). Moult not so advanced at Anna Plains at this time, perhaps because start of moult delayed because more birds undergo first pre-supplemental moult of primaries; median PMS, 20 on 24 Aug. (n=30; none had finished moult) and 31 on 31 Oct. (n=15; seven had finished moult). Little data from Vic. suggest that timing similar to that of Anna Plains rather than Broome (Barter 1987); moult of body finished by Aug.–Sept.; finish date of moult of primaries not known, because birds finishing after end Oct. easily confused with adults; said to be about Dec. (BWP; Barter 1987). Above model of subadult moults complicated by records of birds that have finished moult of primaries but have little breeding plumage and have not gained weight in Mar.–Apr. Barter (1986, 1987) treated these birds as immatures in first austral autumn, but more likely explanation is that they were older, i.e. that at least some subadults spend more than one austral winter in non-breeding areas before first n. migration. Nevertheless, slight wear of outer primaries in a specimen (QM 10837) with primary-moult N²4¹2¹O⁶ on 6 Jan. 1967 could be interpreted as evidence that it was a first-year bird moulting all primaries in first austral summer.

MEASUREMENTS (1–3) A'asia, skins (AM, ANWC, HLW, MV, QM, SAM, WAM): (1) Adults; (2) Immatures in first alternate or second pre-basic; (3) Ages combined. (4–6) Indonesia, skins (BWP): (4) Adults; (5) Juveniles; (6) Ages combined.

	MALES	FEMALES	
WING	(1) 185.2 (5.10; 176–193; 11)	184.6 (4.77; 176–192; 17)	ns
	(2) 174.9 (7.05; 165–188; 7)	180.3 (8.75; 165–191; 6)	ns
	(4) 185 (2.48; 181–189; 7)	192 (5.80; 186–203; 8)	*
	(5) 175 (3.00; 170–179; 14)	184 (3.38; 177–190; 14)	**
TAIL	(1) 65.5 (5.88; 51–71; 11)	65.4 (3.44; 60–72; 17)	ns
	(2) 62.3 (3.50; 56–70; 12)	64.1 (5.33; 57–73; 8)	ns
	(4) 64.3 (1.92; 61–68; 16)	65.8 (2.57; 62–70; 22)	**
	(5) 58.6 (1.79; 56–62; 7)	61.1 (1.29; 59–63; 9)	**
BILL	(3) 43.5 (1.70; 40.2–46.6; 24)	42.8 (2.01; 38.1–46.1; 25)	ns
	(6) 42.1 (1.78; 39–45; 31)	43.8 (0.96; 41–47; 36)	**
	TARSUS (3) 34.9 (1.03; 32.6–37.6; 24)	35.5 (1.26; 32.6–37.6; 26)	ns
TOE C	(6) 35.0 (1.15; 33–37; 25)	35.5 (0.93; 34–38; 31)	ns
	(3) 27.7 (0.90; 25.9–29.5; 21)	27.9 (0.96; 26.3–29.9; 21)	ns
	(6) 27.8 (0.87; 26–29; 23)	28.4 (0.91; 27–30; 30)	*

(7–8) Live adults, sexed by PCF methods of Griffiths (1968): (7) NW. WA (Barter 1986); (8) Vic.; bill measurements from 206 birds and THL from 148 but sex-ratios not given (Barter 1987).

	MALES	FEMALES	
WING	(7) 185.1 (3.51; c. 162)	193.0 (2.78; c. 139)	**
BILL	(8) 42.7 (s.d. = 1.17)	45.1 (s.d. = 0.89)	**
THL	(7) 73.8 (1.60; c. 56)	76.1 (1.46; c. 51)	**
	(8) 74.1 (s.d. = 0.86)	76.5 (s.d. = 1.24)	**

(9–11) NW. WA (Barter 1986) and Vic. (Barter 1987), live: (9) Adults; (10) Immatures with juvenile p10; (11) Immatures with p10 replaced in first pre-basic moult.

	NW. WA	VIC.	
WING	(9) 189.1 (5.3; 347)	191.5 (4.9; 142)	**
	(10) 179.3 (5.8; 33)	184.7 (4.6; 17)	**
	(11) 186.0 (3.8; 29)	189.1 (7.1; 17)	ns
BILL	(9) 44.1 (1.9; 263)	43.6 (1.7; 206)	ns
	(10) 43.9 (1.9; 53)	44.0 (2.0; 11)	**
	(11) 43.9 (1.8; 46)	43.0 (1.6; 14)	ns
THL	(9) 75.1 (2.0; 232)	75.1 (1.8; 148)	ns

Females larger than males (Prater *et al.* 1977; BWP), though differences not apparent in Aust. skins above, possibly because wrongly sexed specimens included. Wing and tail of juvenile significantly shorter than those of adults; when worn juvenile p10 replaced in first pre-supplemental or second pre-basic moult, wing-length increases by c. 7 mm. Measurements of live birds (9–11) suggest wing slightly longer in Vic. than in nw. WA, and bill slightly shorter (differences significant but not known if different sex-ratios in samples are an influence); differences have been attributed to more rapid abrasion of tips of primaries and feathering of culmen in nw. WA (Barter 1987).

WEIGHTS (1–3) Roebuck Bay and Anna Plains, nw. WA, live (Barter 1986): (1) Adults; (2) Immatures in second pre-basic moult; (3) Immatures in first austral summer–autumn.

	ROEBUCK BAY	ANNA PLAINS	
Aug.–Sept.	(1) 147.8 (14.3; 80)	151.8 (17.1; 53)	ns
	(2) 152.3 (13.1; 59)	139.8 (8.9; 29)	**

Oct.–Nov.	(1) 147.7 (12.2; 175)	137.1 (10.3; 342)	**
Mar.–Apr.	(1) 191.9 (33.1; 115–261; 125)	169.8 (23.9; 135–205; 12)	**
	(3) 143.4 (15.4; 76)	130.2 (10.0; 60)	**

Weights of adults at Roebuck Bay apparently fairly stable through much of non-breeding season but gain much weight before migration, Mar.–Apr.; maximum weights recorded 24 Mar. 1994, 204.2 (34.3; 150–261; 54); heaviest birds apparently left on n. migration that evening and average weights had declined c. 20 g in catches over next 2 days, when no individuals weighed more than 240 g. Adults and immatures significantly lighter at Anna Plains compared with Broome, except for adults in Aug.–Sept.; at this time, differences between Broome and Anna Plains may be obscured by newly arrived birds that retain some migratory reserves. Juveniles and first immature non-breeding in nw. WA (localities combined) in Oct.–Nov., 128.5 (12.6; 23); significantly lighter than adults in same period. Piersma & Barter (1991) present some information on body-composition.

(4–6) Vic., live (Barter 1987): (4) Adults; (5) First immature non-breeding; (6) First alternate.

	UNSEXED
Oct.–Nov.	(4) 162.8 (12.2; 44)
Dec.–Jan.	(4) 170.3 (14.0; 177)
	(5) 180.4 (15.7; 11)
Late Mar.	(4) 245, 275, 282
June	(6) 174.3 (3.8; 3)

At all times, Vic. birds significantly heavier than those in nw. WA; especially noticeable in small sample in Mar., which suggests that some in Vic. gained weight for a flight of 8000 km (i.e. direct to coast of s. China) (Barter 1987). Apparent increase in average weight from 164.3 (12.0; 29) in late Nov. to 176.2 (19.8; 33) at end Dec. suggests some might leave Vic. early and stop in n. Aust. (Barter 1987).

STRUCTURE Wings, fairly long and pointed. Eleven primaries: p10 longest, p9 2–6 mm shorter, p8 10–17, p7 22–30, p6 34–44, p5 46–58, p4 62–67, p3 72–78, p2 80–87, p1 88–102; p11 minute. Tips of tertials lie between p6 and p7 on folded wing, 20–35 mm short of tip of p10. Sixteen secondaries, including five long pointed tertials. Tail, almost square; central rectrices slightly pointed; 12 rectrices, t6 1–3 shorter than t1. Bill, long, fairly straight to slightly decurved; base reasonably deep, tapering along length to tip of bill, which is slightly expanded and downcurved. Groove 30–35 mm long on upper mandible from base of bill over nostril, and ending before tip; groove joins nasal groove, and becomes deeper, about one third along bill. Shorter groove on lower mandible. Tarsus, laterally compressed; moderately long; scutellate. Central toe longest, outer two similar in length: outer, c. 82% of middle, inner, c. 79%, hind, short, c. 29%.

AGEING Juveniles distinct (see Plumages). First immature non-breeding, held from about Nov. to Feb., differs from adult non-breeding by: some retained juvenile coverts and tertials (with buff fringes and varying distinct dark shaft-streaks and submarginal lines); and slightly and uniformly worn primaries (actively moulting or very fresh in adults). From Feb. to July, two age-classes separable on condition of primaries: adults have fresh to slightly worn primaries with no active moult

(also develop full breeding plumage, which seldom or never occurs in immatures in first year). Immatures in first austral autumn and winter show a range of patterns of moult of primaries: (1) before any pre-supplemental or second pre-basic moult takes place, primaries uniformly worn (much more worn than those of adults); (2) strong contrast between fresh outer and worn inner primaries in those that have undergone pre-supplemental moult; (3) very early start to second pre-basic moult (often by Mar.–Apr.) results in wave of outwards primary-moult from p1 when adults show no moult; often this is concurrent with first pre-supplemental moult of outer primaries, so primaries have two active moult-centres; (4) active moult of primaries can be suspended in austral winter, so a contrast is evident between fresh inner and worn outer primaries. By Aug. second pre-basic moult of primaries has reached those outer primaries replaced in second pre-basic, so primaries appear to show simple outwards sequence of replacement, only differing from those adults that have returned from breeding grounds by earlier timing. On present knowledge, birds in second basic are not reliably separable from returned adults after Oct.

Age at first migration to breeding grounds, not known. Some birds caught in austral winter with wholly fresh primaries appear not to have been in first year; possibly these were adults that did not migrate, or possibly maturity is delayed till at least 3 years.

GEOGRAPHICAL VARIATION None.

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Sponsors: Ms D Graham, M Simpson



Volume 3, Plate 14

Great Knot *Calidris tenuirostris* (page 214)
 1 Adult breeding; 2 Adult non-breeding; 3 Juvenile; 4, 5 Adult

Red Knot *Calidris canutus* (page 224)
 6 Adult breeding; 7 Adult non-breeding; 8 Juvenile; 9, 10 Adult