

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	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, 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 Glenn 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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Tringa canutus Linnaeus, 1758, *Syst. Nat.*, ed. 10(1): 149 — Europe.

The specific epithet is in honour of Canute (995–1035), King of England, Denmark and Norway (1016–35), of whom it is said that he sat at the seaside ordering the tide to stay out, thus showing to his flattering councillors that he was not all-powerful; according to legend, he regarded the Red Knot, suitably fattened with milk and bread, as a delicacy.

The English name may refer to the Danish name of Canute, Knut, or to the call of the bird.

OTHER ENGLISH NAMES Knot, Common Knot, Iceland Sandpiper, East Siberian Sandpiper.

POLYTYPIC Nominate *canutus* breeds Taymyr Pen., central n. Siberia, New Siberian Is and possibly Yakutia, Siberia. Subspecies *rogersi* Mathews, 1913, breeds ne. Siberia, including Chukotskiy Pen., and possibly areas farther W. Subspecies *roselaari* Tomkovich, 1990, breeds Wrangel I., Siberia, and nw. Alaska. Subspecies *rufa* Wilson, 1813, breeds Canadian Arctic, S of 75°N. Subspecies *islandica* Linnaeus, 1767, breeds islands of Canadian high Arctic and n. Greenland. Subspecies *rogersi* and, probably, *canutus* occur HANZAB region.

FIELD IDENTIFICATION Length 23–25 cm; wingspan 45–54 cm; weight c. 120 g. Medium-small, robust, short-necked, rather dumpy yet long-bodied wader with short straight bill, long wings extending just beyond tip of tail at rest, and short legs. Between Curlew Sandpiper *Calidris ferruginea* and Grey Plover *Pluvialis squatarola* in size. Similar in shape and proportions to Great Knot *Calidris tenuirostris* but smaller and less bulky, with shorter bill, proportionately bigger head, shorter neck, more evenly rounded belly, and slightly shorter wings, which combine to give more rounded, less attenuated appearance. In all plumages, show clear narrow white wing-bar, and off-white patch on rump and uppertail-coverts, obscured by narrow dark barring and appearing pale grey at distance. Sexes similar; female slightly larger, less evenly and extensively chestnut-red on underbody, with more white on rear belly. Marked seasonal variation. Juvenile distinctive. Immatures separable when close.

Description Adult breeding Centre of forehead, crown, nape and hindneck, pale brownish-grey with coarse blackish streaking. Supercilium and rest of face, chin and throat, uniform chestnut-red, except for varying narrow off-white area round base of bill, contrasting dark loreal stripe and patch of dark streaks on ear-coverts. Feathers of mantle, black with broad chestnut-red fringes and narrow pale-grey tips. Back, grey with dark barring. Scapulars vary: most are black with large chestnut-red subterminal bar, typically broken into paired

spots, and narrowly tipped white; others have smaller or no chestnut-red spots, narrow chestnut-red fringes, narrow pale-grey tip and thin white terminal fringe; a few are much duller, brownish grey, with black centres and shaft-streak and narrow white fringe. Tertials also vary: some black with small chestnut-red subterminal paired spots, narrow dull chestnut or off-white fringe and narrow white tip; others much duller, plain brownish-grey with diffuse dusky centres and narrow white fringe. Innerwing-coverts, plain brownish-grey with narrow white fringes, showing as grey panel contrasting with coloured upperparts and underbody; often a few median and greater coverts are new breeding-type feathers, either brownish-grey with contrasting dark submarginal lines and shafts or more

Plate 11

Solitary Sandpiper *Tringa solitaria* (page 157)

1 Adult breeding; 2 Adult non-breeding; 3 Juvenile;
4, 5 Adult

Wood Sandpiper *Tringa glareola* (page 158)

6 Adult breeding; 7 Adult non-breeding; 8 Juvenile;
9, 10 Adult

Common Sandpiper *Actitis hypoleucos* (page 173)

11 Adult breeding; 12 Adult non-breeding; 13 Juvenile;
14, 15 Adult

brightly coloured and patterned like outer scapulars. Chin to belly, chestnut-red, with varying amount of white on lower belly and fine white tips to most feathers; sides of breast and fore-flanks spotted and finely streaked black; rest of underbody, white, with black streaks and spots and scattered chestnut smudging and crescentic black barring on flanks and sides of vent. In flight: show brownish-grey upperwing-coverts and slightly darker, blackish-brown remiges, with contrasting black primary coverts and narrow white wing-bar (white primary shafts and tips of greater secondary and inner primary coverts); off-white rump and uppertail-coverts, heavily barred blackish and contrasting with pale brownish-grey tail; and mostly white underwing with dusky trailing-edge, greyish greater coverts and extensive fine grey markings on leading innerwing-coverts and axillaries. In worn plumage, pale tips and fringes reduced or lost: chestnut areas of upperparts fade and bleach to off-white, mantle and scapulars become darker, black, and either coarsely variegated with white or with only trace of off-white spots and fringes; brownish-grey innerwing-coverts worn and faded; and chestnut-red of underbody fades to orange-chestnut. Bill, black. Iris, dark brown. Legs and feet, dark olive to dark grey. **Adult non-breeding** Differ from adult breeding by: centre of forehead, crown, nape, hindneck and sides of neck, plain brownish-grey, finely streaked black. Chin and throat, white; rest of head and neck, white with fine dark streaking, obvious white supercilium from bill to above rear ear-coverts (often finely streaked darker and less distinct over and behind eye), and dusky eye-stripe formed by narrow grey loreal stripe and patch on ear-coverts. Mantle, scapulars, tertials and innerwing-coverts, plain brownish-grey, all feathers with fine blackish shaft and thinly fringed white when fresh. Underbody, white, with grey suffusion on sides of breast and fine dark streaks or spots from foreneck to upper belly and along sides of belly, which grade to fine wavy dark bars on sides of lower breast and along flanks to sides of vent; some fine dark streaks on lateral undertail-coverts. In flight, like adult breeding except rump and uppertail-coverts have finer dark barring and appear paler and more contrasting (though looking pale grey at distance). Upperparts become browner with wear. Legs and feet vary as breeding but generally paler, dull olive-green. **Juvenile** Like adult non-breeding; differs by: feathers of mantle, scapulars, tertials and innerwing-coverts faintly washed brown, with characteristic pattern of dark shafts, thin dark submarginal lines, and crisp narrow white fringes giving scaly appearance above. Foreneck, breast and upper belly (sometimes entire underbody) have faint pinkish-buff wash, which is soon lost with wear; foreneck and breast tend to be less heavily marked. Legs and feet paler, more yellowish green. Pale fringes on upperparts and innerwing-coverts reduced or lost with wear, but characteristic dark submarginal lines remain. **First immature non-breeding** Like adult non-breeding but distin-

guished by retained worn juvenile innerwing-coverts and, usually, some tertials, which contrast with fresh plumage (plumage uniformly fresh in adult); most also differ by wear and moult of remiges (see Ageing). **First immature breeding** Most birds wintering in HANZAB area stay in first immature non-breeding and acquire only a little breeding plumage (some that migrate N acquire more breeding plumage); during second austral winter—summer in se. Aust. and NZ, distinguished by timing of moult (see Moults, Ageing).

Similar species In all plumages, large size and jizz distinguish from other calidrids. Adult breeding distinguished by boldly variegated black, chestnut and pale-grey upperparts and dark-barred pale rump and uppertail-coverts; and chestnut-red face and underbody (Great Knot never has any chestnut on underbody). In breeding plumage, **Curlew Sandpiper** and **Asian Dowitcher** *Limnodromus semipalmatus* also have chestnut underbody and dark-barred pale rump and uppertail-coverts; Curlew Sandpiper is much smaller and slimmer, with longer, decurved bill, clearer white rump and longer black legs; Asian Dowitcher distinguished by much longer, godwit-like bill. In non-breeding and juvenile plumages, size, jizz, and pale rump distinguish from all other calidrids except **Great Knot**, which IN ALL PLUMAGES: (1) is larger and bulkier in direct comparison; (2) appears to have smaller head, longer neck, flatter profile of back and belly and deeper, heavier chest, which, with longer wings, gives more attenuated shape; (3) has longer slightly heavier and deeper-based bill that tapers to finer, and often slightly drooping, tip; (4) in flight, appears longer-winged and less compact, with slightly narrower, weaker wing-bar, and clearer but narrower and more contrasting white patch on rump and uppertail-coverts (less obscured with dark markings). In NON-BREEDING PLUMAGES, Great Knot also differs from non-breeding Red Knot by: (1) clearer and heavier dark streaking on head and neck; (2) different head-pattern: supercilium less clear, particularly behind eye, and, with diffuse dark triangular area across lores (cf. narrower more distinct dark loreal stripe on Red Knot) and so has greyer, more expressionless face; ear-coverts normally the same colour as nape and hindneck (often contrastingly darker in Red Knot); (3) feathers of upperparts and innerwing-coverts have diffuse dark centres, blackish shaft-streaks and, when fresh, white fringes giving distinctly streaked and more variegated appearance above compared with rather plain brownish-grey upperparts of Red Knot; (4) rump and uppertail-coverts almost unmarked white, contrasting more strongly with greyish upperparts and tail (on Red Knot, same tracts overlaid with narrow dark barring, appearing pale grey and contrasting less); (5) distinctive pattern of underbody: breast heavily spotted dark grey, often with a few large blackish spots, and flanks have series of large triangular streaks or rounded marks (Red Knot can sometimes have similar pattern, but spots on breast typically smaller, and sides of lower breast and flanks marked with many finer and paler grey crescentic bars); (6) legs and feet duller, dark slate or greenish grey, but some overlap. In JUVENILE PLUMAGE, Great Knot differs from juvenile Red Knot by: (1) pattern of head, neck and rump as non-breeding; (2) darker upperparts, with darker blackish centres to feathers of mantle and scapulars and broader blackish subterminal markings to tertials and innerwing-coverts; also, scapulars, tertials and inner few greater coverts have pale-spotted fringes (on Red Knot, upperparts and coverts paler grey, with crisp narrow pale fringes without spots and finer dark submarginal lines, giving more scaly appearance above); (3) larger, much darker blackish-brown spots on breast and flanks, with those on

Plate 12

Wandering Tattler *Heteroscelus incana* (page 188)
1 Adult breeding; 2 Adult non-breeding; 3 Juvenile;
4, 5 Adult

Grey-tailed Tattler *Heteroscelus brevipes* (page 180)
6 Adult breeding; 7 Adult non-breeding; 8 Juvenile;
9, 10 Adult

breast often coalescing to form dark pectoral band, very different from more finely marked underbody of Red Knot; (4) legs and feet usually duller, green, but some overlap. At distance, in flight, might be confused with non-breeding and juvenile **Grey Plover**, but that species has more conspicuous wing-bar, paler and less contrasting off-white tail, and diagnostic black wing-pits that contrast with white underwing.

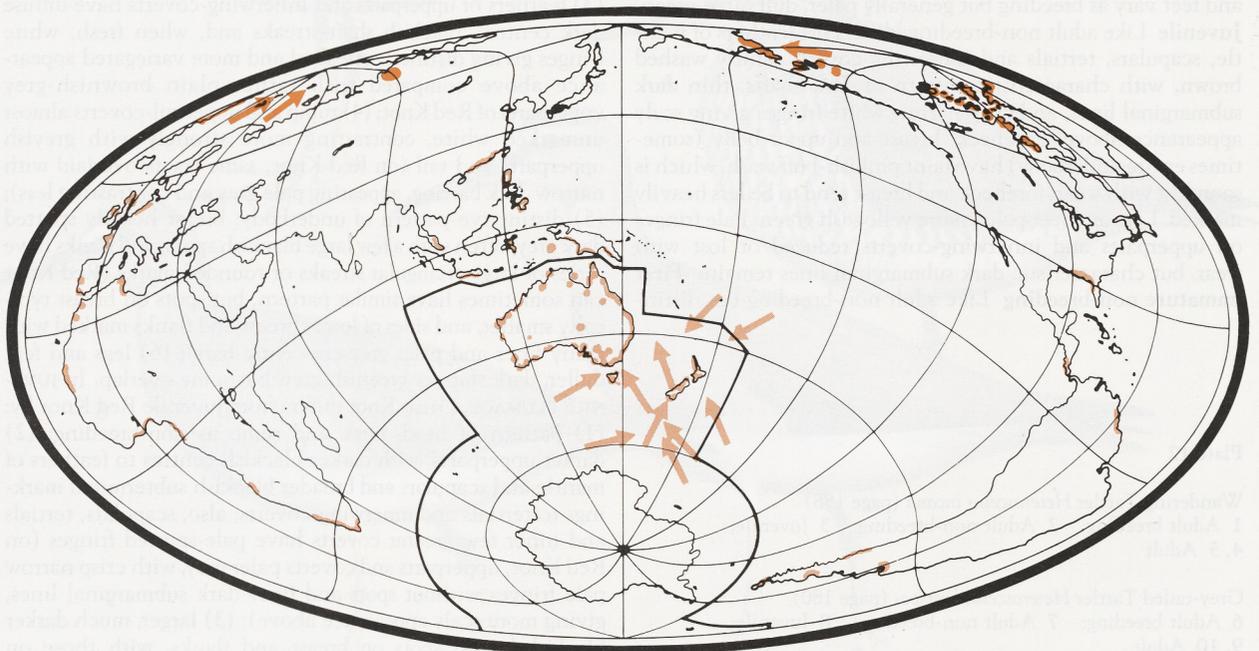
Coastal and highly gregarious in HANZAB region; in small to large flocks (thousands in favoured localities), on large sandy or muddy estuaries or coasts with tidal mudflats. Form dense feeding and roosting flocks and freely associate with other waders, especially Great Knots, godwits, sand plovers and smaller calidrids. Gait and feeding similar to Great Knot, but walk faster and probe more rapidly. Feeding action slower and more methodical than smaller congeners; feed mainly by fast, intense, methodical probing with head held low and bill nearly vertical; also peck at surface. Flight typical of genus, similar to Great Knot, but wing-beats slightly faster and appear shorter-winged and more compact; flying flocks typically ovoid, flat-bottomed when near ground; flocks at distance appear 'grainier' than those of smaller species, and exhibit slower, steadier changes in shade and direction, resembling drifting smoke. Fly in lines or Vs on migration. Quiet in non-breeding season; single individuals almost always silent. Main call similar to that of Great Knot: feeding birds and flocks in flight utter low, slightly harsh monosyllabic *knutt*, *wutt wutt* or *kwet*.

HABITAT In A'sia, mainly intertidal mudflats, sandflats and sandy beaches of sheltered coasts, in estuaries, bays, inlets, lagoons and harbours (Sibson 1979; Martindale 1982; Pegler 1983; Garnett 1989; Peter 1990; Aust. Atlas); occasionally on sandy ocean beaches or shallow pools on exposed wave-cut rock platforms or coral reefs (Gibson 1977; Storr 1977; Congreve & Congreve 1985; Morris 1989). Occasionally on terrestrial saline wetlands near coast, such as lakes, lagoons, pools and pans, but rarely freshwater swamps (Dann 1983; Storr 1984b, 1987; Storr & Johnstone 1988; Lane; Vic. Atlas).

Also sewage ponds and saltworks (Storr 1984a; Lane & Jessop 1985b; Lane; Vic. Atlas). Rarely, inland lakes or swamps (Hobbs 1961; Storr 1977; Badman & May 1983). On Chatham Is, on shallow, brackish lagoon with large sandflats and mudflats (Fleming 1939).

Usually forage in soft substrate near edge of water on intertidal mudflats or sandflats exposed by low tide; at high tide, may feed at nearby lakes, sewage ponds and floodwaters (Sibson 1979; Lane; Vic. Atlas). Also recorded foraging on beds of eelgrass on tidal sandflats (P. Battley), on thick algal mat in shallow water (Dann 1983), and in shallow pools on crest of coral reef (Domm & Recher 1973). Roost on sandy beaches, spits and islets, and mudflats; also in shallow saline ponds of saltworks; in NZ, roost on short wet pastures near coast (Sibson 1979; Lane; Vic. Atlas; A. Riegen & S. Davies).

DISTRIBUTION AND POPULATION Breed North America, Russia, Greenland and Spitsbergen: nw. and n. Alaska round Seward Pen. and De Long Mts and, rarely, at Pt Barrow and Cooper I.; n. Canadian Arctic Arch., including Queen Elizabeth Is, from Prince Patrick and Melville Is, S to Prince of Wales and Somerset Is, and W to Devon and Ellesmere Is; also s. Victoria I. (possibly also on Adelaide Pen.), e. Melville Pen. and islands in n. Hudson Bay, including Southampton, Coats and Mangel Is; nw. and e. Greenland and, occasionally nw. Spitsbergen; Taymyr Pen., New Siberian Is, Wrangel I. and mountainous regions of Chukotskiy Pen., from Yuzhnyy Anyuyskiy and Vernyy Anyuyskiy Ras, E through Chukotskiy (Anadyrskiy) and Ekiatapskiy Mts, E to Tenkany Ra., and S to just S of Arctic Circle (Dement'ev & Gladkov 1951; AOU 1983; Tomkovich 1987, 1992; Boyd 1992; Godfrey 1992; Morrison & Harrington 1992; BWP). On passage, occur Canada, USA, n. South America; Iceland; n. and ne. Russia, Scandinavia, Baltic countries, Iberian Pen., n., nw. and w. Africa; e. Asia, from Kamchatka Pen. through e. Siberia, Korean Pen., Japan, e. China, Philippines, Malaysia, Indonesia and Irian Jaya. Non-breeding visitor to most continents. Small numbers in North America, in w. Florida, Gulf of Mexico





and Caribbean. In Central America, round Costa Rica and Panama. In South America, mostly Argentina, from Valdes Pen. to Tierra del Fuego; occasionally L. Maracaibo in nw. Venezuela, French Guyana, and n.-central Brazil and Pacific coast of Peru and Chile. In w. Europe, mostly British Isles, France and the Netherlands, with a few on Iberian Pen. In Africa, mostly s. Morocco and Mauritania and in S between nw. Namibia and Natal. Small numbers in e. and se. Asia, from e. China, through Philippines, S to Indonesia, and W to Malaysia and to A'asia. Vagrant to India, Thailand, Mongolia, Hawaii, Palau, Fiji, e. Africa, e. South Africa, s. Mozambique and Botswana (Dick *et al.* 1976; Ali & Ripley 1980; de Schauensee 1984; Coates 1985; Pratt *et al.* 1987; Urban *et al.* 1986; Morrison & Harrington 1992; Piersma & Davidson 1992b; AWB 1993; BWP).

Aust. **Qld** Passage migrant along coast N of 19°S, sometimes in large numbers (Roberts 1975; Draffan *et al.* 1983; Garnett & Bredl 1985; Garnett 1989; Aust. Atlas). Widespread along coast S of Townsville (Storr 1984b; Qld Bird Reps; Aust. Atlas). Inland record from Toomba L. (Qld Bird Rep. 1985). **NSW, Vic.** Widespread round coast, but few records between Bermagui and Lakes Entrance, and from w. Bellarine Pen. to Warrnambool. Few inland records, including L. Goran, Fivebough Swamp and area N to L. Menindee, W to Wentworth, S to L. Albacutya and Kerang Ls and E to Wakool; occasionally round lakes in Colac district (Hobbs 1961; Thomas 1970b; Lowe 1981; Morris *et al.* 1981; Henle 1989; NSW Bird Reps; Vic. Bird Reps; Vic. Atlas; Aust. Atlas). **Tas.** Regular visitor in small numbers on coast and on King and Flinders Is. On n. coast, recorded in NW from Kangaroo, Robbins and Perkins Is; also Port Sorell, Kelso, George Town and C. Portland. Isolated record at Swansea on e. coast; in SE, many records from Marion Bay, W to Sorell and S to Bruny I. On w. coast, recorded at Melaleuca, Bond Bay, Port Davey, Strahan,

Four Mile Beach and Pieman Heads (Thomas 1970a, 1979; White 1985; Schulz 1993; Tas. Bird Reps; Aust. Atlas). **SA** Rarely in SE; mostly from The Coorong, N and W to Yorke Pen. and Port Pirie. On Eyre Pen., recorded Port Augusta, and from s. Eyre Pen. to Streaky Bay (Eckert 1974; SA Bird Reps; Aust. Atlas). Isolated inland record from L. Eyre (Cox & Pedler 1977). **WA** Scattered in S, from Eyre W to Albany, and from Flinders Bay to N of Perth. Occasionally round Peron Pen. and Carnarvon. Widespread along coast from Ningaloo and Barrow I. to sw. Kimberley Div. Isolated inland record near Leonora (Davies & Chapman 1975; Howard 1983; Johnstone 1983; Halse & Halse 1988; Jaensch *et al.* 1988; Aust. Atlas). **NT** Mainly recorded Darwin, but also at Lalungang Ck, Melville I., Groote Eylandt, Sir Edward Pellew Is and McArthur R. (Crawford 1972; Schodde 1976; Storr 1977; Aust. Atlas; H.A.F. Thompson & D.K. Goodfellow).

NZ Widespread but unevenly distributed round much of coast (NZCL). Rarely inland, where records include L. Tarawera and L. Wairarapa (Cunningham 1946; CSN 30, 37). **NI** Widespread in harbours, from Parengarenga Harbour, S to Manukau Harbour and w. Firth of Thames; occasionally Coromandel Pen. Widespread Bay of Plenty, from Bowentown to Te Araroa, probably on passage (NZCL). Between East C. and C. Palliser, occasionally at Muriwai and Waiapu R., but mostly round Hawke Bay; single record from estuary of Porangahau R. Scattered records from Petone to Waitotara R. and at several locations round New Plymouth between Pungaerare Stream and Waitara R. Also round Kawhia and Aotea Harbours. **SI** Mostly Farewell Spit, Golden Bay and Tasman Bay; occasionally Marlborough, at Wairau R. and L. Grassmere. In Canterbury, mostly between Waipara and Ashburton R. estuary; also Kaikoura and Wainono Lagoon. Few records Otago, round Otago Pen. and at Inch Clutha. Widespread se. and s. Southland, in lagoons between Catlins

L. and Te Waewae Bay. Uncommon w. coast, but a few records scattered from Karangarua, N to estuary of Orowaiti R. and Karamea (CSN; NZ Atlas). Stewart I.

Norfolk I. Unknown number, 1839 (Schodde *et al.* 1983); single, early 1970 (Hermes *et al.* 1986); two, 28 Oct., 20–21 Nov. 1979 (Moore 1981); 1–2, 5–18 Nov. 1980 (Moore 1981); up to five, 31 Oct.–16 Nov. 1981 (Moore 1985); two, 12 Oct. 1984 (Hermes *et al.* 1986); single, 9–24 Dec. 1984 (Moore 1985).

Lord Howe I. Single specimen, 10 Sept. 1853 (Hindwood 1940); single, 19 Sept. 1963 (McKean & Hindwood 1965).

Macquarie I. Single specimen, 7 Nov. 1913 (Falla 1937).

Kermadec Is Raoul I.: single specimen, 17 Oct. 1910 (Oliver 1911, 1912; Merton 1970) (not 29 July as stated by Sorensen [1964]); single, specimen, 20 Dec. 1966 (Merton 1970); 4–6, 21 Aug.–Oct. 1977 (CSN 26); unconfirmed record, Sept. 1908 (Sorensen 1964).

Chatham Is Summer visitor to Chatham I.; flocks of 500–1500 recorded (Fleming 1939; Freeman 1994; CSN; NZCL).

Auckland Is Straggler (NZCL): recorded before 1972 (Yaldwyn 1975).

Campbell I. Four (two specimens), 21 Dec. 1945; previously, unconfirmed report of birds that may have been Red Knot, 10 Dec. 1943 (Bailey & Sorensen 1962).

Population Aust. Estimated 153,000 (Watkins 1993). Totals for summer and winter counts, 1986–91, summarized in Table 1 (Hewish 1986, 1987a,b, 1988, 1989a,b, 1990a,b; Anon. 1992; Naismith 1992). Sites of significance and maximum or average counts for summer and winter surveys, 1981–85, were: Eighty Mile Beach, WA, 80,700; se. Gulf of Carpentaria, Qld, 79,100; Roebuck Bay, WA, 11,200; Spencer Gulf, SA, 4800; Corner Inlet, Vic., 2720; Gulf St Vincent, SA, 11,200; Port Phillip Bay, Vic., 730; w. coast of Eyre Pen., SA, 710 (Lane). Other areas of international importance (Watkins 1993) include Roper R. area, NT (3100) and L. Macleod, WA (2566).

Table 1

Year	Summer Total	No. Sites	Winter Total	No. sites
1987	9433	22	1896	23
1988	5517	23	1800	23
1989	7392	22	2878	21
1990	4668	21	991	21
1991	6401	21	–	–

NZ Totals for summer and winter counts, 1983–93, summarized in Table 2; mean total summer count (n=10 summers): NI, 36,036 (s.d. = 9986); SI, 16,953 (s.d. = 4069) (OSNZ Nat. Wader Count; P.M. Sagar). Sites of importance, with mean summer counts given below; maximum counts that exceeded maxima from OSNZ Nat. Wader Counts are also given. **NI** Parengarenga, 4897 (3868; 155–13,500); Houhora, 1876 (676; 1100–2855); Rangaunu Harbour, 1839 (818; 100–2500), also 6000, 28 Oct. 1983; Whangarei Harbour, 2528 (1159; 856–4198); Kaipara Harbour, 7846 (4981; 381–16,910); Manukau Harbour, 16,083 (4472; 9950–22,433), also 23,200, summer 1981–82 (CSN 30) and, at Kidd's Bay, 12,000, Mar. 1978 (CSN 25, 30), and 20,000, 20 Jan. 1985 (CSN 33); Firth of Thames, 3848 (900; 1901–5200), also 11,400, 20 Oct. 1974 (CSN 22) and, at Miranda, 8000, 10 Oct. 1982 and 28 Oct. 1983 (CSN 31, 32). **SI** Farewell Spit, 14,538 (3957; 9206–24,227), also 27,370, Jan. 1961 (Edgar 1962). Other sites of

Table 2

Year		Winter Total	No. Sites	Summer Total	No. Sites
1983	NI	–	–	30,280	31
	SI	–	–	16,760	43
1984	NI	1966	42	26,423	44
	SI	401	68	25,512	73
1985	NI	3151	60	36,933	79
	SI	352	83	12,183	65
1986	NI	4848	91	30,733	75
	SI	569	77	16,644	73
1987	NI	3067	66	37,621	54
	SI	317	53	20,240	63
1988	NI	4540	58	45,867	65
	SI	388	66	19,235	54
1989	NI	6584	56	24,275	30
	SI	561	65	17,589	56
1990	NI	4928	34	25,333	31
	SI	420	49	17,466	40
1991	NI	4178	33	54,255	37
	SI	528	47	13,121	35
1992	NI	7815	45	48,640	34
	SI	373	52	10,783	44
1993	NI	5757	43	–	–
	SI	1266	42	–	–

importance (counts of ≥ 5000 birds; CSN 19–39) include: Karaka, 20,000, 20 Jan. 1985 (CSN 33); Tapora, c. 7000, 2 Mar. 1991 (CSN 39); Mangere Sewage Farm, 5500, 2 Dec. 1990 (CSN 39).

In NZ, some illegal shooting persists (P. Battley).

MOVEMENTS Migratory. Breed in high Arctic and move S to non-breeding areas between 58°N and 50°S. Five subspecies, separable into seven migratory populations; one subspecies known to occur in A'asia; a second may occur. Nominate *canutus* probably comprises three migratory populations: population breeding Taymyr Pen. possibly migrates to w. Europe; population breeding New Siberian Is migrates along coast of e. Asia, possibly to Aust. and NZ; breeding range of a third population of relatively long-billed nominate *canutus*, which migrates through w. Europe to w. and s. Africa, is not known but possibly Yakutia, Siberia. Subspecies *rogersi* breeds ne. Siberia, including Chukotskiy Pen. and possibly farther W, and migrates mainly to Aust. and NZ (Barter 1992; Piersma & Davidson 1992b; Tomkovich 1992; BWP). Route of migration to HANZAB region not known; may move in loop, migrating S across w. Pacific Ocean and N along e. Asian coast (Barter 1992). Tend to make long non-stop flights between only a few staging areas; weight increases greatly before migration (BWP). Known to migrate overland and visit inland wetlands while migrating (Beehler *et al.* 1986). Only nominate *canutus* breeding New Siberian Is and subspecies *rogersi* discussed below.

Departure Nominate *canutus* probably move across inland e. Siberia to coast of e. Asia; subspecies *rogersi* move to Sea of Okhotsk (Tomkovich 1992). Juveniles move through Ussuriland from late Aug. (Dement'ev & Gladkov 1951). Recorded Korea, Aug.–Sept. (Gore & Won 1971). Uncommon or in small numbers in: Japan, China, Hong Kong, se. Asia and s. Pacific during s. migration (see AWB 1993; Lane). Banding suggests birds do not move along coast of e. China, though in 1991 small numbers moved through Jiangsu Province during Aug., and others, probably juveniles, recorded

Shanghai, mid-Sept. (Wang Tian Hou & Qian Gouzhen 1988; Barter 1992; Hui 1992). Juveniles caught Hong Kong, Sept.–Nov. estimated to be able to fly non-stop to n. Aust. (Barter 1992). Lack of abundance and banding recoveries in Asia during s. migration and evidence from radar studies at Guam suggests birds fly non-stop across w. Pacific Ocean from ne. Asia (Barter 1992). Rare on Pacific islands (Pratt *et al.* 1987), though recorded Fiji, Tonga, Samoa, between Fiji and NZ, and Kermadec Is (Jenkins 1978; Watling 1982; Oliver). In New Guinea, huge flocks recorded Trans-Fly region, and many regularly stage in se. Irian Jaya, Oct.–Nov.; vagrant farther E in PNG; irregular passage migrant in sw. Torres Str. only (Draffan *et al.* 1983; Coates 1985; Beehler *et al.* 1986; Hicks 1990).

Aust. Most arrive nw. coast and Gulf of Carpentaria; banding shows that birds occurring se. Aust. and NZ do not move through nw. Aust. on either migration, but birds may move from w. Aust. to NZ between non-breeding seasons (Barter 1992; see Banding). Arrive nw. Aust., end Aug. to early Sept., with rapid increases in weight before migrating farther; numbers decline by 50% in Nov. (Watkins 1993). Numbers peak Darwin in Sept. and Oct. (Lane). In Gulf of Carpentaria, large numbers Sept., with evidence that tens of thousands pass through in Sept. and Oct. before numbers drop by Dec. (Garnett 1986; Lane); Gulf probably main staging area for birds moving to NZ, though some move to se. Aust., arriving from end Sept.; some move from se. Aust. to NZ (Barter 1992). Do not usually visit Norfolk and Lord Howe Is. **NZ** Arrive from end Sept. (Barter 1992).

Non-breeding Subspecies *rogersi* apparently only in large numbers in Aust. and NZ (de Schauensee 1984; Barter 1992). **Aust.** Most remain in N with <10,000 in s. Aust. (Lane). Move S, mostly along coasts, with some inland records, Sept.–Nov. (Cox & Pedler 1977; Aust. Atlas). Apparently arrive sw. Aust. from Sept. (Storr & Johnstone 1988); arrive Gulf St Vincent, SA, Sept.–Nov. (Hindwood & Hoskin 1954; Gibson 1977; Close & McCrie 1986; Lane); small numbers regularly arrive Tas., Aug.–Sept. (Thomas 1970b) though sometimes large numbers in nw. Tas. (Ashby 1991). Recoveries of bands shows high site-fidelity in nw. Aust. and Vic.: few movements recorded, all in Vic. and ≤ 27 km, and mostly first-year birds (Barter *et al.* 1988b). However, large fluctuations in numbers in Gulf St Vincent indicate much movement (Close & McCrie 1986; Hewish 1987a). In Vic., adult and first-year birds have different distributions, e.g. first-year birds 81–95% of population in Westernport Bay (Barter *et al.* 1988b). **NZ** Probably many birds on passage in Far North on s. migration (CSN; P.A. Battley). At Firth of Thames, numbers increase late Sept. to early Nov. (McKenzie 1967). At Manawatu Estuary, numbers increase from late Sept. to Dec. (P. Battley). Generally scarce passage migrant on e. coast (Sibson 1979). Movement between NI and SI confirmed by single recovery (Riegen & Davies 1993) and sightings of leg-flagged birds (P. Battley).

Sometimes noted in tight single-species flocks in nw. Aust. before migration (Lane & Jessop 1985a). Pre-migratory flighting observed during Mar. in NZ (McKenzie 1967). At Farewell Spit, birds called much when leaving, flocks gradually changing from a cluster to a V or echelon (P. Battley).

Return NZ Leave late Mar. to early Apr. (Barter 1992), though influx Manukau, Jan.–Feb. (McKenzie 1967) may have been early n. passage. At Farewell Spit, in 1994, departures recorded 8–27 Mar. (though some birds in breeding plumage that remained after this date may have left later); mean size of departing flocks, 33.7 birds (13–75; 15); most flocks left on incoming tide and within 3 h of dusk; mean direction of

departure, 333°7' (n=10 flocks) (P. Battley); no evidence for passage of birds at Farewell Spit (P. Battley; J. Hawkins *contra* McKenzie 1967). No evidence for suggestion that NZ birds stop in se. Aust. (Starks & Lane 1987), though banding recoveries in se. Qld and Irian Jaya suggest NZ birds might stop in Gulf of Carpentaria (Barter 1992). Estimated flight-ranges suggest NZ birds capable of flying non-stop to Gulf of Carpentaria (3900 km) (Barter *et al.* 1988a). **Aust.** Leave Tas., Feb.–May (Thomas 1970b); influxes recorded at some sites in SA before departure (Close & McCrie 1986). Leave se. Aust., late Mar. to early Apr. (Barter 1992), though in 1985 birds recorded leaving s. Aust., late Feb. (Starks & Lane 1987). Estimated flight-ranges of birds in se. Aust. indicate many could fly non-stop to staging areas in n. Aust. or beyond; Gulf of Carpentaria probable staging site (Barter 1992). Inland records show some birds might move overland on n. migration from se. Aust. No evidence of passage through Darwin (Lane). Small flocks move along coast of e. Qld, mid-Mar., then pass through Gulf of Carpentaria, Mar. and Apr. (Lane; Garnett 1989). Regularly stop in large numbers in se. Irian Jaya, Apr. to early May (Coates 1985). Leave nw. Aust., late Mar. to end Apr. (Barter 1992); influx in mid-Apr. and weights indicate staging occurs in nw. Aust., but birds probably not from se. Aust. or NZ (Barter 1992 *contra* Lane). Estimated flight-ranges indicate nw. Aust. birds able to fly directly to Shanghai, China (5500 km) with evidence that this occurs (Barter & Wang Tian Hou 1990; Barter 1992). Radar studies indicate average heading of birds leaving Broome, nw. Aust., is 320° (cf. 360° direct to Shanghai), thus route apparently compensates for prevailing E to NE winds over e. Asia in Mar. and Apr. (Barter 1992).

Extralimitally, only small numbers pass through se. Asia, e.g. Olango I., Philippines (Magsalay *et al.* 1990; Magsalay 1991). Biometrics indicate that birds migrate along e. Asian coastline and, though staging sites poorly known, band recoveries suggest staging on e. coast of China (Shanghai) in Apr. and early May (Wang Tian Hou & Qian Gouzhen 1988; Barter 1992). Large numbers counted Korea, Apr. and May (AWB 1993).

Breeding Aust. Mainly stay in N, but as far S as Vic. (Aust. Atlas; Vic. Atlas); sometimes recorded Tas. and sw. WA during winter (e.g. Hewish 1988, 1990b). Some young non-breeders may remain during winter. Reporting rates in summer 0.72%, and in winter 0.22%. Percentage of summer population wintering at counted sites, 1982–86, 7–44% (Hewish 1987a), though at some sites, such as Gulf St Vincent, SA, proportion varies from year to year (Close & McCrie 1986). Some counted sites not occupied in all years (Hewish 1987a). Much movement suggested by fluctuations in numbers at Gulf St Vincent, SA, e.g. large influx June–July in some years (Close & McCrie 1986). **NZ** Commonly winter, sometimes in thousands (e.g. Auckland district) (McKenzie 1967). At Firth of Thames, 1970–77, average 11% of summer population remained over winter (Sibson 1988).

Banding, Colour-marking Birds banded se. Aust. recovered NZ (one recorded moving Vic. to NZ twice), China and Siberia; birds banded sw. Aust. recovered at least 1 year later in NZ; birds banded nw. Aust. recovered China (data to 28 Feb. 1993; ABBBS 1992, 1993). Twelve international recoveries of birds banded NZ to Aug. 1992: Qld (n=2), Irian Jaya (n=2), China (n=4) and e. Siberia (n=3) (Riegen & Davies 1993). All recoveries on coasts of Qld, Irian Jaya and China on n. migration (Barter 1992). Single bird banded nw. Aust. recovered near Shanghai, China, 1 month later (ABBBS 1992). All

recoveries in Siberia (except undatd recoveries) and all movements from Aust. to NZ are on smigration (Barter 1992). Birds colour-marked in Vic. sighted Qld (n=2) and NZ (n=24, but some possibly same bird) (Maton 1993); birds colour-marked Qld sighted NZ; one color-marked NZ sighted Vic. (A. Riegen & S. Davies).

32S151E	01	1+ U	112	1268	358	ABBBS
38S144E	03	1 U	28	1893	3	ABBBS
33S137E	12	P U	6	1646	357	ABBBS
38S144E	11	1 U		1412	358	ABBBS
33S137E	12	P U	79	806	349	ABBBS
37S175E	11	1+ U	5	384	316	NZNBS
17S122E	10	3+ U		964	5	ABBBS
38S144E	03	2+ U	109	015	339	ABBBS
38S144E	10	1 U	42	015	339	ABBBS
38S144E	10	3+ U	18	010	339	ABBBS
33S137E	12	1+ U	31	993	346	ABBBS
33S137E	12	1+ U	40	983	343	ABBBS
32S151E	12	2+ U	111	740	332	ABBBS
33S137E	12	1+ U	30	965	342	ABBBS
33S137E	12	1+ U	30	965	342	ABBBS
19S121E	04	2+ U	59	572	1	ABBBS
19S121E	04	2+ U	1	540		ABBBS
18S122E	04	2+ U	24	474	359	ABBBS
18S122E	04	2+ U	12	429	359	ABBBS
18S122E	03	2+ U	85	426	359	ABBBS
18S122E	04	1 U	13	424	359	ABBBS
31S115E	10	1+ U	28	320	112	ABBBS
31S115E	10	1+ U	28	320	112	ABBBS
31S115E	10	1+ U	28	308	112	ABBBS
31S115E	10	1+ U	28	308	112	ABBBS
35S117E	03	2+ U	15	082	110	ABBBS
35S117E	03	2+ U	15	082	110	ABBBS
22N114E	09	J U	36	591	168	BTO
38S144E	11	1 U	47	686	97	ABBBS
38S144E	06	1 U	11	651	96	ABBBS
38S144E	06	1 U	11	651	96	ABBBS
38S144E	06	1 U	11	645	97	ABBBS
38S144E	06	1 U	11	645	97	ABBBS
38S144E	01	J U	13	641	95	ABBBS
38S144E	01	J U	13	641	95	ABBBS
38S144E	01	1 U	95	639	96	ABBBS
38S144E	01	J U	13	636	95	ABBBS
38S144E	01	J U	13	636	95	ABBBS
38S144E	10	3+ U	4	631	95	ABBBS
38S144E	10	2+ U	51	624	95	ABBBS
38S144E	10	3+ U	16	624	95	ABBBS
38S144E	02	2+ U	72	624	95	ABBBS
38S144E	11	3+ U	3	624	95	ABBBS
38S144E	11	1 U	27	624	95	ABBBS
38S144E	06	1 U	32	624	95	ABBBS
38S145E	01	1 U	17	617	97	ABBBS
38S145E	08	2 U	10	610	96	ABBBS
38S145E	08	2 U	10	610	96	ABBBS
38S145E	07	1 U	17	609	96	ABBBS
38S145E	08	2 U	4	547	95	ABBBS
37S175E	08	2+ U	7	509	297	NZNBS
37S175E	11	1+ U	34	351	291	NZNBS
27S153E	11	1 U	19	342	123	ABBBS
36S174E	02	1+ U	55	266	292	NZNBS
27S153E	10	2+ U	28	245	122	ABBBS
27S153E	10	U U	28	244	122	ABBBS
32S151E	12	1+ U	36	106	108	ABBBS
35S117E	03	2+ U	-36	793	12	ABBBS

32S151E	12	1+ U	22	626	13	ABBBS
38S146E	03	2+ U	2	195	284	ABBBS
18S122E	04	2+ U	35	177	218	ABBBS
18S122E	04	2+ U	35	177	218	ABBBS
38S145E	01	1 U	2	130	114	ABBBS
38S145E	01	1 U	2	130	114	ABBBS
38S146E	03	1 U	4	118	287	ABBBS
38S146E	03	1 U	4	118	287	ABBBS
38S146E	03	1 U	6	117	287	ABBBS

FOOD Omnivorous: worms, bivalves, gastropods, crustaceans and echinoderms. Extralimitally, also take shoots, bulbs, seeds and roots, especially early in breeding season; hydrozoans, arachnids, insects, fish and kitchen scraps. **Behaviour** Diurnal and nocturnal. In non-breeding areas, activity regulated by tide: feed less just before and after high tide, but timing of cessation of feeding and roosting depends on time of year and height of tides (Tulp & de Goeij 1991; BWP). In nw. Aust., follow receding edge of tide and fly to edge of water when a few meters of exposed mudflats between bird and the water (Tulp & de Goeij 1994). Feed in large mixed flocks with Great Knots, Bar-tailed Godwits *Limosa lapponica* and Grey-tailed Tattlers *Heteroscelus brevipes* (Tulp & de Goeij 1994). In NZ, individuals maintain space of 7–10 bird-lengths round them while foraging (Piersma 1991); at Farewell Spit, feeding birds appear to be more widely spaced than in Europe (P. Battley). Locate prey mostly by touch; sometimes by taste (Gerritsen *et al.* 1983); sometimes locate prey by sight, picking snails from eelgrass (P. Battley). In Aust. and NZ, feed mainly by probing vertically into substrate with full length of bill and slowly rotating head. Often probe 1–5 times followed by short run, then repeat pattern; said to be less hasty than other *Calidris* (Cunningham 1946; McGill 1947; BWP). Glean from surface, especially on upper shore, for 2 h either side of high tide. Recorded ploughing: probing c. 1 cm into mud with bill then pushing bill forward 1–3 cm. Sometimes immerse head fully or wade up to belly. Recorded taking whelks off rocks above edge of water (Thomas 1986). Also feed by continuous pecking (sewing-machine action), rarely lifting bills completely from mud (Tulp & de Goeij 1994; P. Battley). Size of molluscs taken varies with latitude of feeding site; can swallow *Macoma* and *Siliqua* up to 23 and 29 mm long respectively (Tulp & de Goeij 1994). Most indigestible material excreted as faeces, though sometimes regurgitate pellets of indigestible material. Feeding rate of 27.6 feeding movements/min recorded (Dann 1983). May be stimulated to feed by other species feeding, e.g. Bar-tailed Godwit (Howell & Harrison 1981). Birds on L. Reeve, e. Vic., spent same amount of time feeding on dry algal mat and wet mud (Dann 1983). Shells crushed in stomach (Piersma 1991).

Adult At Miranda, NZ (30 faeces; Piersma 1991): Molluscs: bivalves: *Myadora* 90% dry wt; *Nucula* 5; *Tellina* 5. Also at **Miranda** (50 faeces, Aug. 1992; P. Battley): Molluscs: bivalves: *Nucula* 98%; *Chione* 2. At **Farewell Spit, NZ** (20 faeces; Piersma 1991): Molluscs: gastropods: Trochidae (*Micreleuchus tenebrosus*; *Diloma subrostrata*) 35; bivalves: *Nucula* 35; *Tellina* 15; *Chione* 15. Also at **Farewell Spit** (P. Battley): Molluscs: bivalves: pipi *Amphidesma australis*; *Nucula*; *Tellina*; *Chione*; gastropods: unident. (small). Crustaceans: amphipods *Paracorophium*. At **Roebuck Bay, nw. WA** (430 min obs.; Tulp & de Goeij 1994): Annelids: polychaetes 14.6% of total prey taken; Molluscs: bivalves (incl. *Macoma*, *Siliqua*) 65.8%; gastropods 4.8; Crustaceans 9.7; Echinoderms 4.8.

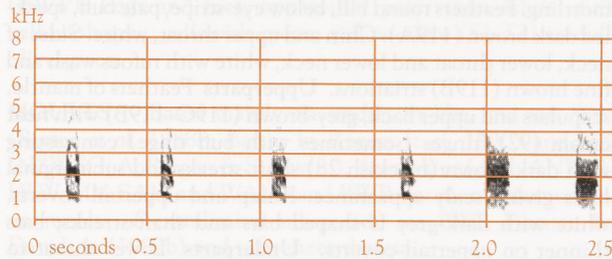
Other records Annelids: polychaetes: lugworm

Abarenicola, unident. (P. Battley); oligochaetes. Molluscs: gastropods (Dann 1983): Nassariidae: *Nassarius* (Thomas 1986). Crustaceans: amphipods (Dann 1983); decapods: prawns (P. Battley). Insects: Diptera (P. Battley). Fish: small flounder (P. Battley).

Intake Theoretical study by Piersma (1991) and Piersma *et al.* (1991); see also references therein and BWP.

VOICE No detailed studies but sonagrams in Bergmann & Helb (1982), Glutz von Blotzheim *et al.* (1977), Maclean (1985) and BWP. Not very vocal and single birds usually silent. Soft calls heard from feeding flocks but not noisy.

Adult **KNOT-CALL**: a muttered *knut*; common outside breeding season (BWP); sonagram A shows two slightly different short explosive sounds: (1) a typical *knut* call; (2) a longer more rasping call. These are similar to some calls of Great Knot (q.v.), but deeper and mellower. **ALARM CALL** (sonagram B): described as *kvee-kvee* or *veek-veek* and *quick-ick*, *twit-wit*, or *whit-whit-whit-whit* (see BWP); similar call given by Bartailed Godwit (q.v.).

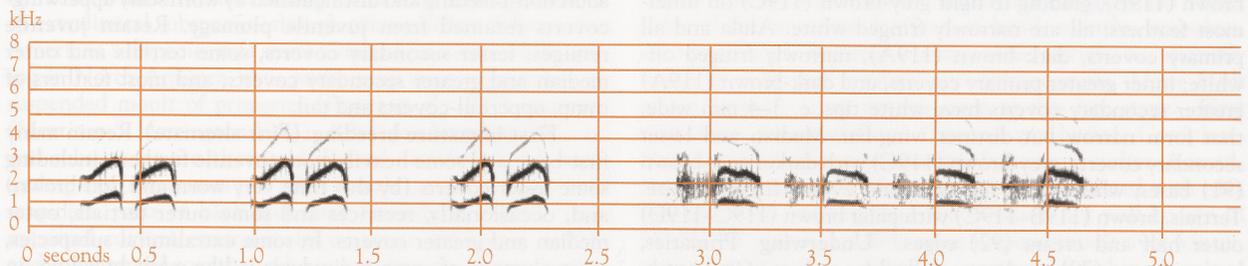


A E. Slater & P.J. Fullagar, Broome, WA, Oct. 1992

PLUMAGES Prepared by K. Bartram and D.I. Rogers. Partial first pre-basic moult to immature non-breeding juvenile plumage begins in late stages of s. migration or shortly after arrival in non-breeding areas. Often moult varying number of outer primaries in first pre-supplemental moult during austral autumn. Remain in non-breeding areas through first austral autumn and winter, developing a little breeding plumage in first pre-alternate moult and then beginning complete second pre-basic moult to adult non-breeding plumage. Thereafter moult twice annually: undergo a partial pre-breeding (pre-alternate) moult to breeding plumage, mostly just before n. migration; and a post-breeding (pre-basic) moult to non-breeding plumage, mostly after s. migration. Age of first breeding and n. migration not well known; delayed until at least 2 years old in HANZAB region. Subspecies *rogersi* (described below), only subspecies recorded in HANZAB region but nominate *canutus* may occur.

Adult male breeding (Second and subsequent alternate). **Head and neck** Feathers of forehead to nape, dull

rufous (c139) with broad grey-black (89) shaft-streaks, and light grey-brown (44) edges; when very worn, grey-brown edges lost. Top of head greyer than sides of head, where more rufous-brown (c139) is exposed. Nape and upper neck like crown, except grey-black shaft-streaks much finer. Most of rest of throat, face, including supercilium, rufous-brown (139) with dull off-white tips to feathers which are lost with wear. Ear-coverts patterned like upper neck, contrasting slightly with rufous face. Chin, rufous (c139), finely mottled white. **Upperparts** Feathers of upper mantle, dark olive-brown (129) with paler (partially concealed) bases, and broad light-brown (39) edges; on lower mantle, centres of feathers become blacker, indented by light-brown (39) spots along narrow light grey-brown edges; tips, light grey-brown (119C); with wear, light grey-brown tips and edges reduced or lost. Scapulars vary; base and centre of feathers, black-brown (119) with large paired cinnamon-rufous (39–38) spots separated by black shafts; usually broadly fringed white; some smaller scapulars, black, edged rufous, and with broad pale-grey (brownish 86) tips bisected by black shafts. Larger scapulars, similar but with black-brown (119) submarginal stripes that isolate rufous-brown spots from pale rufous-brown to off-white edges. Feathers of back, pale light-brown (c39) with dark-brown (119A) subterminal bars and off-white tips; rump similarly patterned but ground-colour, white. Lateral uppertail-coverts, white, with brown (119B) bars and crescents; central coverts, rufous-brown (38–39) with dark-brown (119A) bands and off-white tips. **Underparts** Rufous-brown (38 or 340) to brown (rufous 37) (with slightly yellow tinge when worn); hidden bases of feathers, paler rufous-brown; feathers very narrowly tipped white when fresh. Feathers of sides of breast have dark olive-brown (129) striations and paler edges than on centre of breast; striations continue down flanks. Axillaries, white (sometimes faintly tipped rufous), banded with irregular brown variegations and elongated chevrons. Lower belly and lower sides of flanks, yellowish white, with irregular dark-brown (119A) bands and spots. Vent, undertail-coverts and feathers of tibia, white, sometimes with light rufous-brown (39) wash; undertail-coverts have small dark-brown (119A) blotches on centre of feather. **Uppertail** Central feathers (t1–t2): dark olive-brown (129) with light rufous-brown (139) margins, two light rufous-brown (139) subterminal spots and thin white tips. Rest of tail, generally retained from adult non-breeding (q.v.). **Upperwing** Mostly retained from adult non-breeding (q.v.). Usually attain varying amounts of darker breeding plumage admixed in secondary coverts: greater coverts, brownish grey (79) with darker centres, submarginal stripes, and white tips; median coverts, dark olive-brown (129) with narrow off-white fringes and irregular cream to light rufous-brown (139) blotches on sides; lesser coverts, dark olive-brown (129) with rufous wash to some inner coverts and a few marginal coverts; inner tertial coverts, like smaller scapulars. Also usually develop two or



B C. Chappuis; Bay of the Somme, w. France, spring; *Sounds of Migrant and Wintering Birds — Western Europe*. Cassette 2: #71

three dark-brown (119B) to black-brown (19) tertials with cream (92) or white fringes; inner ones each have light rufous-brown (39–139) lateral spots and pair of blotches on either side of shaft at tip. **Underwing** Retained from adult non-breeding (q.v.).

Adult female breeding (Second and subsequent alternate). Difficult to reliably sex birds on breeding grounds and probably impossible in HANZAB region; differences slight and varying. Generally like male but: duller; often have buff or white (not cinnamon) markings on hindneck; grey-white tips to feathers of mantle and scapulars, broader; white patch of rear-belly, rear-flanks, vent and undertail-coverts usually larger, without rufous suffusion; often have a few white feathers (probably retained from non-breeding) scattered on centre of breast. Dullest females also differ by: almost no cinnamon on upperparts (except sides of crown and a few scapulars); often retain some non-breeding scapulars; rufous of underparts, duller, more strongly tinged cinnamon, and white tips of fresh feathers may be broader; upper breast sometimes finely speckled by small black subterminal spots or bars on feathers; white patch of rear-belly can extend onto lower breast as subdued mid-ventral stripe.

Adult non-breeding (Second and subsequent basic). **Head and neck** Forehead to hind-crown, light grey-brown (119C) with brown (28) shaft-streaks that are more obvious when plumage worn. Hindneck, pale grey-brown (119D) with fine brown (28) shaft-streaks. Supercilium, distinct, extending from bill, over eye, to rear of ear-coverts; dull white with small dark-brown streaks (especially behind eye). Eye-stripe, dull brown (119B) with off-white speckling. Lower face, white with brownish wash and dark-brown striations. Chin and throat, white. **Upperparts** Feathers of mantle, light grey-brown (119C) with darker-brown (28) shaft-streaks and pale grey-brown (119D) or off-white fringes. Scapulars, like mantle except dark-brown (119B–119A) centres of feathers, broader. Back, intermediate between rump and mantle in pattern. Feathers of rump and most uppertail-coverts, white heavily marked by dark-brown (119A–119) U-shaped submarginal markings enclosing irregularly patterned dark-brown bands. Central uppertail-coverts, dark brown (119A) with white bands through centres and white tips. **Underparts** Mostly white, suffused light grey-brown (119C) on sides of breast; rather varying brown (119B–119A) speckles, bars or streaks on breast extend onto upper belly and sides of foreneck and sparsely along flanks and sides of belly as distinct grey-brown (c119B) chevrons. Undertail-coverts, white with a few rows of small dark-brown (119A) marks. **Tail** Brown (27–119B) with darker brown (119C) submarginal marks and light grey-brown (119C) fringes, tinged buff. Shaft, whitish horn. **Upperwing** Primaries, dark to blackish brown (119A–219) with most of base of inner web, pale greyish-brown; base of outer web of inner eight primaries, edged white; shafts, dull yellow-white. Secondaries, brown (119B), grading to light grey-brown (119C) on innermost feathers; all are narrowly fringed white. Alula and all primary coverts, dark brown (119A), narrowly fringed off-white; inner greater primary coverts, and dark-brown (119A) greater secondary coverts have white tips, c. 3–4 mm wide, that form narrow but distinct wing-bar. Median and lesser secondary coverts, grey-brown (119C) with darker grey-brown (91) bases; when fresh, narrowly and evenly fringed white. Tertials, brown (119B–119C) with paler brown (119C–119D) outer half and cream (92) edges. **Underwing** Primaries, brownish grey (79), grading to dull white on base of inner web. Secondaries, pale grey (86) with darker submarginal bands and

white edges. Greater primary coverts, pale grey (86) with darker grey (85) submarginal bands and white edges; other primary coverts, white, with grey-black (82) markings throughout; marginal coverts, more heavily marked, especially round carpal. Greater secondary coverts, white with pale grey bands along each side of feather; central secondary coverts, white. Marginal and smaller coverts, white with small grey-black (82) centres, imparting slightly darker leading-edge to underwing.

Juvenile Head and neck Forehead and crown, light brown (223C) with black-brown (119A–119) shaft-streaks, sometimes broad enough to form capped effect; nape and hindneck, light grey-brown (119C) with less obvious, finer, dark-brown (119A) streaks. Supercilium, varies; sometimes as striking as in adult non-breeding; sometimes pale grey-brown (whitish 119D) (only slightly paler than crown) with faint dark-brown striations. Eye-stripe, brown (119B), darker brown (119A) at rear of lores. Upper half of ear-coverts, light grey-brown (119C) with dark-brown (119A) streaks; lower ear-coverts, white with rufous tinge and faint brown (119B) mottling. Feathers round bill, below eye-stripe, pale buff, speckled dark brown (119A). Chin and upper throat, white. Sides of neck, lower throat and lower neck, white with rufous wash and fine brown (119B) striations. **Upperparts** Feathers of mantle, scapulars and upper back, grey-brown (119C–119B) with neat cream (92) fringes (sometimes with buff tinge) contrasting with dark-brown (blackish 28) shaft-streaks and submarginal lines giving scaly appearance. Rump and uppertail-coverts, white with dark-grey U-shaped bars and shaft-streaks; bars thinner on uppertail-coverts. **Underparts** Lower throat to breast, white, with rufous wash when fresh and fine brown (119B) striations or speckles, forming faint gorget; sides of breast, pale grey-brown with dense brown striations. Flanks, light grey-brown (119C), initially with faint pink-buff wash and dark-brown (119A) vermiculations. Axillaries, off-white with light grey-brown (119C) wavy bands. Centre of belly, cream (92), whiter when worn. Undertail-coverts, cream (92) with fine dark-brown (119A) striations on anterior half of shafts of each feather. **Tail** Feathers, brownish grey (80–119C) (slightly darker brown at centre) with dull-white shafts, light brown-grey (whitish 44) fringes, and dark-brown (121) submarginal lines; t6 has faint off-white bands through feather and white basal third of inner web. **Upperwing** Mostly like adult non-breeding. Greater, median and lesser secondary coverts, light grey-brown (119C) with neat broad cream (92) fringes and dark-brown submarginal arcs; smaller lesser coverts, brown (119C) with dull pale grey-brown (119D) fringes. Marginal coverts, brown (119C) with white fringes. Tertials, like secondaries, except fringes slightly broader and submarginal bands slightly more obvious. **Underwing** As adult non-breeding.

First immature non-breeding (First basic). Very like adult non-breeding and distinguished by worn scaly upperwing-coverts retained from juvenile plumage. Retain juvenile remiges, lesser secondary coverts, some tertials and outer median and greater secondary coverts, and most feathers of rump, uppertail-coverts and tail.

First immature breeding (First alternate). Retain many first-basic and some heavily worn juvenile feathers, including some lesser coverts (by this time very worn and dull brown) and, occasionally, rectrices and some outer tertials, outer median and greater coverts. In some extralimital subspecies, most plumage of some individuals is like adult breeding; in HANZAB region, most or all develop only traces of alternate

plumage, often with new feathers intermediate in appearance between those of adult breeding and adult non-breeding.

Second immature non-breeding (Second basic). Almost identical to adult non-breeding, except that plumage reached c. 2 months before adults, and so plumage slightly more worn in austral spring.

Second immature breeding (Second alternate). Remiges said to be rather more worn than those of adult breeding (BWP); this not confirmed in HANZAB region. Some males in this plumage slightly duller than full adult males, and easily confused with adult females.

BARE PARTS From BWP, photographs (Pringle 1987; Chandler 1989; Aust. RD; NZRD; unpubl.: H.M. Gibbs) and unpubl. notes (AWSG). **Adult** Bill, black (119–89). Iris, dark brown (219, 22). Legs and feet: olive, greyish olive (50, 42), grey-brown (45, 91), dark olive (49, 129) to dull black (c82) with light-olive tinge in breeding plumage (BWP); joints often slightly darker. Claws, black (89). **Juvenile** Bill, dull black, with dark-olive (47) or grey tinge at base of lower mandible (BWP). Legs and feet, apparently paler than adult: dull yellowish-grey, yellowish green, yellow-olive (51–52) to dull olive-green.

MOULTS Based mainly on studies in Vic. and nw. WA (Barter *et al.* 1988b; Barter in Rogers *et al.* 1990) and NZ (NZWSG; A. Riegen & S. Davies), Aust. skins (AM, ANWC, HLW, MV, SAM and WAM) and BWP. For more information on moults of extralimital subspecies, see BWP, Piersma & Davidson (1992b) and references therein.

Adult post-breeding (Third and subsequent pre-basic). Complete; primaries outwards. Based on extralimital subspecies, some probably begin moult of body on breeding grounds, with a few feathers of chin, neck, upper breast, sides of breast, flanks, mantle and scapulars; most moult of body completed in s. part of migration. In nw. Aust., still retain 30–40% of breeding plumage in late Aug. to early Sept.; moult of primaries begins in second half of Aug., upon arrival; in late Oct. to early Nov., median PMS 30; completion date, not known. In Vic., moult of primaries begins c. 6–7 weeks later, in late Oct. to early Nov.; completed late Feb. to early Mar.; last traces of breeding plumage lost in Nov. Estimation of starting date and duration of moult of primaries in Vic. complicated by: (1) in Oct.–Nov. some birds may use Vic. as staging area *en route* to NZ (Barter *et al.* 1988b) and delay moult till reaching there; their inclusion in Vic. samples could make estimates of starting date late; (2) many (at least 20%) arrive in Vic. with primary-moult suspended and PMS of c. 20–30 by late Oct. to early Nov.; not known where these birds undergo moult of inner primaries and not known whether any are staging. Few data on start of moult in NZ but timing apparently similar to that in Vic.; median and average PMS 33–34 on 22 Dec. (n=102), when PMS is c. 30 in Vic. General strategies similar to extralimital subspecies, though timing differs. Claims that American subspecies *rufa* starts moult of primaries while staging in North America, thus performing most migration with suspended moult of primaries (Prater *et al.* 1977) incorrect (Morrison & Harrington 1992). **Adult pre-breeding** (Second and subsequent pre-alternate). Partial. Involves head, neck, underparts (sometimes not all in female), mantle, most or all scapulars, parts of back and rump (mainly in males), some uppertail-coverts, central rectrices, inner and longer tertials, and some tertial coverts, and some median and lesser coverts. In Vic., begins Feb. and often not completed before departure;

on average, have attained c. 60% breeding plumage by late Mar. In nw. Aust., extent of pre-alternate moult before departure varies, e.g. from 23 Mar. to 6 Apr. 1985, average c. 60% breeding plumage; in 1988, when adverse weather delayed departures, average c. 85% breeding plumage. In NZ, begin moult earlier than in Aust. At Farewell Spit, SI, almost 25% beginning moult 18–26 Jan. 1994; by 9–16 Mar., 80%–95% had much or complete breeding plumage (P. Battley). However, at Kaipara Harbour, NI, average amount of breeding plumage only 35% on 7 Mar. 1993 (n=348), though a few had almost full breeding plumage (NZWSG). **Post-juvenile** (First pre-basic). Partial. Little information for Aust., but appears similar to other subspecies. Begins early Sept. to late Oct.; completed, Oct.–Dec. Involves head, most feathers of body (sometimes not back or uppertail-coverts), varying numbers of rectrices (sometimes none), and sometimes a few upperwing-coverts and tertials. **Post-juvenile moult of primaries** (First pre-supplemental). Apparently restricted to trans-equatorial migrants; only known to occur in South Africa (Prater *et al.* 1977) and HANZAB region (could occur in subspecies *rufa* in South America but no information). Partial, usually involving varying number of outer primaries (replaced in outwards sequence) and associated primary coverts. Can overlap with early moult of inner primaries in second pre-basic, as occurs in Great Knot (q.v.); presumably this is why BWP and Prater *et al.* (1977) suggested (probably incorrectly) that first pre-supplemental occurred from Jan.–June and may include outer, inner or all primaries. In Vic., moult can start Jan., but usually occurs late Feb.–Apr.; first pre-supplemental does not occur in all birds and those from Vic. that do so apparently more apt than others to move to other areas in mid-winter. A few in Vic. (<10%) and many in nw. WA (at least 20%) moult all primaries in austral autumn and remain in HANZAB region through austral winter. Barter *et al.* (1988b) suggested these were in their first year (implying moult of all primaries in first pre-supplemental) but this needs confirmation; possibly they included some birds delaying maturity until at least third year. Delayed maturity further suggested by limited NZ data: of 233 moult-records from unaged birds caught 4 July, 71.2% had completed moult of primaries (improbable if all these birds were in their first year); 8.5% of birds in this catch retained all juvenile primaries, 5.5% had active moult of primaries (in most or all cases, early stages of second pre-basic), and 14.5% had performed partial first pre-supplemental moult of primaries or suspended second pre-basic moult of primaries, with average PMS 18.5 (12.58; 5–45; 36). **First immature pre-breeding** (First pre-alternate). Partial; Mar. or Apr. to June. Completed when inner primary dropped in first immature post-breeding. Extent of body-moult varies; in some, like adult pre-breeding (BWP) but in HANZAB region, average amount of breeding plumage attained only 20%. In Vic., 70–80% of birds gain traces of breeding plumage over austral autumn and winter (Barter *et al.* 1988b), usually on throat, upper chest, sides of breast, some feathers of head, mantle, scapulars, occasionally on uppertail-coverts, some tertials, occasionally much of belly and median upperwing-coverts. Many birds retain juvenile lesser coverts even at this late stage. **First immature post-breeding** (Second pre-basic). Complete. Sequence like adult post-breeding but occurs earlier. According to BWP, start late May to mid-July; completed with p10, late July–Dec. Starting date and duration not well known in HANZAB region; possibly some suspend moult over winter, as in Great Knot (q.v.). In Vic., some are finishing moult of primaries in mid-Oct. and median PMS, 30 (adults are just

beginning moult at this time and median PMS does not reach 30 till mid-Dec.); as in Vic. adults, some in Oct.–Nov. captured with suspended moult of primaries (Barter *et al.* 1988b). In nw. WA, median PMS 40–50; as in Vic., second pre-basic usually finished at about same time that adults begin moult of primaries.

MEASUREMENTS (1–7) A'asia, skins (AM, ANWC, HLW, MV, NMNZ, QM, SAM, WAM): (1–3) SA and e. coast Aust. (mostly S of Brisbane): (1) Adults; (2) Juveniles and immatures with juvenile p10; (3) Ages combined. (4–6) WA: (4) Adults; (5) Juveniles and immatures with juvenile p10; (6) Ages combined. (7) NZ, ages combined.

	MALES	FEMALES	
WING	(1) 162.4 (3.82; 158–170; 7)	162.2 (4.62; 154–167; 8)	ns
	(2) 157.3 (2.66; 154–161; 6)	156.0 (3.39; 152–160; 5)	ns
	(4) 156, 162	–	
	(5) 154, 152	150, 153, 153	
	(7) 165.5 (3.94; 159–171; 15)	169.0 (6.32; 162–179; 10)	ns
TAIL	(1) 58.5 (2.93; 56–65; 8)	57.0 (3.60; 50–62; 11)	ns
	(2) 57.9 (1.35; 56–60; 7)	54.6 (3.51; 51–60; 5)	ns
	(4) 53, 54, 57	–	
	(5) 50, 50	50, 51, 53	
BILL	(3) 31.2 (1.53; 28.5–33.6; 15)	32.5 (1.36; 30.1–35.2; 16)	*
	(6) 31.3 (1.17; 29.5–32.7; 5)	31.2, 31.5, 33.8	ns
	(7) 32.4 (1.37; 30–35; 16)	33.8 (1.73; 31.8–37.0; 10)	*
TARSUS	(3) 30.6 (1.02; 29.1–32.4; 15)	30.6 (1.19; 28.8–32.8; 16)	ns
	(6) 30.5 (1.50; 28.2–32.3; 5)	29.1, 31.4, 30.8	ns
TOE	(3) 24.9 (0.67; 23.9–26.1; 14)	24.7 (0.94; 23.3–26.5; 15)	ns
	(6) 24.4 (0.53; 23.7–24.8; 5)	24.7, 24.8	

(8–11) Breeding grounds, assumed to be adults, skins; wings measured as flattened, unstraightened chord and thus not directly comparable with maximum chord measurements in HANZAB; comparison of published maximum and flattened chord data for subspecies *icelandica* (Tomkovich 1992; BWP) suggests average wing-lengths might be c. 6 mm shorter than they would have been if measured with HANZAB methods; difference may not be so marked for wings of *rogersi*, as most skins in this sample were measured before they had completely dried out and may not have undergone all of usual 1.7–2.9% shrinkage (Tomkovich 1992): (8) Nominat *canutus*, Taymyr Pen.; (9) Nominat *canutus*, New Siberia Is; (10) Subspecies *rogersi*, Chukotskiy and Anadyr; (11) Subspecies *roselaari*, Wrangel I.

	MALES	FEMALES	
WING	(8) 162.3 (2.2; 159–166; 18)	168.6 (4.2; 164–173; 6)	**
	(9) 155.1 (3.5; 151–160; 5)	160.1 (2.7; 158–164; 4)	ns
	(10) 159.3 (5.7; 150–166; 10)	166.1 (3.1; 162–171; 10)	**
	(11) 166.8 (3.6; 160–173; 17)	170.4 (3.5; 166–176; 12)	*
BILL	(8) 32.5 (1.8; 29.0–35.2; 15)	34.9 (1.8; 33.2–37.3; 7)	*
	(9) 30.0 (0.9; 29.0–31.0; 7)	33.4 (0.6; 32.8–34.4; 6)	**
	(10) 31.7 (1.5; 28.9–33.5; 10)	33.6 (1.1; 31.5–35.3; 10)	**
	(11) 36.1 (1.8; 33.3–38.9; 18)	36.6 (1.4; 34.7–38.3; 11)	ns
TARSUS	(8) 31.0 (1.8; 28.7–35.8; 18)	32.3 (1.5; 30.5–33.9; 7)	ns
	(9) 29.5 (1.7; 26.0–30.9; 7)	31.4 (1.2; 30.0–33.4; 6)	ns
	(10) 30.4 (1.3; 28.6–32.7; 10)	30.9 (1.3; 29.5–32.8; 10)	ns
	(11) 32.5 (1.1; 30.6–35.5; 19)	32.9 (1.3; 30.7–35.5; 12)	ns

(12–13) Aust., live, sexes combined (Barter *et al.* 1988b): (12) Adults; (13) Juveniles and immatures in first year (most with juvenile p10).

	VIC.	NW. WA	
WING	(12) 165.5 (4.40; 149–177; 380)	165.8 (4.42; 148–177; 570)	ns
	(13) 158.8 (5.6; 146–174; 312)	160.1 (6.3; 146–168; 68)	ns
BILL	(12) 32.8 (1.69; 27.1–39.4; 443)	32.8 (1.64; 29.0–38.5; 432)	ns
	(13) 32.8 (1.8; 28.3–37.9; 371)	32.5 (1.4; 29.7–35.6; 45)	ns
THL	(12) 61.0 (2.19; 55.1–66.0; 205)	60.9 (2.07; 55.1–66.0; 258)	ns
	(13) 60.9 (2.1; 57.3–68.5; 139)	61.1 (1.0; 58.6–62.6; 20)	ns

(14) NZ, live, adults (NZWSG; S. Davies & A. Riegen).

UNSEXED			
WING	(14) 169 (4.62; 141–182; 1214)		
BILL	(14) 32.5 (1.56; 28.5–37.5; 147)		

Females have slightly longer wings and bills than males. Juvenile wing significantly shorter than in adult; tail of juveniles also probably shorter than in adult (BWP) but not evident in small samples above; bill, tarsus and toe of juveniles similar to adults after about Aug. (BWP). BWP considered seasonal variation in length of wing to be negligible provided birds with obviously frayed wing-tips were removed from samples.

WEIGHTS (1) Aust., live, adults (Barter *et al.* 1988b).

	VIC.	NW. WA	
Aug.–Sept.	(1) –	110.2 (7.7; 91–128; 83)	
Oct.–Nov.	(1) 117.5 (11.6; 92–150; 265)	111.8 (8.1; 95–152; 81)	**
Dec.	(1) 122.6 (7.2; 110–140; 27)	–	
Feb.	(1) 127.5 (9.4; 110–142; 20)	–	
2nd half Mar.	(1) 175.1 (13.2; 150–200; 21)	135.9 (16.9; 100–187; 518)**	
1st week Apr.	(1) –	142.1 (15.1; 94–179; 190)	
Mid-Apr.	(1) –	121.4 (13.21; 95–153; 215)	

(2) Aust., immatures through first year (Barter *et al.* 1988b).

	VIC.	NW. WA	
Oct.–Nov.	(2) 112.7 (13.4; 88–143; 86)	100.5 (10.5; 81–119; 30)	**
Dec.	(2) 126.6 (13.6; 86–168; 77)	–	
Jan.–Feb.	(2) 116.0 (7.9; 98–131; 69)	–	
2nd half Mar.	(2) 128.4 (20.1; 87–158; 9)	100.9 (10.2; 86–130; 60)	**
1st week Apr.	(2) –	99.1 (7.3; 85–112; 26)	
June	(2) 128.7 (15.8; 104–162; 31)	–	
July	(2) 114.8 (9.4; 95–141; 70)	–	
Aug.–Sept.	(2) –	108.7 (8.8; 96–121; 34)	

(3) NZ, live; immatures in first austral summer, autumn or winter (NZWSG; A. Riegen & S. Davies).

	ADULT	IMMATURE	
3 Nov.	(3) 109.3 (7.97; 98–128; 39)	135	
22 Dec.	(3) 108.1 (7.17; 88–122; 102)	–	
23 Feb.	(3) 141.6 (12.10; 110–176; 376)	112.8 (7.98; 100–128; 25)	**
28 Feb.	(3) 152.1 (13.97; 110–198; 471)	117.3 (16.63; 92–170; 74)	**
7 Mar.	(3) 162.5 (14.55; 119–200; 357)	129.1 (19.22; 110–168; 17)	**
4 July	(3) 117.7 (8.08; 99–114; 41)	112.2 (8.56; 100–130; 37)	**

No information on differences in weight between sexes in HANZAB region; females probably slightly heavier. Adults and immatures apparently have similar and rather stable weights through much of non-breeding period; Vic. birds significantly heavier than those in nw. WA, and appear heavier than those in NZ. Gain in weight before migration noticeable in NZ by late Feb.; in Vic. by early Mar.; in nw. WA by late Mar. Available data suggest departure weights from nw. WA may be considerably lower than those from Vic. and NZ. For reviews of changes in weight over time in other subspecies, see BWP, Morrison & Harrington (1992), Piersma *et al.* (1992) and Davidson & Wilson (1992); for information on body-composition, see Piersma & Barter (1991) and Piersma (1994b).

STRUCTURE Wings, rather long and pointed. Eleven primaries; p10 longest, p9 2–6 mm shorter, p8 10–15, p7 21–27, p6 32–40, p5 44–53 p4 54–63, p3 65–75, p2 74–86, p1 83–95; p11 short and slender, concealed by primary coverts; no emarginations; primaries extend 25–50 mm past tertials on folded wing. Sixteen secondaries, including five long pointed tertials. Tail, square; 12 rectrices; central rectrices, slightly pointed, usually slightly shorter than outer rectrix; t1 1–4 mm shorter than t6. Bill, c. 1.3 x length of head (much shorter than bill of Great Knot); straight, but slightly concave ventral surface can cause subtly decurved appearance; slightly expanded at base, gradually decreasing in width, tip slightly expanded. Grooves, along upper and lower mandible, ending before tip. Tarsus, slightly laterally compressed; proportionately longer than tarsus of Great Knot; scaling, small and rounded. Central toe longest, outer two fairly similar in length; outer c. 82% of middle; inner c. 79%, hind, c. 29%.

AGEING On moult of primaries, as in Great Knot (q.v.)

GEOGRAPHICAL VARIATION Five subspecies recognized, based on slight differences in measurements and subtle and varying differences in breeding plumage (though juveniles in HANZAB region differ from most extralimital subspecies by slightly broader dark submarginal lines on feathers of mantle and scapulars). Studies of mitochondrial DNA show little genetic variation between populations, subspecies possibly beginning to diverge c. 10,000 years ago, after last glaciation had restricted Red Knot to small breeding population in Berengian or e. Atlantic glacial refuge (Baker 1992; Baker *et al.* 1994; Piersma 1994a). Following summary based largely on BWP, Tomkovich (1992) and brief examination of Siberian skins (ZMM); see also Roselaar (1983), Godfrey (1992), Piersma & Davidson (1992b) and references therein, and except where stated, discusses usual appearance of males in breeding plumage. Identification of subspecies complicated by slight difference in size and plumage between sexes; in particular, plumage of adult females is usually duller than that of adult males, so that even in most brightly coloured subspecies (e.g. *canutus*) duller females may resemble males of duller subspecies (*rufa*). In general, plumage varies from subspecies with dark backs, dark rufous underparts and small white patch on belly in W of breeding range (*icelandica* and *canutus*) to subspecies with silvery variegated upperparts, pale rufous underparts and large white patch on belly in E (*rufa*). Variation in size not so easily summarized, but smallest birds breed e. Siberia (*rogersi* and populations of *canutus* on New Siberian Is), and largest in North America and on Wrangel I. (*rufa* and *roselaari*).

Subspecies *rufa*. Palest, and one of largest, subspecies (see BWP). Breeds central Canadian Arctic; apparently migrates

to South America (Morrison & Harrington 1992). Differs from A'asian birds by: (1) paler mantle and scapulars, with smaller black centres, smaller duller cinnamon spots, and broader grey-and-white fringes and tips to feathers; upperparts often appear grey, richly variegated black, with little cinnamon (almost none on females); and (2) underparts, duller rufous-cinnamon, with rear-belly, vent and undertail-coverts, white.

Subspecies *islandica* breeds n. Greenland and Canadian Arctic islands and migrates to w. Europe. Nominate *canutus* breeds Siberia, apparently in three disjunct populations that differ in measurements; birds from n. Taymyr Pen. similar in size to subspecies *icelandica* (see Measurements). Piersma *et al.* (1992) noted that bills of subspecies *canutus* in non-breeding areas of w. Africa are c. 1 mm longer than those from Taymyr Pen., and argued that they come from an undiscovered breeding population, perhaps in highlands of Yakutsk. Tomkovich (1992) identified population on New Siberian Is as subspecies *canutus* (using plumage characters) and found birds there were at least as small as subspecies *rogersi* (previously considered smallest subspecies). Subspecies *icelandica* differs from nominate *canutus* in slightly paler upperparts and, arguably, shorter bill; see Roselaar (1983) and BWP for information on identification. Together, nominate *canutus* and subspecies *icelandica* have darkest mantle and scapulars, appearing mainly black and rufous-cinnamon, even when fresh; compared to subspecies *rogersi* in A'asia: feathers have broader black centres and subterminal bars, darker cinnamon-rufous fringes and paired spots, and much narrower white tips; underparts generally slightly deeper rufous, colour extending over much of rear-belly and undertail-coverts.

Subspecies *rogersi* and *roselaari*. Breeding distribution of subspecies *rogersi* poorly known, thought to be Chukotskiy and Anadyr. Subspecies *roselaari* (previously treated as *rogersi*) breeds Alaska and Wrangel I. (see Tomkovich 1992). Patterns of upperparts and colours of underparts intermediate between nominate *canutus* and subspecies *rufa*. Subspecies *rogersi* small (see Measurements), usually with clean white patch on rear-belly, vent and undertail-coverts (only five of 18 examined had extensive rufous tinge in these areas; Tomkovich 1992). Subspecies *roselaari* much larger than *rogersi* (especially bill-length; see Measurements) and, differs by usually having much rufous on rear-belly to undertail-coverts.

Subspecies occurring Aust. and NZ not certain and more than one subspecies may occur. In Aust., considered to be subspecies *rogersi*, based on small size (Barter *et al.* 1988a) but nominate *canutus* from New Siberian Is has been found to be at least as small as Aust. birds and could occur here. Important measurements of wing from breeding grounds (Tomkovich 1992) cannot be compared directly with Aust. measurements because methods of measuring differed. Banding and colour-marking (q.v.) show that population in nw. WA distinct from that in e. Aust., and that there is much movement between e. Aust. and NZ. Available data, mostly from unsexed birds, do not show any difference in size between nw. WA and e. Aust., though subtle differences might be obscured by differences in sex-ratios. However, average length of wing and bill from NZ significantly longer than those from e. Aust. (see Measurements), which suggests that at least two populations of differently sized birds reach NZ: one the same as that which occurs commonly in e. Aust. (based on band-recoveries), and a second population larger than those commonly in e. (and nw.) Aust. Bill-length from NZ seem too short for subspecies *roselaari* from Wrangel I. and suggest the large birds might be subspecies

rogersi (as defined by Tomkovich 1992). Study of breeding plumages probably needed to solve problem but this difficult in HANZAB region because few reliably sexed skins in full breeding plumage and many migrate N before attaining such. Further, extent of white on rear-belly to undertail-coverts is critical in subspecific identification but all subspecies probably pass through stage late in pre-alternate moult, when rear-belly and undertail-coverts have yet to be moulted and thus appear superficially similar to white-bellied subspecies *rufa* and *rogersi*.

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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