

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	seed-snipes; 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.
Jacaniidae	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, Jacaniidae) and charadriids and allies (Chionididae, Burhinidae, Haematopodidae, Recurvirostridae, Ibidiorhynchidae, Charadriidae, Pluvianellidae, Dromadidae, Glareolidae, Stercorariidae, Rhynchopidae, Laridae, Sternidae, Alcidae); Strauch (1978) treated Alcidae as separate lineage, but skeletons may be so highly modified for foot-propelled diving that they do not reflect relations well (Sibley & Ahlquist 1990); gulls and allies have also been regarded as a separate lineage (Christian *et al.* 1992) or as allied to charadriids (e.g. Sibley & Ahlquist 1990). Further relationships within the Order discussed in introductions to families.

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

COLOUR PLATE FACING PAGE 368

Tringa pugnax Linnaeus, 1758, *Syst. Nat.*, ed. 10 (1): 148 — Europe = Sweden.

The generic name is derived from the Greek φίλος, loving, fond of, and μάχη battle, combat. The specific epithet is derived from the Latin *pugnax*, combative, fond of fighting. Both generic and specific names refer to the lekking behaviour of males when breeding. The name of the female, Reeve, is thought to be a stem or vowel mutation of the male name.

MONOTYPIC

FIELD IDENTIFICATION Length: male 26–32 cm, female 20–25 cm; wingspan 46–59 cm; weight: male 180 g, female 110 g. Medium-sized (male) to medium-small (female) wader with distinctive, gangly jizz: small head with low sloping forehead enhancing drawn-out facial appearance (more marked in non-breeding and juvenile plumages); long neck; bulky, deep-bellied body often with hunched back; short to medium-length, slightly decurved bill; and medium-length legs. At rest, folded primaries level with tip of tail; almost no primary projection in adults, short in juveniles. Male close in size to Common Greenshank *Tringa nebularia*, female to Ruddy Turnstone *Arenaria interpres* or tattlers. In direct comparison, male much bigger than Sharp-tailed Sandpiper *Calidris acuminata*, and even female is bigger, with longer neck and legs, and stands taller. In adult breeding plumage, both sexes show much variation in colour and pattern of plumage and bare parts, with no two individuals exactly alike; and the male has unique ornamental plumes on head and bare skin on face. In all plumages, flight-pattern distinctive, with narrow white wing-bar, and broad oval-shaped white patches at base of tail, which usually join. Sexes differ: male larger; differ in breeding plumage but similar in non-breeding. Marked seasonal variation, especially in male. Juvenile distinctive. Immatures separable.

Description Adult breeding male In May–June, lose feathering on forehead and round eye to reveal bare warty skin, and acquire ornamental plumes on head. Ear-tufts that cover sides of nape, and ruff that covers neck and breast vary considerably and do not match in colour: chestnut, buff, white or black, with purple gloss, spotted or barred black on some. Mantle, back, scapulars and tertials similar, though each tract can vary. Innerwing-coverts mostly grey-brown, narrowly fringed white; some inner coverts like mantle and scapulars. Chin, white. Throat and foreneck a mixture of light cinnamon, brown and rufous feathers with black subterminal markings, and some duller grey-brown non-breeding feathers. Sides of breast and flanks usually glossy purple-black, flecked with white, though sometimes as ruff. Belly, vent and undertail-coverts, white. In flight: mostly grey-brown innerwing-coverts contrast with slightly darker blackish-brown remiges and primary coverts; show clear narrow white wing-bar along tips of greater coverts; rump and narrow line through centre of uppertail-coverts, dark brown, with white lateral coverts forming two large ovals that almost reach tip of tail and, on some, join just above tail to form large white U; tail, grey-brown, usually with conspicuous black and cinnamon bars and spots on central pair and often on others; underside of remiges, light grey-brown grading to white at bases; rest of underwing, white except for narrow band of dark mottling along leading-edge. After ornamental plumes lost and facial feathering regained,

may resemble more strongly marked adult breeding females, from which best distinguished by size. Bill varies from yellow to orange or pinkish red, with or without black tip; occasionally, leaden grey, red-brown or black (sometimes with yellow to orange tip), especially in birds with black ear-tufts or ruff. Facial skin varies from green or yellow to orange or red. Iris, dark brown. Legs and feet usually pinkish red or orange-red, occasionally yellow when breeding. **Adult female breeding** Plumage varies. palest birds: head, neck and upperparts vary from light brownish-grey to cinnamon, with head and neck finely streaked and mottled black (and often also plainer and paler round base of bill), and feathers of mantle, scapulars and tertials with varying black bars or wider subterminal markings (scapulars sometimes all-black) and finely fringed dull white; foreneck, breast and fore-flanks, pale buff-brown with dark-brown or black mottling or barring; rest of underbody, white, with some fine dark streaks along flanks; like adult male breeding in flight. Strongly marked birds are like breeding male, but without bare facial skin, ear-tufts and ruff; general pattern of plumage similar to pale birds but: head and neck more heavily mottled black; feathers of upperparts mainly black with contrasting pale-grey to off-white subterminal markings on feathers of mantle and scapulars, and bold barring through tertials, giving strikingly variegated appearance; foreneck, breast and fore-flanks, pale grey to off-white, with much bolder, messy black barring and V-shaped marks on sides of lower breast and fore-flanks. Some birds like pale birds but with strong rufous tones and barring, with sides of head, neck, chest and flanks uniform rufous or rufous with black spots and bars. Bill, blackish brown but may have orange base as in male; legs and feet, orange. **Adult non-breeding** Differ from adult breeding by: crown, nape, hindneck and sides of head and neck, plain grey-brown, very finely streaked darker and grading to off-white on lower cheeks, chin, throat and round base of bill, giving characteristic pale, open-faced expression; and with indistinct dark smudge in front of eye and hint of short narrow dark stripe behind eye. Rest of upperparts and innerwing-coverts, grey-brown with diffuse darker centres to feathers and, often, darker blackish subterminal spots or short bars on longer scapulars and tertials (most prominent on latter); all feathers narrowly fringed dull white when fresh. Foreneck, breast and fore-flanks washed and mottled light grey-brown; rest of underbody, white; some whiter below, with sharp contrast between dull-white sides of neck and grey-brown hindneck, and foreneck and central breast, white with grey restricted to sides of breast and fore-flanks. A few (almost always males) have conspicuous patch of white or cream on breast and round base of neck, or have white head, neck and breast (and sometimes also upper mantle). Bill, black, with brown or orange at base in some. Legs and feet often yellow or

dull orange, though usually little different from breeding. **Juvenile** Distinct till Nov. Plumage similar to adult non-breeding; differs by: Head and neck washed rich buff, with nape and hindneck faintly streaked darker and crown more boldly streaked black, giving slightly capped appearance; slightly darker and more prominent narrow dark stripe behind eye and smudge in front of eye; indistinct narrow buff supercilium. Rest of upperparts and innerwing-coverts vary: feathers of mantle, scapulars, tertials and coverts, black, with narrow buff fringes giving neat scaly appearance above and, often, forming narrow buff mantle V; less often, tertials and innerwing-coverts, paler, grey, grading to black toward tips, with dark areas on larger coverts showing as diffuse broad submarginal blackish lines bordering neat buff fringes; rarely, black tertials and coverts have scalloped buff fringes and bold buff internal bars and markings giving coarsely barred appearance. Foreneck, breast and fore-flanks, buff, with, at best, a few indistinct fine dark streaks on sides of breast; rest of underbody, white. With wear, buff fringes on upperparts reduced and paler, cream; and buff of head, neck and chest fade to duller greyish-buff or pale grey-brown. Crown, mantle and scapulars appear nearly uniform black when very worn. Bill, black with brown base. Legs and feet, dull yellow-brown, green or olive-grey. **First immature non-breeding** As adult non-breeding but separable till late in first austral spring by varying number of retained worn juvenile innerwing-coverts and tertials; best distinguished by dull legs, either like legs of juveniles or green, mottled with yellow or orange. **First immature breeding** Some males, especially those returning to breeding grounds, acquire facial warts and some breeding plumage on head, neck, chest and upperparts, though ear-tufts and ruff usually shorter and less thick than those of adult. Many, especially those remaining in non-breeding areas, develop only a little breeding plumage, hardly any head plumes, and in males, no or only a few facial warts. Distinguished from adults by retained worn juvenile remiges or, in a few females, contrast between newly replaced outer few primaries and worn juvenile inner primaries (primaries uniformly fresh in adults); and by much duller or mottled legs as first immature non-breeding, though at least some that breed when 1 year old can have bill and leg like those of adults.

Similar species Adult male breeding, unmistakable, but not likely to be seen in HANZAB region. In non-breeding and juvenile plumages, generally easily distinguished from similar waders by combination of large size, gangly jizz, plain-faced appearance, with pale area round base of bill; orange or pinkish legs; distinctive flight-pattern; and lack of calls. Non-breeding adults and juveniles, especially females, might be confused with same plumages of **Sharp-tailed Sandpiper** and **Buff-breasted Sandpiper** *Tryngites subruficollis*, and non-breeding adults could also be confused with **Common Redshank** *Tringa totanus*; see those accounts for differences.

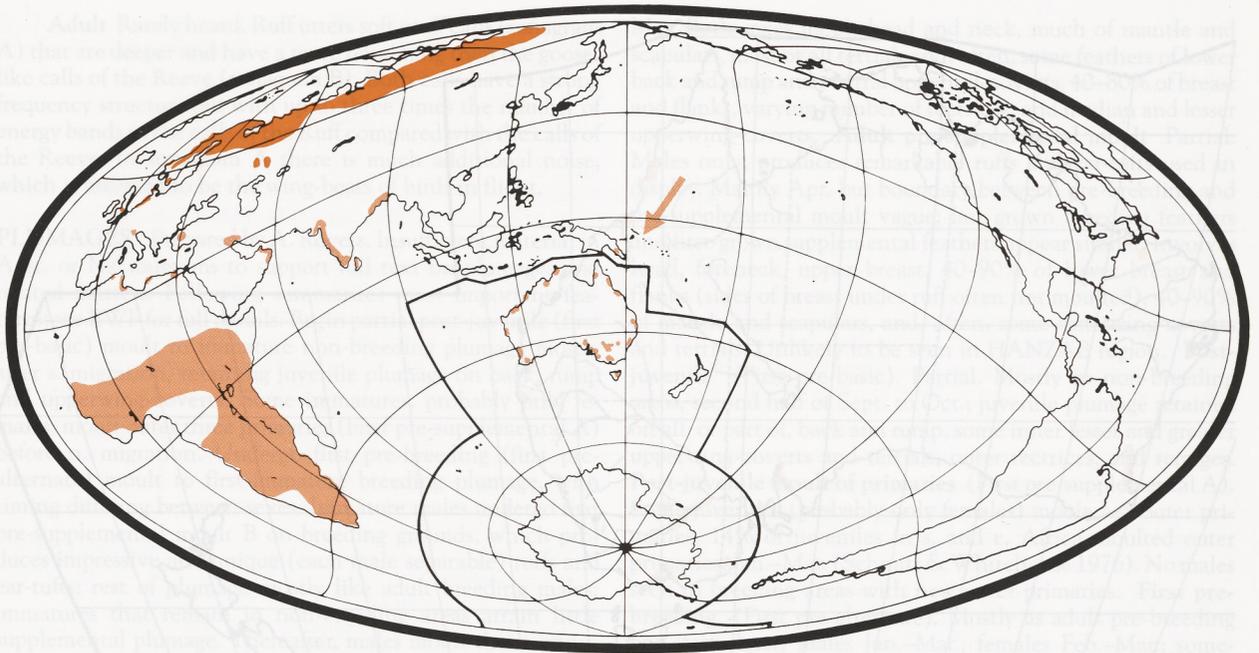
Gregarious in normal range, though seldom in large flocks; in HANZAB region, usually seen singly or occasionally in pairs or small groups. Freely associate with other small waders and, in HANZAB region, often seen feeding and roosting with Sharp-tailed Sandpipers. In non-breeding season, found on variety of coastal and inland wetlands, preferring muddy margins of freshwater and brackish swamps and lakes; often seen in sewage farms and commercial saltfields. Generally wary, rarely allowing close approach. Forage methodically along muddy margins in steady walk with body held horizontal, head held below hunched back, and tail raised, picking and probing rapidly at mud; sometimes dart after food; wade freely through flooded grass and in pools, often submerging entire head; on

saline lakes, may also swim, somewhat like phalaropes, pecking at surface; often also forage with head up and slightly clumsy run when in open. When stationary and when alarmed, adopt upright stance with small head held high on long neck; often raise mantle feathers when foraging, especially in hot weather. Rise steeply when suddenly flushed. In flight, look long-winged and powerful; flight loose and lazy, with deep slow irregular wing-beats and effortless languid flight; generally keep low; often glide in flight, and glide slowly before landing; feet project clearly beyond tip of tail and, with pattern of tail, are ready distinctions from other similar waders. Normally very quiet, only rarely uttering low hoarse grunting notes such as *kurr*, *kuk-uk* and *kook*.

HABITAT In A'asia, generally fresh, brackish or saline wetlands with exposed mudflats at edges. Usually terrestrial wetlands, including lakes, swamps, pools, lagoons, tidal rivers, swampy fields and floodlands (Ford 1966; Sympson 1966; Carter & Smith 1968; McKean *et al.* 1976; Curry 1979); occasionally on sheltered coasts, in harbours, estuaries and on seashores (Fisher 1964; MacKenzie & McKenzie 1965; Sympson 1966; Holmes 1972); also sewage farms and saltworks (Colemane 1973; Lane & Jessop 1985). Wetlands sometimes surrounded by dense vegetation, including grass, sedges, saltmarsh and reeds (Sympson 1966; Carter & Smith 1968; Thompson 1978; Curry 1979). Usually on exposed mud, but also observed on sand spits and other sandy habitats; sometimes on shingles (MacKenzie & McKenzie 1965; Sympson 1966; Morris 1975).

Mainly forage on exposed mudflats (Fisher 1964; Ford 1966; McKean *et al.* 1976), in shallow water (Carter & Smith 1968; Curry 1979), or occasionally on dry mud (Curry 1979; R.P. Jaensch). Also among dry waterside plants (Curry 1979) and in swampy area next to aeration tanks in sewage farm (Colemane 1973). Mainly roost among short vegetation (Carter & Smith 1968). Once seen roosting on sheltered shingle beach (Sympson 1966).

DISTRIBUTION AND POPULATION Breed Europe, n. Russia and nw. Kazakhstan: scattered and irregular records British Isles, and Belgium, N to Denmark, and E through Poland to e. Baltic countries; Alaska; in Norway, on w. and n. coasts and in central regions, to n. Sweden and most of Finland; Russia, from borders with Scandinavia, Baltic countries and Poland, E to n. Chukotskiy Pen.; occur S to c. 50°N near Polish border, but not S of 65°N in Urals; E of Urals, S to c. 62°N round Ob R., to N of Arctic Circle farther E. Isolated breeding also farther S, round Ural'sk region on Ural R., Irtysh R. round Omsk, Ob R. round Tomsk, L. Baikal area, Magadan region, Sakhalin I., and headwaters of Ob and Yenisey Rs (Dement'ev & Gladkov 1951; Gibson 1977; Flint *et al.* 1984; Tomkovich 1992; BWP; P.S. Tomkovich). During non-breeding period, mostly in Africa, Indian subcontinent and, less often, s. Europe: in Africa, along Mediterranean coasts and Nile R.; mainly S of line from s. Mauritania to junction of Blue and White Nile Rs, E to coast of Red Sea; scattered records Arabian Pen. and Persian Gulf; widespread Indian subcontinent, E to n. Bay of Bengal; Indochina and se. China; uncommon Indomalaya, E to Philippines, S to Indonesia, Micronesia and New Guinea. Occasionally recorded North America, Caribbean, Central America, Hawaii, Greenland, Iceland, The Faeroes and C. Verde Is (Gibson 1977; Ali & Ripley 1980; AOU 1983; de Schauensee 1984; Coates 1985; Pratt *et al.* 1987; Urban *et al.* 1987; AWB 1993; BWP; R.P. Jaensch).



Aust. Rare but regular visitor. **Qld** Widely scattered localities: Edward R.: five, Dec. 1979; single, 21 Mar. 1980 (Garnett & Bredl 1985; Garnett 1989; Aust. Atlas); single, Hasties Swamp, Atherton Tableland, 6 Nov. 1986, 19 Nov. 1987 (Qld Bird Reps 1986, 1987); single, Townsville, 25 Feb. 1985 (Qld Bird Rep. 1985); single, Alva, 12 Mar. 1989 (Qld Bird Rep. 1989). Several records in SE, at Lytton, Myrtle town, Luggage Pt, Nudgee and Dyer's Lagoon (Roberts 1979; Storr 1984; Qld Bird Reps 1983, 1988; Aust. Atlas; AWSG). Unverified report, single, Cairns, 12 Nov. 1987. **NSW** First record, 25 Sept. 1971, Kurnell (NSW Bird Rep. 1971). Most records round Sydney (Morris *et al.* 1981; NSW Bird Reps; AWSG). Elsewhere: Tomki, Casino and Ballina; often at Kooragang I. (Holmes 1972; NSW Bird Reps); Broadwater Lagoon, Little Cattai Ck, 5 Feb. 1977 (NSW Bird Rep. 1977); Dubbo, 20–31 Oct. 1987 (NSW Bird Rep. 1987); at several places in the Riverina, including Windouran Swamp and Wanganella, with many records at Fivebough Swamp and Tullakool Saltworks (NSW Bird Reps). **Vic.** Many records round Port Phillip Bay; other records in s. Vic. include singles at L. Murdeduke, 12 Feb. 1966 and 2 Jan. 1981 (Carter & Smith 1968; Vic. Bird Rep. 1981). In nw. Vic., singles recorded Ryan's Swamp, Merbein, 11 Jan. 1978 and Mildura Sewage Farm, 11 Dec. 1982 (Sonter & Allan 1983; Vic. Bird Rep. 1982); several records in Murray Valley between Swan Hill and Cohuna (Lowe 1981; Vic. Bird Reps; Vic. Atlas; AWSG data), including first Vic. record at Mystic Park, 22 Jan. 1966 (Wheeler 1967; Thomas 1970b). Unverified reports: Tankerton, French I., 24 Apr. 1966 (Sympson 1966), and single, L. Corangamite, 6 Feb. 1993. **Tas.** Vagrant. Single, Orielson Lagoon, 8 Nov. 1987–7 Mar. 1988 (Tas. Bird Reps. 1987, 1988); 1–2, Orielson Lagoon–Barilla Bay, Dec. (possibly Oct. also) 1991 to 9 Feb. 1992 (Tas. Bird Rep. 1992; AWSG). Two unconfirmed records, of up to 60, C. Portland, Mar. 1966 (Thomas & Wall 1966) and five, se. Tas., Sept. 1966 (Thomas 1970a). **SA** First record, specimen, Buckland Park, 14 Jan. 1962 (McEvey 1963). In SE, recorded at Bool Lagoon, 26 Jan. 1980, 21–23 Mar. 1981 (Aust. Atlas); Langhorne Ck and Tolderol–Mosquito Pt, 10 Dec. 1966–1 Jan. 1967, Feb. 1982

(SA Bird Rep. 1966–67; AWSG); several sites round Gulf St Vincent, especially at ICI (St Kilda) Saltworks–Buckland Park; Whyalla Saltfieds, 29 Oct.–2 Nov. 1978, Feb. 1981 (Garrett 1980; AWSG); Bird I., Wallaroo, 1 Apr. 1967 (Condon 1969). **WA** First record, specimen, lower King R., c. 9.5 km NE of Albany, 28–29 Oct. 1963 (Fisher 1964). Mostly in SW, from Vasse R. estuary, N to Namming L. with maximum count of five at L. McLarty (Jaensch *et al.* 1988; *West. Aust. Bird Notes*; AWSG; R.P. Jaensch). Sporadically recorded elsewhere: Hamelin Pool Stn, 14–15 Nov. 1964 (Ford 1966); Port Hedland, Apr. 1979 (Aust. Atlas); Kununurra, Nov. 1980 (Aust. Atlas); Argyle Diamond Mine, 13 Mar. 1993 (O'Connor 1993). Unverified reports: Curlewis Camp, Millstream Chichester NP, 14 Nov. 1990; Broome–Roebuck Bay, 23 Jan. 1991, 29 July 1992. **NT** Round Darwin (e.g. McKean *et al.* 1976; Thompson 1978; McKean & Hertog 1980; Aust. Atlas; H.A.F. Thompson & D.K. Goodfellow). Unverified claim of single, Alice Springs, 17 Nov. 1990–Feb. 1991. **NZ** Vagrant (singles unless stated): unconfirmed, Karaka, 11 Apr. 1964 (MacKenzie & McKenzie 1965); Colac Bay, 9 Dec. 1984–16 Mar. 1985 (Miskelly & Cooper 1985); 1–2, L. Ellesmere, 30 Dec. 1984–20 Jan. 1985 (Harrison & Fennell 1985); L. Poukawa, 1 Nov. 1985 (CSN 34); L. Wainono, 1–10 Nov. 1987 (Maloney 1988). **Populations** A total of 37 recorded in regular summer surveys round Aust., 1981–91, with maximum of eight in any one year; totals 1981–91: Qld, 1; NSW, 5; Vic., 16; Tas, 1; SA, 6; WA, 7; NT, 1 (AWSG). There were 65 records during the RAOU Field Atlas (1976–81) (Aust. Atlas). **MOVEMENTS** Migratory. Breed Eurasia and nw. Alaska; migrate to SW (AOU 1983; BWP). Origins of birds in HANZAB region not known; birds that breed ne. Siberia recorded India, Europe and Africa (McClure 1974; BWP). **Departure** Males, late June or early July; females, mid-July (BWP); juveniles, late July and Aug. (P.S. Tomkovich). Mainly travel SW across Eurasia, with smaller passage through far-e. Russia, Mongolia, China, Japan (higher numbers on s. migration), Korea (apparently Aug. and Sept.), Taiwan, Hong



Kong (mainly early Sept. to early Oct.), Brunei, Bali (rare Aug. and Sept.) and Philippines (Gore & Won 1971; Ash 1984; Chalmers 1986; AWB 1993). Small numbers, irregularly, move through PNG; usually arrive Port Moresby district, late Sept. (females apparently earlier than males) then mostly move on by mid-Nov. (Coates 1985; Hicks 1990). Occasionally on Pacific coast of North America and in Pacific; rare to Hawaiian Is and Micronesia (AOU 1983; Pratt *et al.* 1987).

Non-breeding Visit Aust., Sept.–Apr. (Holmes 1972); vagrant to NZ, Nov.–Apr. (Falla *et al.* 1981; Maloney 1988). In Vic., mainly recorded Jan. and Feb. (Vic. Atlas); Gulf St Vincent, SA, Sept.–Feb. (Close & McCrie 1986); Swan Coastal Plain, sw. WA, late summer (R.P. Jaensch). Some movements in Aust. apparently dispersive. Singles sometimes recorded at one locality for extended periods (e.g. Miskelly & Cooper 1985; Tas. Bird Rep. 1989; R.P. Jaensch).

Return Extralimitally, mid-Feb. to May with some arriving breeding grounds in Siberia from mid-May, till June (BWP; P.S. Tomkovich). On breeding grounds on Tamal Pen., no site fidelity (Ryabitsev 1993). Usually leave Port Moresby district by Jan., with records from Apr. (Hicks 1990). Smaller numbers move through Japan and Hong Kong; very few recorded South Korea, Apr. and May (Chalmers 1986; AWB 1993). Return passage from main non-breeding areas in Europe and Africa to E of s. passage (BWP).

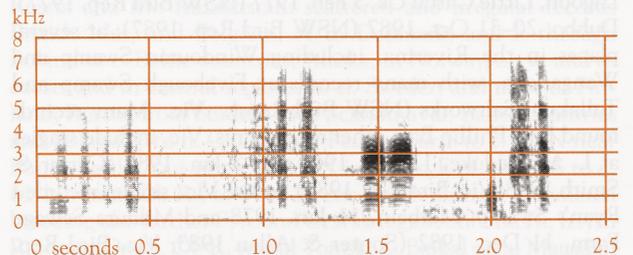
Breeding Occasionally winter extralimitally (AOU 1983; Hayman). Most apparently leave HANZAB region, though one recorded WA in winter (Curry 1979).

FOOD Insectivorous on breeding grounds; omnivorous elsewhere; take grain from fields (Tomkovich 1992). **Behaviour** Extralimitally, diurnal and nocturnal (Witherby *et al.* 1940). Probe and peck in water, on dry land and among dead vegetation at edge of water. Sometimes crane neck to glean

items above head (Curry 1979). May wade up to belly, swim and follow plough when foraging (BWP).

Adult No information for HANZAB region. Extralimitally: moss and plant fibre, seeds, annelids, molluscs, crustaceans, spiders, insects, fish and amphibians (BWP).

VOICE No detailed studies. Few calls and quiet, remarkably so for a wader (see van Rhijn 1991; BWP). Typically silent in HANZAB region.



A Ruf: C. Chappuis; *Sounds of Migrant and Wintering Birds — Western Europe*. Cassette 2: #84



B Reeve: C. Chappuis; *Sounds of Migrant and Wintering Birds — Western Europe*. Cassette 2: #84

Adult Rarely heard. Ruff utters soft gruff calls (sonagram A) that are deeper and have a more nasal tang than the goose-like calls of the Reeve (sonagram B). Both calls have a strong frequency structure but with up to three times the number of energy bands in the calls of the Ruff compared with the calls of the Reeve. In sonagram A there is much additional noise, which is assumed to be the wing-beats of birds in flight.

PLUMAGES Prepared by A. Rogers. Insufficient material in Aust. or NZ museums to support full text on plumages and related matters. Following summarizes most important features; see BWP for full details. Begin partial post-juvenile (first pre-basic) moult to immature non-breeding plumage mostly after s. migration, retaining juvenile plumage on back, rump and upperwing-coverts. Some immatures, probably only females, moult outer three primaries (First pre-supplemental A) before n. migration. Undergo first pre-breeding (first pre-alternate) moult to first-immature breeding plumage, with timing differing between sexes. Immature males undergo first pre-supplemental moult B on breeding grounds, which produces impressive and unique (each male separable) ruffs and ear-tufts; rest of plumage mostly like adult breeding males; immatures that remain in non-breeding areas attain little supplemental plumage. Thereafter, males moult thrice annually and females twice: (1) adult post-breeding (pre-basic) moult to non-breeding plumage, mostly on, or near breeding grounds in males, and later, mostly in non-breeding areas, in females; (2) adult pre-breeding (pre-alternate) moult to breeding plumage in non-breeding areas, with timing differing between sexes; and (3) males undergo adult pre-supplemental moult to extraordinary display plumage, mostly on breeding grounds. Adult non-breeding plumage first attained in complete second pre-basic moult. Females probably first breed when 2 years old, males probably later.

MOULTS Based mainly on BWP; no data from HANZAB region. For further information see BWP, Hogan-Warburg (1966), Schmitt & Whitehouse (1976), Pearson (1981), Koopman (1986) and Münster (1991).

Adult post-breeding (Second and subsequent pre-basic). Complete. Primaries outwards. Timing differs in males and females. **MALES:** start on, or near, breeding grounds, early June to early July, with moult of face, neck, upper breast and some feathers of mantle and scapulars; moult of head, body and upperwing-coverts almost complete by late July to early Aug. Moult of primaries begins late June to early Aug.; some complete moult of primaries before s. migration, some suspend moult while migrating and complete it in non-breeding areas in Africa. The few males that reach South Africa in Aug. arrive with all primaries old, or with only inner three replaced (though most moult of body complete at this time); moult of primaries starts, or resumes, on arrival and is completed by about Dec. **FEMALES:** timing of start of moult varies according to breeding success. Failed and non-breeders (mostly 1-year-olds) start moult of body at the same time as males and sometimes start moult of primaries near breeding areas in early Aug., suspend moult on migration, and complete it in non-breeding areas. Successful breeders begin moult later; moult of primaries usually starts early Sept. in non-breeding areas, and is completed mid-Dec. Both sexes start to moult secondaries inwards when moult of primaries about two-thirds complete. **Adult pre-breeding** (Second and subsequent pre-alternate). Partial. Males start Nov. to early Jan. and finish early Feb. to early Mar.; females start moulting later, from Dec. or Jan. to

Mar. Both sexes moult head and neck, much of mantle and scapulars, most or all tertials and, often, some feathers of lower back and rump and central uppertail-coverts, 40–80% of breast and flanks, varying number of rectrices, and median and lesser upperwing-coverts. **Adult pre-supplemental moult** Partial. Males only; produces remarkable ruffs and ear-tufts used in display. Mainly Apr. but boundary between pre-breeding and pre-supplemental moult vague; last grown breeding feathers and first-grown supplemental feathers appear similar. Involves head, foreneck, upper breast, 40–90% of lower breast and flanks (sides of breast under ruff often not moulted), 40–90% of mantle and scapulars, and, often, some innerwing-coverts and tertials. Unlikely to be seen in HANZAB region. **Post-juvenile** (First pre-basic). Partial. Mostly in non-breeding areas, second half of Sept. to Oct.; juvenile plumage retained on all, or part of, back and rump, some inner lesser and greater upperwing-coverts and tertials, outer rectrices, and remiges. **Post-juvenile moult of primaries** (First pre-supplemental A). Some juveniles (probably only females) moult 2–3 outer primaries; 14% of juveniles in s. and e. Africa moulted outer primaries, Jan.–Mar. (Schmitt & Whitehouse 1976). No males seen in breeding areas with new outer primaries. **First pre-breeding** (First pre-alternate). Mostly as adult pre-breeding but starts later; males Jan.–Mar., females Feb.–Mar.; sometimes moult fewer wing-coverts and feathers of underbody; some immatures that remain in non-breeding areas attain only a scattering of breeding plumage on head and body. **Immature pre-supplemental moult** Partial. Males only. In immatures that migrate to breeding areas, mostly as adult males but ruff and ear-tufts smaller. Full density of tuft and ruff feathers not attained for several years (Hogan-Warburg 1966). Immatures that remain in non-breeding areas attain very little supplemental plumage.

MEASUREMENTS (1–3) Netherlands, skins (RMNH, ZMA; BWP): (1) Adults, mainly Apr.–June; (2) Juveniles, mainly Aug.–Sept.; (3) Ages combined.

	MALES	FEMALES	
WING	(1) 191 (3.43; 180–200; 191) (2) 186 (3.81; 173–193; 186)	158 (3.03; 154–164; 158) 157 (3.37; 152–164; 157)	** **
TAIL	(1) 65.9 (2.18; 62–70; 67) (2) 65.6 (1.39; 64–68; 6)	54.3 (2.07; 51–60; 23) 52.9 (2.62; 49–55; 6)	** **
BILL	(3) 35.0 (1.29; 33–37; 74)	30.9 (1.26; 29–33; 31)	**
TARSUS	(3) 50.2 (1.61; 47–54; 77)	42.9 (1.53; 40–46; 31)	**
TOE	(3) 37.9 (1.30; 35–41; 67)	33.4 (1.51; 30–35; 26)	**

Wing of juvenile male significantly shorter than that of adult male; other measurements similar to those of adults. Size of adult males is related to colour and, possibly, pattern of ruff and ear-tufts in supplemental plumage. Those with darker or more boldly patterned plumage are slightly larger (van Rhijn 1973; Höglund & Lundberg 1989), e.g. average length of wing, tail, bill and tarsus of black males, 187, 69.6, 35.2 and 51.7 respectively; in white males, same measurements 182.8, 66.8, 34.4 and 49.4 (Höglund & Lundberg 1989). Differences may be related to display strategy, as dark males form territories on a lek while white males behave as satellites (e.g. Hogan-Warburg 1966; van Rhijn 1973, 1983). Breeding females also show plumage polymorphism, albeit much less marked (Chandler 1987); apparently not known if this also related to size.

WEIGHTS Summarized from BWP: (1) Central e. and s.

Africa, ages combined; (2) On spring migration in n. West Germany; (3) Adults, after crossing the Sahara; (4) Netherlands, exhausted adults.

	MALES	FEMALES	
Aug.–Sept.	(1) 171 (13.0; 141–230; 52)	101 (9.10; 72–125; 348)	**
Oct.–Nov.	(1) 170 (21.2; 130–210; 100)	102 (9.59; 78–147; 1001)	**
Dec.–Feb.	(1) 172 (21.0; 130–220; 33)	99 (10.4; 74–11; 575)	**
Mar.	(1) 188 (19.8; 132–210; 24)	97 (13.3; 76–139; 283)	**
Mar.–Apr.	(2) 210 (185–254; 20)	132 (98–170; 11)	
Apr.	(1) 180 (28.5; 130–230; 11)	114 (13.1; 82–150 164)	**
	(3) 98, 100, 110	78	
	(4) 91, 95, 101	64 (3.67; 59–68; 5)	**

AGEING On arrival in non-breeding areas, immatures (first basic) have fresh primaries while adult primaries old or moulting. By about Dec., adults have completed moult of primaries and immatures separable by more worn primaries and lack of pre-breeding plumage. Adult males start first pre-alternate moult, Nov. to early Jan., immature males, Jan. to early Mar.; adult females, Dec. to early Mar., immature females, Feb.–Mar. Some immature females replace 1–4 inner primaries and show contrast between worn outer and new inner ones. After second pre-basic moult, as adult, though males in pre-supplemental plumage do not attain full density of ruff and ear-tuft feathers for several years. Colour of legs also important in determining age (see Field Identification). For additional information, see BWP and Pearson (1981).

GEOGRAPHICAL VARIATION None.

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Volume 3, Plate 21

Ruff (and Reeve) *Philomachus pugnax* (page 341)

1 Adult male breeding, red plumage; 2 Adult male breeding, black-and-white plumage; 3 Adult female breeding, typical plumage;
4 Adult female breeding, striped plumage; 5 Juvenile; 6 Adult male non-breeding; 7 Adult female non-breeding; 8, 9 Adult