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Higgins, P.J. & Davies, S.J.J.F. (editors) 1996. Handbook of Australian, New Zealand & Antarctic Birds. Volume 3, Snipe to pigeons. Melbourne, Oxford University Press. [Vol. 2, pages 648-649] Vol. 3, pages 25-28, 347-352; plate 13.

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648 Charadriiformes

## Order CHARADRIIFORMES

A large, diverse assemblage of small to medium-large (12–75 cm long) limicoline, pratincoline, aquatic or terrestrial birds. Cosmopolitan from Arctic to Antarctic regions; in all sorts of maritime, freshwater and open terrestrial habitats (including deserts) with a few (woodcocks and snipes) even using dense forests. Once known as Limicola or Laro-limicola (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.    |
| Ibidorhynchidae  | Ibisbill; monotypic, central Asia.   |
| Charadriidae     | plovers and lapwings; c. 60 species, cosmopolitan.                                       |
| Pluvianellidae   | Magellanic Plover; monotypic, S. America.  |
| Dromadidae       | Crab Plover; monotypic, Arabian region.  |
| Glareolidae      | pratincoles, coursers, and Egyptian Plover; c. 15 species, widespread in Old World.      |
| Stercorariidae   | skuas and jaegers; about seven species, mostly in Arctic and Antarctic regions.          |
| Rhynchospidae    | 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. Pteroclidae (sandgrouse) probably sister-group of Charadriiformes (e.g. Fjeldså 1976, 1977; Sibley & Ahlquist 1990; BWP), though whether best placed within Charadriiformes or in separate order is debated. Flamingoes (Phoenicopteridae) and divers (Gaviidae) have also been treated as Charadriiformes (Olson & Feduccia 1981; Fjeldså 1976, 1977) but DNA-DNA hybridization studies (Sibley & Ahlquist 1990) inconsistent with these theories. Affinities to other orders still controversial; DNA-DNA hybridization has suggested closest links are to large waterbirds, such as storks, herons and allies, Pelicaniformes, Procellariformes, penguins, grebes, divers (Gaviidae) and also Falconiformes. All these were combined in huge order Ciconiiformes by Sibley & Ahlquist (1990).

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

Because the Order comprises so many species and adaptations are so diverse, few characters shared by all species; those that are shared are mostly anatomical features of the skull, e.g. most or all have schizorbinal nostrils, schizognathous palates, well-developed vomer, lachrymals fused with ectethmoid 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 *Scopopax 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, rhynchoskeinesis 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); hind toe, 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 Westernport 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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## Subfamily PHALAROPODINAE phalaropes

Small (18–24 cm) swimming scolopacids, with distinctive breeding behaviour and migratory habits. Three species in two genera: (1) *Phalaropus*, with two species (Red-necked Phalarope *P. lobatus*, Grey Phalarope *P. fulicaria*) that breed in Arctic and Subarctic and migrate to pelagic non-breeding areas in Tropics and farther S; and (2) *Steganopus*, with single migratory species (Wilson's Phalarope *S. tricolor*) in New World. All recorded HANZAB region; Red-necked Phalarope a rare summer visitor, the other two accidental. Studies of osteology (Campbell 1979), allozymes (Dittman *et al.* 1989) and mitochondrial DNA (Dittman & Zink 1991) have shown *Steganopus* to be generically distinct. Structure, behaviour, appearance, reversed sexual dimorphism, moults and aquatic adaptations are unusual and rather uniform, so they have long been regarded as a 'natural' unit (BWP) and often treated as a full family. However, some analyses of allozymes and mitochondrial DNA suggest *Steganopus* is no more closely related to *Phalaropus* than to some Calidridinae or Tringinae, and monophyly of group remains unproven (Dittman *et al.* 1989; Dittman & Zink 1991; Rubega & Obst 1993). Despite uncertainties about affinities, studies of osteology and jaw musculature (Lowe 1931; Strauch 1978; Burton 1974), allozymes and mitochondrial DNA (Dittman *et al.* 1989; Dittman & Zink 1991; Sibley & Ahlquist 1990) show phalaropes are clearly scolopacids, as do patterns of downy young, which are very similar to those of sandpipers in tribe Tringini (Jehl 1968; Fjeldså 1977).

Neck, slender; head, small, with narrow forehead; musculature of jaw, weak but that of tongue well developed, especially in Grey Phalarope. Bill, straight and needle-like in Wilson's and Red-necked Phalaropes; in at least latter species, fine bill structure associated with feeding mechanism in which zooplankton transported rapidly from bill-tip to mouth by forces resulting from surface tension of water surrounding prey (Rubega & Obst 1993). Grey Phalarope may have different filter-feeding mechanism; bill is broader and a few well-developed papillae at inside tip of lower mandible probably act as strainers (Olson & Feduccia 1980). Bodies, slim and sandpiper-like; underparts more densely feathered than other scolopacids, presumably for improved waterproofing and buoyancy while swimming. Wings, narrow, pointed; flight low, fast, and direct. Swim readily and well (but do not dive), with structure of short legs and feet modified accordingly: tarsi are strongly laterally compressed and front toes are lobate, each broadly fringed by independent, scutellate webs (arrangement of scales and webs differs in each species). Anterior toes also have small basal webs; hindtoe relatively long, raised.

Sexual dimorphism reversed: females larger with more brightly coloured breeding plumage than males. Breeding plumage attained in partial pre-alternate moult and is highly decorative, with various combinations of rufous or maroon and white, black, grey, and buff, making females among the most colourful waders. Attain non-breeding plumage in complete pre-basic moult; plumage pale grey above, white below. Juvenile plumage distinct, with dark upperparts scaled buff, and white underparts often washed grey to orange-buff on foreneck and breast. Pre-basic moult (post-breeding and post-juvenile) occur earlier than in most scolopacids, often beginning near breeding grounds and well advanced by early stages of s. migration. Adult post-breeding moult usually starts earlier in females than males; genuine moult-migration reported in Wilson's Phalarope (q.v.; Jehl 1987). Down of precocial young, soft and silky; mainly rich buff above, grading to white on centre of underparts. Dorsal pattern similar to striped type of Tringinae, with three bold black bands on upperparts; most down-feathers have fine, deep purplish-grey terminal filaments (Fjeldså 1977).

Breed in open habitats, usually with some pools, lakes or other standing water nearby, from Arctic tundra (most Grey Phalaropes) and Subarctic (most Red-necked Phalaropes) to temperate prairies and taiga (Wilson's Phalarope). Wilson's Phalarope spends non-breeding season in inland wetlands of South America; non-breeding *Phalaropus*, tend to be strictly pelagic, spending non-breeding season at sea in tropical or subtropical waters where upwellings occur (though can occasionally occur on inland wetlands, especially during migration).

Characteristically feed while swimming, picking invertebrate prey from surface of water or just below it; when doing so in still water, often spin rapidly in tight circles, presumably to bring food into view or within reach (e.g. Höhn 1971). Wilson's Phalarope spins less often than *Phalaropus*, and feeds more while swimming directly or wading. When breeding, all three species have more diverse feeding behaviours and may also feed on land (e.g. Kistchinski & Chernov 1973; Höhn & Barron 1963; BWP).

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## *Steganopus tricolor* Wilson's Phalarope

COLOUR PLATE FACING PAGE 256

*Steganopus tricolor* Vieillot, 1819, *Nouv. Dict. Hist. Nat.* 32: 136 ex Azara, 1802–1805, *Apuntamientos para la historia natural de los Paxaros del Paraguay y Rio de la Plata* — Paraguay.

The generic name is from the Greek στεγανόποτος, web-footed. The specific epithet is from the Late Latin *tricolor* for three-coloured, presumably referring to the breeding colour of the female.

The English name is from Plate LXXIII, Figure 3 of A. Wilson, 1814, *American Ornithology*.

### MONOTYPIC

**FIELD IDENTIFICATION** Length 22–24 cm; wingspan 35–38 cm; weight: male c. 50 g, female c. 70 g. Small wader with very distinctive shape: straight, medium-length, needle-like bill; small head (with sloping forehead); long slender neck; wide-bodied and pot-bellied appearance; and short legs. Larger than other phalaropes, with smaller head, slimmer neck, longer bill and legs (but less strongly lobed toes) and longer outline, both on ground and on water. In flight, distinguished from other phalaropes by: lack of wing-bar; square white patch across uppertail-coverts; and projection of feet beyond tip of tail. Most terrestrial of the phalaropes. Sexes separable in breeding plumage, with male much duller and varying. Marked seasonal variation. Juvenile distinct. Immatures separable.

**Description** **Adult female breeding** Forehead and crown, light grey grading to almost white on nape and hindneck; short narrow white fore-supercilium (not extending to bill), finely bordered black; bold black band extends from bill, through eye to ear-coverts, and continues down sides of neck to merge with dark-chestnut band on side of lower neck and side of mantle; chin and throat, white. Rest of mantle, scapulars and tertials, blue-grey, with chestnut stripe running through central scapulars; tertials narrowly fringed rufous-brown. Back and rump, dark grey. Uppertail-coverts, white, with some dark-grey smudging on central feathers. Tail, grey, with narrow white fringes to feathers. Upperwing, dark brownish-grey grading to black on primary coverts and outer primaries; shaft of outermost primary, white; all wing-coverts have fine white fringes. Underbody, white, with rich orange-rufous wash on sides of neck, foreneck and upper breast, grading to paler orange-rufous on sides of lower breast and flanks. Underwing, white, with slightly contrasting pale-grey remiges and greater primary coverts and some fine dark mottling along leading-edge of innerwing. In flight, show almost uniform dark-grey upperwing with no wing-bar, and square white patch (like that of Curlew Sandpiper) across uppertail-coverts, contrasting with dark upperparts and pale-grey tail. Bill, black. Iris, dark brown. Legs and feet, brownish grey to black when breeding, changing to yellowish (as non-breeding) from June. **Adult male breeding** Duller than female (and smaller; see Measure-

ments), but plumage varies much; brightest birds like breeding female; dullest birds like non-breeding birds. Brightest differ from breeding female by: forehead and crown, darker grey; white supercilium longer, usually extending closer to bill and behind eye also; upperparts, duller grey-brown with more mottled appearance caused by dark brown or black centres to feathers and dull orange-brown fringes to some feathers of mantle and scapulars (cf. smarter, blue-grey and chestnut upperparts of breeding female). Most males also differ by: blackish eye-stripe narrower and duller, continuing down sides of neck as faint dark border to rather dull chestnut wash on ear-coverts and sides of neck; pale area on central hindneck smaller and less distinct; wash on foreneck and upper breast, duller orange, and on flanks, duller grey-buff. Dullest males (very few like this) also have little or no chestnut on neck or breast and differ from non-breeding birds mainly by darker, more mottled upperparts and blackish legs and feet. **Adult non-breeding** Centre of forehead, crown, nape, hindneck and narrow stripe from beneath eye to sides of nape, pale grey; rest of head and neck, white (though some show hint of greyish loral stripe and, rarely, rear supercilium washed pale grey and much less distinct). Rest of upperparts and innerwing-coverts, uniform, pale grey, all feathers narrowly fringed white when fresh. Underbody, white, with pale-grey wash on sides of lower breast and flanks. Flight-pattern and bare parts as breeding except: legs and feet, yellow or bright yellow, gradually darkening from middle of non-breeding season. **Juvenile** Superficially like dull adult male breeding, especially in pattern of head and neck; differs by: forehead, crown and narrow eye-stripe, dark brown, with feathers of crown faintly fringed cinnamon; chin, throat and supercilium, white; nape and hindneck, pale grey, mottled dark grey and buff. Mantle, back, rump and scapulars, dark brown or black, with buff scaling or striping, especially on mantle (broad buff fringes to feathers, which are sometimes broken at tips by black shafts). Tertiaries and innerwing-coverts like rest of upperparts but paler and greyer (and usually with narrow darker submarginal line bordering buff fringe). Underbody, white, with buff wash on foreneck, sides of breast and fore-flanks and grey mottling on sides of breast; occasionally buff tinge on rear flanks and black

tips to longer undertail-coverts. With wear, buff fringes on upperparts and wash on underbody fades to off-white. Legs and feet, yellow or greenish yellow. Birds in full or mostly juvenile plumage unlikely to occur in HANZAB area. **First immature non-breeding** Like adult non-breeding, but separable till late in spring by retained worn juvenile innerwing-coverts and, usually, some tertials, contrasting with fresh pale-grey plumage of rest of upperparts; many probably inseparable from adult non-breeding after summer (see Ageing, Moult).

**Similar species** For distinctions from **Red-necked** and **Grey Phalaropes**, see those accounts. In non-breeding and juvenile plumages or when behaviour is atypical for a phalarope (e.g. when feeding on land), may be confused with other species, such as **Marsh Sandpiper** *Tringa stagnatilis*, **Stilt Sandpiper** *Micropalama himantopus* and **Lesser Yellowlegs** *Tringa flavipes* (q.v. for distinctions).

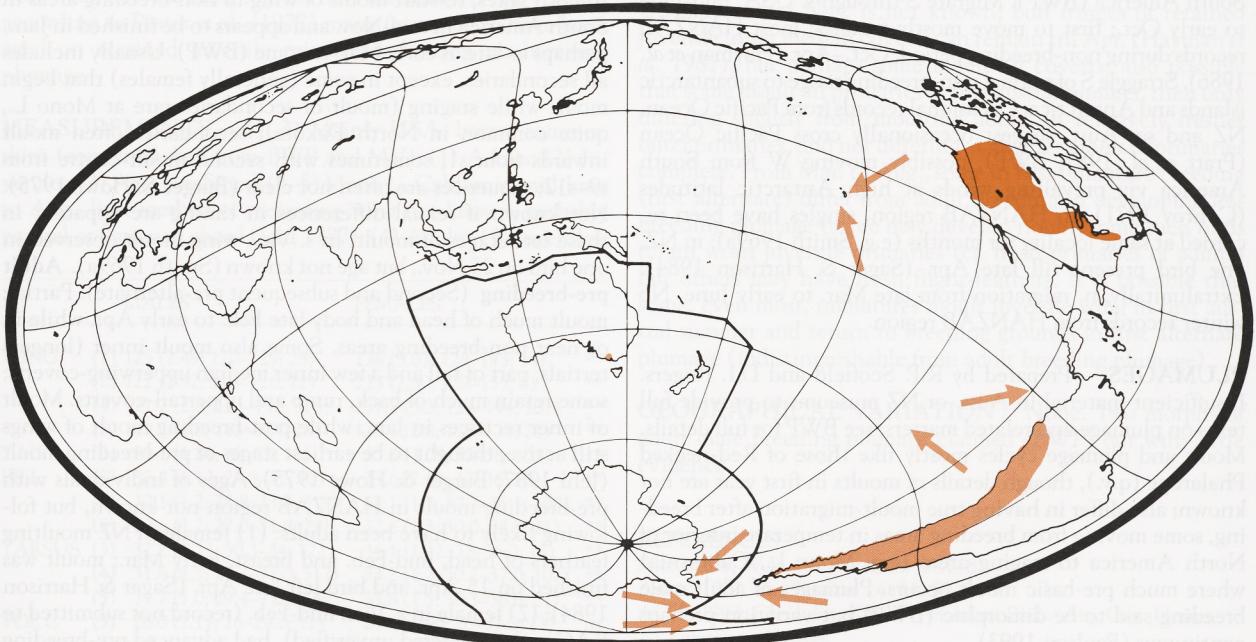
Gregarious in normal range where typically seen in small parties; only solitary vagrants recorded in HANZAB region. Outside breeding areas, mostly on inland wetlands and only rarely reported at sea. Freely associate with other waders, such as Red-necked Phalarope, stilts, and avocets; more loosely with small calidrids and species of *Tringa*. Often very tame and approachable. Very active. Swim like other phalaropes, but not persistently; much more terrestrial than other phalaropes, foraging as much by wading in shallows or walking along muddy edges. When swimming, spin less than other phalaropes, feeding mainly by picking at surface but also by thrusting open bill into water while moving forward quickly or by up-ending. When wading in shallows, move bill rapidly from side to side in scything motion like that of Greenshank *Tringa nebularia*. When foraging on land, gait freer than that of other phalaropes, typically running about more actively and erratically than most other shoreline sandpipers; actions include high-stepping walk (often with more erect stance than other phalaropes) and fast but wavering run with hint of gallop when pursuing insects. Picking actions while on land may be quick and erratic or slow and methodical, combining with forward-tilted stance, unusual pot-bellied shape and crouching gait to give very

distinctive jizz; sometimes also stalk insects with head and bill stretched out parallel to ground. Flight looser and slower than that of other phalaropes, recalling flight of smaller *Tringa* (as does flight-silhouette). Rather quiet outside breeding season; sometimes utter soft grunting *aangh*, *chu* or *yup* in flight.

**HABITAT** Less aquatic than other phalaropes. In non-breeding periods, rarely in pelagic or coastal habitats, except for sheltered tidal areas, such as pools, lagoons, estuaries and beaches with mudflats; mainly occur round terrestrial wetlands, both fresh and saline, frequenting swamps, shallow lakes, pools and the like (Bent 1962; Hein 1967; Blake 1977; Myers & Myers 1979; Bomberger 1984; Colwell & Oring 1988a,b; BWP). Few records at sea (Alexander 1927; Anon. 1961; Bourne 1964, 1967; Bourne & Dixon 1973–74).

In Aust., recorded in shallow water of brackish lake and shallow freshwater swamp, among low emergent vegetation, on mudflats or mats of waterweed; also on flat grassy islet (Smith 1968, 1969a,b); also in saltworks (Vic. Bird Rep. 1981). In NZ, recorded in shallow water and on open mudflats of near-coastal lagoon and estuary (Moore & Moore 1984; Sagar & Harrison 1984). On Signy I., observed swimming on lake and sitting on rocks at edge of lake (Rootes 1988). At Alexander I., Antarctica, individual found several hundred kilometres inland from edge of ice (Conroy 1971). In A'sia, recorded feeding in shallow water, either open or among low emergent or floating vegetation; on exposed mudflats; among small rocks. Seen roosting on sand at edge of wetland and standing in water 1 cm deep at grass-fringed edge of swamp, with other waders (Smith 1968, 1969a,b; Moore & Moore 1984; Sagar & Harrison 1984).

**DISTRIBUTION** Widespread breeding throughout much of s. Canada and w. USA; n. limit from s. Yukon and n. British Columbia and Alberta, SE to s. Ontario and sw. Quebec; extends S to central regions of California, Nevada and New Mexico and n. Texas; thence NE to n. Indiana and Ohio. On migration, transient through islands of Caribbean and Central



America. Spend non-breeding period in South America, from s. Peru, Chile (from Arica, S to Valdivia), Bolivia, Paraguay, Argentina (S to Chubut) and Uruguay; occasionally farther S, to Tierra del Fuego and Falkland Is. Rarely Galapagos Is and once recorded at sea between Galapagos and Easter Is, c. 1600 km from nearest land. Accidental to Scandinavia, central and w. Europe, including Mediterranean countries; recently recorded as regular visitor to Britain and Ireland; vagrant to Morocco and South Africa. In central Pacific, vagrant to Hawaii, Johnston and Easter Is. Vagrant to A'asia, S. Orkney Is, S. Georgia and Antarctica (Alexander 1927; Johnson 1965; Blake 1977; AOU 1983; Urban *et al.* 1986; Murphy; BWP).

**Aust.** Only one (unacceptable) record has been submitted to the RAC. Other published records with descriptions (all singles): L. Murdeduke, Vic., 6 Feb. 1966 (Smith 1968); Altona, Vic., 5 Nov. 1967–7 Jan. 1968, 17 Nov. 1968, 7 May 1977 (Smith 1969a,b; Aust. Atlas). Unverified records include: single, Altona, 7 May 1977 (Aust. Atlas); single, Laverton, Vic., 10 Feb.–1 Mar. 1971 (Vic. Bird Rep. 1981); L. Woorinen, 28 Oct.–4 Nov. 1980 (Lowe 1981). Unacceptable records: three, Moolap, Vic., 6–17 Dec. 1981 (Aust. Atlas; RAC); single, Tullakool Saltworks, NSW, 3–5 Apr. 1988 (Disher 1990; not accepted by NSWORAC).

**NZ** Single, estuary of Manawatu R., 25–29 Sept. 1983 (Moore & Moore 1984); L. Ellesmere: one, 19 Nov.–25 Apr. 1984; second bird present, 22 Dec.–28 Jan. (Sagar & Harrison 1984; J.L. Moore).

**South Orkney Is** Singles, Signy I., 23 Mar. 1982 (Rootes 1988), Dec. 1981–Feb. 1982 (Hemmings 1985); see Rootes (1988).

**South Georgia** Single, Bird I., date unknown (Lidstone Scott 1983).

**Antarctica** Specimen, Alexander I., 13 Oct. 1968 (Conroy 1971); the most southerly record of any wader (Hayman *et al.* 1986).

**MOVEMENTS** Migratory; breed North America, and move through Central America to non-breeding areas in inland South America (BWP). Migrate S through s. USA, mid-June to early Oct.; first to move mostly females; most HANZAB records during non-breeding period, Oct.–Apr. (Hayman *et al.* 1986). Straggle S of normal non-breeding range to subantarctic islands and Antarctica. Occasional records from Pacific Ocean, NZ and se. Aust. suggest occasionally cross Pacific Ocean (Pratt *et al.* 1987; BWP), possibly moving W from South America via prevailing winds at high Antarctic latitudes (Conroy 1971). In HANZAB region, singles have been recorded at same locality for months (e.g. Smith 1969a); in NZ, one bird present till late Apr. (Sagar & Harrison 1984). Extralimitally, n. migration from late Mar. to early June. No winter records from HANZAB region.

**PLUMAGES** Prepared by R.P. Scofield and D.I. Rogers. Insufficient material in Aust. or NZ museums to provide full texts on plumage and related matters; see BWP for full details. Moult and plumage cycles mostly like those of Red-necked Phalarope (q.v.), though details of moults in first year are not known; also differ in having true moult-migration after breeding, some moving from breeding areas in temperate interior of North America to staging areas (e.g. Mono L., California) where much pre-basic moult occurs. Plumages of adult male breeding said to be dimorphic (BWP) but variation perhaps continuous (Paulson 1993).

**MOULTS** Based mostly on Burger & Howe (1975), BWP and Jehl (1987). Only moults that occur while in North America are adequately known. **Adult post-breeding** (Second and subsequent pre-basic). Complete; primaries outwards. Best known from study at Mono L., California (Jehl 1987) where tens of thousands stage on s. migration, moulting body, much of tail and inner primaries in 32–40 days before suspending moult and continuing migration to South America, where moult finished. Moult of body begins early, from mid-June, with timing of onset differing between sexes. Females do little or no moult on breeding grounds and arrive at staging areas in mid-June with worn breeding plumage. Moult begins by July, on upper back, breast and tertials (sequence varies, and scapulars or rectrices can be moulted first) and spreads to most other tracts of body within several days. Moult of tail begins with central rectrices, then outer pair or pairs, and then rest; typical sequence: t1–t6–t2–t5–t3–t4. Sequence of tertials, inwards in some, centrifugal in others. Moult of primaries begins 1–2 weeks after moult of body starts; usually p1 and p2 dropped simultaneously, then subsequent primaries not lost till adjacent inner primary fully grown (see Jehl 1987 for variation in pattern); some upperwing-coverts (especially median coverts) often moulted at same time as inner primaries. Non-breeding appearance often attained by third week of July and most females have finished moult of body by 5 Aug.; before departure (usually in last days July or first week Aug.), 60–70% have moulted all rectrices, and most have replaced three primaries, some as many as five (a few, none). Males follow similar general sequence, but arrive at staging areas later than females and usually begin moult while still on breeding grounds (one known to have been moulted while still attending chicks); moult usually begins 1–2 weeks later than in females, and thus extent of moult in staging areas differs slightly from females. A few finish moult of body by end July (earliest 22 July) but most have not done so when leaving in first half Aug., when most have moulted 6–8 rectrices (a few finish moult of tail by 31 July) and 2–4 inner primaries (maximum, six); a few have not started moult of tail or primaries before departure, and an aberrant male had not even started moult of body by 21 Aug. In both sexes, re-start moult of wing in non-breeding areas in South America in mid-Nov. and appears to be finished in Jan., perhaps as late as early Mar. in some (BWP). Usually includes all secondaries, except in some (generally females) that begin moult while staging (moult of secondaries rare at Mono L., quite common in North Dakota); secondaries often moult inwards from s1, sometimes with second moult-centre from s9–s12; sequences are often not clear (Burger & Howe 1975). Not known if sexual differences in timing are apparent in these late stages of moult. In s. Vic., wing-moult observed in one bird on 25 Nov., but age not known (Smith 1969a). **Adult pre-breeding** (Second and subsequent pre-alternate). Partial; moult much of head and body late Feb. to early Apr. while in or near non-breeding areas. Some also moult inner (longer) tertials, part of tail and a few inner median upperwing-coverts; some retain much of back, rump and uppertail-coverts. Moult of inner rectrices in Jan., while post-breeding moult of wings still active, thought to be earliest stages of pre-breeding moult (Jehl 1987; Burger & Howe 1975). Ages of individuals with pre-breeding moult in HANZAB region not known, but following likely to have been adults: (1) female in NZ moulting feathers of head, mid-Feb. and breast, early Mar.; moult was finished on 15 Apr. and bird left late Apr. (Sagar & Harrison 1984); (2) female in s. Vic., mid-Feb. (record not submitted to RAC and considered unverified), had advanced pre-breeding

moult; left 1 Mar. (Vic. Bird Rep. 1981: photo). **Post-juvenile** (First pre-basic). Early stages, rapid; usually start to moult head and body in late July (soon after fledging), and most in first-immature non-breeding plumage when leaving staging areas in late Aug., retaining only juvenile remiges, tertials, wing-coverts, back, rump, uppertail-coverts and tail (a few have juvenile plumage scattered elsewhere [photo in Pringle 1987: 421] and one had not started moult by 27 Aug.). Extent of moult thereafter, poorly known. Juvenile coverts and tertials retained till at least Nov., when active moult of median coverts recorded (Burger & Howe 1975); said to retain some buff-fringed inner median coverts till Apr.–May (Prater *et al.* 1977). Information on moult of flight-feathers, contradictory; it is not clear whether mistakes have been published or whether there is individual (or geographical) variation in moult-strategies, like that in Red-necked Phalarope. Small sample from Mexico indicated primaries replaced between middle of austral summer and Mar.–Apr., though one had not moulted primaries by Apr. (BWP). Burger & Howe (1975) considered first pre-basic to be complete, with flight-feathers moulted at about the same time as adults; these were aged by slight wear on old (retained juvenile) primaries (analogous ageing character is helpful in Sharp-tailed Sandpipers *Calidris acuminata* in Aust.). Jehl (1987) argued that the specimens were wrongly aged as Burger & Howe were not aware that some adults migrate with moult suspended; the argument is not soundly based as this should not have any effect on the wear of retained (outer) primaries, but it is true that waders moulting all juvenile primaries in first austral summer pose ageing problems. Like Prater *et al.* (1977) and Hayman *et al.* (1987), Jehl stated that first pre-basic does not involve primaries but did not present supporting evidence. **First pre-breeding** (First pre-alternate). Poorly known. Analogy with other phalaropes suggests that those replacing primaries in first austral summer thereafter perform first pre-alternate like adult pre-breeding, and return N to breed. Paulson (1993) also suggested this moult is as extensive as adult breeding, but some individuals apparently differ; several specimens from Mexico still in first basic by Mar. and one (with fresh primaries) moulted directly from worn non-breeding to fresh non-breeding in Aug. (BWP); according to Prater *et al.* (1977) many (assumed to have been aged on retained juvenile primaries) develop no breeding plumage.

**MEASUREMENTS** (1–3) Mainly USA, boreal summer, skins (combined data from BWP and MV): (1) Adults; (2) Juveniles; (3) Ages combined. (4–5) Mono L., California, mid-June to Aug., live; method of measuring wing not known, probably natural or flattened chord (Jehl 1987): (4) Adults; (5) Juveniles.

|       | MALES                          | FEMALES                    |    |
|-------|--------------------------------|----------------------------|----|
| WING  | (1) 125 (2.49; 120–129; 28)    | 136 (3.03; 128–143; 34)    | ** |
|       | (2) 122 (2.92; 118–126; 12)    | 133 (2.50; 129–135; 6)     | ** |
|       | (4) 121.2 (2.8; 115–132; 318)  | 131.7 (3.3; 124–144; 101)  | ** |
|       | (5) 119.5 (3.0; 113–124; 28)   | 129.4 (2.8; 125–134; 21)   | ** |
|       | (3) 50.1 (1.84; 48–52; 10)     | 53.6 (3.09; 50–58; 10)     | ** |
| TAIL  | (3) 30.4 (1.12; 28.8–32; 10)   | 33.6 (1.54; 32–36; 10)     | ** |
|       | (4) 30.1 (1.2; 25.8–33.8; 319) | 33.1 (1.3; 30.2–36.1; 100) | ** |
|       | (5) 29.6 (1.2; 27.0–31.8; 29)  | 32.8 (1.3; 30.0–34.9; 21)  | ** |
| BILL  | (3) 32.2 (1.23; 30.3–34; 12)   | 34.1 (1.42; 32–36.0; 13)   | ** |
|       | (4) 31.6 (1.3; 27.3–37.0; 317) | 33.2 (1.2; 30.2–37.0; 101) | ** |
|       | (5) 31.7 (1.0; 29.4–33.4; 28)  | 33.6 (1.5; 30.3–36.0; 21)  | ** |
| TOE C | (3) 28.0 (1.17; 26–29.0; 12)   | 28.6 (1.90; 26–32.0; 13)   | ns |

Females larger; Jehl (1987) gives discriminant function for sexing. In samples above, wing of juveniles significantly shorter than in adults; variation related to age negligible for other measurements (BWP), though measurements of Jehl (1987) show slight but significant difference between juvenile and adult males in length of bill ( $P<0.05$ ). For additional measurements, see Höhn (1967), Prater *et al.* (1977), Colwell & Oring (1988b) and Murphy.

**WEIGHTS** Breeding adults: (1) Alberta, Canada, May to mid-July (Höhn 1967), excluding female of 34 g; (2) Saskatchewan, Canada (Colwell & Oring 1988b; Dunning 1993); does not include gravid females with formed eggs in oviduct, weighing 79.0 (4.9; 31).

|     | MALES                   | FEMALES                |    |
|-----|-------------------------|------------------------|----|
| (1) | 50.2 (5.24; 30–64; 100) | 68.1 (8.44; 55–85; 53) | ** |
| (2) | 51.8 (4.10; 155)        | 68.1 (7.10; 48)        |    |

Differences between sexes significant. Weights of males decrease during incubation. Few data available from outside breeding range, even though many have been handled or collected during studies of moult. Non-breeding male, Peru, Feb., 45.8 (Sanft 1970); on migration in USA, male 42.4 (June) and females 49.8, 56.8, 48.5 (May–July); vagrant female, Netherlands, 78.3 (BWP).

**AGEING** From late Aug. till about Mar., adult non-breeding can be confused with FIRST IMMATURE NON-BREEDING (first basic). Latter differs till at least Nov. by: (1) retained black juvenile tertials with broad buff (124) fringes (adults have pale grey tertials); (2) retained juvenile median upperwing-coverts, and, less obviously, juvenile feathers on rump, uppertail-coverts and tail; all these have buff fringes and black-brown submarginal lines, which are so broad that brown centres of feathers often not visible; (3) may be distinguished by slight, uniform wear of retained juvenile primaries (adults have suspended or active moult of primaries). Reliability of above characters after Nov. is not known; buff fringes of retained juvenile inner median coverts can remain till Apr. (Hayman *et al.* 1987), but perhaps some moult all coverts; also possible that some moult all primaries in first austral summer, then only differing slightly from moulting adults in relatively fresher outer primaries, and not differing at all after moult of primaries complete. From Mar. to Aug., some in first immature breeding (first alternate) differ from adult breeding in developing less breeding plumage (some may develop none); some such birds retain worn juvenile primaries (cf. fresh primaries of adults) but others may have fresh flight-feathers. It is possible that some, even most, immatures moult juvenile wing in first austral summer and return to breeding grounds in first alternate plumage (indistinguishable from adult breeding plumage).

**GEOGRAPHICAL VARIATION** None. Two morphs of adult male breeding plumage claimed (BWP) but with little evidence.

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Volume 3, Plate 13

Ruddy Turnstone *Arenaria interpres* (page 194)

1 Adult male breeding; 2 Adult female breeding; 3 Adult non-breeding; 4 Juvenile; 5, 6 Adult

Wilson's Phalarope *Steganopus tricolor* (page 348)

7 Adult male breeding; 8 Adult female breeding; 9 Adult non-breeding; 10 Juvenile; 11, 12 Adult