

Order CHARADRIIFORMES

A large, diverse assemblage of small to medium-large (12–75 cm long) limicoline, pratincoline, aquatic or terrestrial birds. Cosmopolitan from Arctic to Antarctic regions; in all sorts of maritime, freshwater and open terrestrial habitats (including deserts) with a few (woodcocks and snipes) even using dense forests. Once known as Limicolae or Laro-limicolae (e.g. Mayr & Amadon 1951); colloquially, the assemblage (excluding alcids, skuas, gulls, terns and skimmers) is often referred to as waders (especially in Britain) or shorebirds (especially in North America).

About 350 species in 19 families, though taxonomic treatments vary. Following families recognized (mostly based on recent reviews of Order [Sibley *et al.* 1988; Sibley & Ahlquist 1990; Sibley & Monroe 1990]):

Thinocoridae	seedsnipes; four species, S. America.
Pedionomidae	Plains-wanderer; monotypic, Aust.
Scolopacidae	sandpipers, snipes and allies; c. 85 species, cosmopolitan.
Rostratulidae	painted snipes; two species, s. America and Old World.
Jacanidae	jacanas; seven species, pantropical.
Chionididae	sheathbills; two species, Antarctica and subantarctic islands.
Burhinidae	thick-knees, stone-curlews; nine species, widespread in Old World and two in Neotropics.
Haematopodidae	oystercatchers; c. 11 species, worldwide in tropics and temperate regions.
Recurvirostridae	avocets and stilts; about seven species, worldwide in tropical and temperate regions.
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.
Rhynchopidae	skimmers; three species, pantropical.
Laridae	gulls; c. 47 species, cosmopolitan.
Sternidae	terns; c. 42 species, cosmopolitan.
Alcidae	auks; c. 20 species, Arctic and temperate regions of n. hemisphere.

Apparently monophyletic. Pteroclididae (sandgrouse) probably sister-group of Charadriiformes (e.g. Fjeldså 1976, 1977; Sibley & Ahlquist 1990; BWP), though whether best placed within Charadriiformes or in separate order is debated. Flamingoes (Phoenicopteridae) and divers (Gaviidae) have also been treated as Charadriiformes (Olson & Feduccia 1981; Fjeldså 1976, 1977) but DNA–DNA hybridization studies (Sibley & Ahlquist 1990) inconsistent with these theories. Affinities to other orders still controversial; DNA–DNA hybridization has suggested closest links are to large waterbirds, such as storks, herons and allies, Pelicaniformes, Procellariiformes, penguins, grebes, divers (Gaviidae) and also Falconiformes. All these were combined in huge order Ciconiiformes by Sibley & Ahlquist (1990).

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

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

breeding and partial pre-breeding; some jacanas and alcids have flightless periods when moulting remiges. Young, downy, usually with intricate cryptic patterns on upperparts of three chief types: pebbly, spotted and striped, matching characters of habitat (Fjeldså 1976, 1977): precocial, nidifugous usually, self-feeding or not depending greatly on parents.

Thirteen families recorded in HANZAB region, with 54 species breeding, 41 occurring as regular non-breeding migrants and c. 38 as accidentals or probable accidentals. Scolopacidae, Stercorariidae, Laridae and Sternidae will be dealt with in Volume 3 of HANZAB.

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Family CHARADRIIDAE plovers and lapwings

Small to medium-sized, mostly terrestrial, waders of open habitats. About 65 species, placed in varying number of genera. Evidently monophyletic by behaviour and structural characters. Distributed worldwide and separable into two distinct sub-families: Charadriinae (plovers) and Vanellinae (lapwings), both of which are represented in HANZAB region and are discussed in more detail below. Most closely related to Recurvirostridae, Haematopodidae and possibly Burhinidae (Sibley & Ahlquist 1990; Christian *et al.* 1992).

Bodies, compact. Size differences between sexes negligible; sometimes males and sometimes females slightly larger. Necks, short and thick; 15 cervical vertebrae. Wings, long and usually pointed but rounded in some lapwings; 11 primaries, p11 minute; 14–19 secondaries. Tails, short to medium-long, square or rounded; 12 feathers. Bill, short, somewhat swollen at tip and narrower centrally; no sensitive nerve-endings at tip and prey located by sight rather than touch. Nostrils, holorrhinal, impervious, slit-like. Head, rounded; forehead steep and broad. Legs, fairly short or medium in length; bare part of tibia short; tarsi, reticulated, rarely with some transverse scutes. Usually three, rather short toes, slightly webbed at base in some plovers; no hind toe in most plovers and in some lapwings; hallux, short and vestigial if retained. No crop. Caeca present. Eyes large. Supraorbital salt-glands, often large; size related to salinity of habitat and influences structure of skull and appearance of head. Plane of *foramen magnum* of occiput nearly horizontal.

Plumages generally boldly patterned in brown, olive-grey, black and white; markings often have cryptic disruptive effect. Bill, bicoloured in some species, especially plovers. Stance erect with head held high. Fast runners for good distances but often proceed in short bursts with halts, especially when feeding. Post-breeding moult complete; primaries outwards; pre-breeding moult varies considerably. Young, precocial, nidifugous and always feed themselves; down of pebbly-pattern type (Fjeldså 1977).

See accounts of sub-families (below) for additional details.

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Sub-family CHARADRIINAE plovers

Generally small birds, usually smaller than lapwings (Vanellinae). Apparently a monophyletic assemblage. About 40 species in five (Voous 1973; Strauch 1978; BWP) to 10 genera (Sibley & Ahlquist 1990; Sibley & Monroe 1990; Christian *et al.* 1992), with most species in two genera, *Pluvialis* and *Charadrius*, and varying number of genera composed of only one or a few species (e.g. *Anarhynchus*, *Phegornis*, *Thinornis*, *Elseyornis*). The affinities of *Phegornis* (Diademed Sandpiper-plover of South America) have not been resolved (Sibley & Monroe 1990). Recent studies of allozymes of Aust. plovers and lapwings (Christian *et al.* 1992) indicate that Red-kneed Dotterel *Erythrogonys cinctus* is a lapwing (Vanellinae; q.v.).

We recognize the following genera within the Charadriinae in HANZAB region:

Pluvialis. Two regular non-breeding migrants (*fulva*, *squatarola*), two doubtfully recorded (*dominica*, *apricaria*). We follow Connors *et al.* (1983, 1993) and treat *fulva* and *dominica* as full species.

Charadrius. Four breeding species (*obscurus*, *ruficapillus*, *bicinctus*, *australis*), six non-breeding migrants (*hiaticula*, *dubius*, *mongolus*, *leschenaultii*, *asiaticus*, *veredus*), one accidental (*tricoloris*); one doubtfully recorded (*alexandrinus*). Inland Dotterel *C. australis* is a typical *Charadrius* plover (Maclean 1976; Christian *et al.* 1992 *contra* Jehl 1968); we follow NZCL in placing New Zealand Dotterel in *Charadrius*.

Thinornis. Two endemic species: *novaeseelandiae* and *rubricollis*.

Allozymes of *rubricollis* form a cluster (with *Elseyornis melanops*) well separated from those of typical *Charadrius*; placed in *Thinornis* on basis of similarities in morphology (Christian *et al.* 1992) and behaviour (Phillips 1980).

Elseyornis. Single species *melanops*, endemic to Aust. Allozymes, with those of *Thinornis rubricollis*, well separated from *Charadrius* (Christian *et al.* 1992).

Anarhynchus. Single species *frontalis*, endemic to NZ.

Thus, in HANZAB region, eight breeding species, eight non-breeding migrants, and four accidental or not acceptably recorded.

General features of the sub-family are outlined under Charadriidae. The plumages of *Pluvialis* are spangled in white or gold and black above, black below when breeding, and never with white band across nape; plumages of *Charadrius* and other genera in general plain brownish above and white below, boldly marked with black on face and head, at least when breeding;

usually with one or two black or chestnut bands across breast and often with white band across nape. Two moults per cycle: complete post-breeding moult, primaries outwards; and partial pre-breeding moult, which often brings in much brighter breeding plumage; supplemental plumage occurs in at least one species (Eurasian Golden Plover *Pluvialis apricaria*). Down of pebbled pattern (Jehl 1968; Fjeldså 1977, 1988; BWP). Juvenile plumage duller than adults in most species, with pale dorsal scalloping. Adult plumage attained at 1–2 years. Most probably first breed at 1–2 years, maturity perhaps delayed further in some migratory species (e.g. Gréy Plover *Pluvialis squatarola*).

Inhabit open places; when not breeding, many are typically birds of ocean beaches, coastal mudflats and estuaries; others use rivers and freshwater wetlands, often ephemeral; still others characteristic of dry habitats, including gibber plains, grasslands and steppes. Breeding may occur in any of these habitats, or in tundra or high-altitude moorlands. Most species probably migrate to some extent; about 15 species are long-distance transequatorial migrants. Diet consists of terrestrial and coastal invertebrates. When foraging, tend to spread out and feed separately over wide area, rather than feeding in flocks as do many scolopacids. In general, gregarious but less so than many scolopacids. Roost communally. Usually territorial when breeding; some species may defend feeding territories in wintering areas. Various mating systems recorded in different species: monogamy, polyandry (associated with sexual reversals), polygyny and polygamy. While breeding, generally rather aggressive, defending and advertising territories with displays on the ground and in the air, often with butterfly-like flights and song (long melodious trills). Courtship and mating behaviour often complex or stereotyped. Anti-predator strategies, injury-feigning and distraction displays generally elaborate and well developed. Most vocal during breeding season with variety of peeps, trills and mellow or liquid whistles.

Breed seasonally. Nest, a simple scrape on the ground, sparsely lined with plant stems, grasses and other objects; in open, often unvegetated places. Several scrapes may be prepared by male and one then selected by female. Eggs, oval, short oval or even somewhat pyriform; smooth, not glossy; ground-colour, buff, brown or grey, heavily blotched and spotted dark, well camouflaged. Clutch-size, 2–4, often consistently of one size in a species (e.g. two in *C. ruficapillus*). Laying at intervals of 24–60 h. Replacement laying, up to several times. Incubation by both sexes in monogamous species but share varies and is by male alone in Eurasian Dotterel *Eudromias morinellus*, the only plover in which female more brightly coloured than male. Incubation period, 24–31 days. Young hatched in natal down; precocial, nidifugous. Usually tended by both parents but feed themselves from hatching. Fledge in 3 (smaller species) to 5 (larger species) weeks.

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Anarhynchus frontalis **Wrybill**

COLOUR PLATE FACING PAGE 801

Anarhynchus frontalis Quoy & Gaimard, 1830, *Voy. Astrolabe*, *Zool.* 1: 252 — Hauraki Gulf, North Island, New Zealand.

Anarhynchus combines the Greek ἄνω- (upwards and backward) and ῥύγχος (bill), referring to diagnostic twisted bill; *frontalis* is modern Latin, meaning 'fronted' or 'browed'.

OTHER ENGLISH NAMES Wry-billed or Crook-billed Plover, Crockbill, Scissor-bill.

The English name refers to the distinctly bent bill.

MONOTYPIC

FIELD IDENTIFICATION Length 20–21 cm; weight 47–71 g. Small heavy-bodied plover with unique right-hand bend in narrow bill; bill slightly longer than length of head. Short-legged, short-necked appearance, somewhat reminiscent of Ruddy Turnstone *Arenaria interpres*. Combination of uniformly grey upperparts and single black breast-band unlikely to be confused with any other species in NZ. Sexes separable in breeding plumage. Seasonal variation. Juvenile separable.

Description Adult male breeding Head and upperparts, grey, with white supercilium to just behind eyes; white forehead, often flecked grey-brown; narrow black frontal bar between forehead and crown; and, usually, pale areas below and behind eye. In flight, upperparts mostly light-grey, with black outer primaries and narrow white wing-bar, mainly on greater primary coverts, broadening on bases of inner primaries. In fresh plumage, edges of wing-coverts, white. Underparts and underwing, white, except for wide even black breast-band. Bill, black and narrow with tapering tip slightly upturned and bent to right. Iris, dark brown. Legs, fairly short, greenish black or grey-blue. **Adult female breeding** No or very faint black frontal bar; supercilium sometimes not extending past eye; breast-band, narrower, with more ragged lower edge, and duller. **Adult non-breeding** No or very faint frontal bar; supercilium less distinct; no black breast-band, though as plumage wears, grey patches form at sides of breast, which gradually become darker and larger, forming breast-band. **Juvenile** Similar to adult non-breeding; some grey on sides of breast; feathers of upperparts have narrow dark subterminal bands, narrowly fringed white.

Similar species When seen, right-hand bend in bill diagnostic. **Red-capped Plover** *Charadrius ruficapillus* smaller, with rufous nape and, usually, crown. **Double-banded Plover** *Charadrius bicinctus*, smaller, with brown upperparts, pale legs and traces of double breast-band in all plumages.

While breeding, solitary and secretive, with grey plumage blending with shingle. During non-breeding season, highly gregarious, feeding and roosting in large flocks. When in flock with other species, generally stand together on edge. Often with stints and other small charadriids. Breed on braided river beds of central-e. SI; migrating N along coast to mudflats of n. NI estuaries and harbours. Short-legged hurried gait, typical of plovers. Run fast with hunched neck and head tucked-in. Usually stand on one leg to roost. Flight fast and manoeuvrable; in non-breeding season, often in tight whirling flocks, often of hundreds or thousands. Probe and sweep under stones at edges of rivers using curved bill; peck, probe and scythe on mudflats. Shrill call made in flight and as an alarm call; aggressive chirring calls made on breeding grounds.

HABITAT Braided watercourses during breeding season, estuarine and sheltered coastal habitats during non-breeding season. Breed to at least 700 m asl round Cass R.–L. Tekapo (Pierce 1979).

Breed inland, in beds of large braided rivers with large areas of bare shingle and sand, free of weeds and drifts. Prefer large, glacier-fed rivers and high flow-rates during breeding season; and dynamic shingle banks (Turbott 1970; Pierce 1979; Hughey 1985). Less often in smaller rivers with catchments in foothills, less braiding and reduced flows during breeding season; occasionally on lake shores, up to 3 km from rivers (Pierce 1983; Hughey 1985). Nest among large smooth rounded shingles, or in sand (Oliver 1937; Pierce 1979). Before migration, some may congregate at drying ponds after flooding (Pierce 1983).

In non-breeding season, mainly shallow estuaries and sheltered coasts with large tidal mudflats and no cover; very rarely,

mudflats on inland lakes or on ocean beaches (Sibson 1963; Waters 1969); prefer soft silty or muddy substrate; less often sand (Oliver 1937; Urquhart & Sibson 1952; Sibson 1963; Turbott 1970; Owen & Sell 1985). Occasionally in ploughed paddocks, reclaimed saltmarsh or muddy margins of small mountain lakes (tarns) (Urquhart & Sibson 1952; Sibson 1963; Pierce 1979). On arrival near breeding grounds (e.g. L. Tekapo), congregate on shingle, sand or silt deposits at mouth of river, before dispersing upstream (Pierce 1983).

During breeding season, forage in shallow riffles, pools and backwaters, and on shingle banks and at edge of water where debris has collected in riparian habitats (Pierce 1979, 1983; Hughey 1985); occasionally at inland wetlands near usual river-bed habitat (Pierce 1980). When foraging on mudflats, prefer soft mud at edge of receding tide (Sibson 1943; Turbott 1970; Owen & Sell 1985; CSN 6).

Roost on bare or sparsely vegetated shingle banks, shell banks and sandbanks; often near high-water mark; prefer dynamic banks where weeds not established, because stable banks unsuitable when choked with weeds; occasionally roost on sheltered beaches, saltmarsh, or bare patches along saltings above high-water mark (Sibson 1943, 1963).

Nesting and roosting areas, especially in lowlands, sometimes invaded by exotic weeds (e.g. Broom *Cytisus scoparius*, Gorse *Ulex europaeus*, lupin *Lupinus*, willow *Salix*) that render site unsuitable, and may cause declines in local populations (Oliver 1937; Pierce 1979; Hughey 1985). Floods are a major cause of breeding failure, so flood mitigation through dams and irrigation, which level flood-peaks, may be beneficial (Hughey 1985); however, construction of dams destroys some nesting habitat through permanent flooding. Roosting sites threatened by reclamation of saltmarsh; control of water-levels and embankments may be deleterious (Sibson 1963).

DISTRIBUTION AND POPULATION Endemic to NZ. Breed between 43°S and 45°S in Canterbury and n. Otago in many rivers E of Southern Alps.

NI Generally coasts in n. half of NI, N of 38°S. Small numbers regularly reach Far North, but most birds occur Firth of Thames, Manukau and Kaipara Harbours. Often in smaller numbers at other estuaries and harbours in Bay of Plenty and farther N (Sandager 1889; CSN; NZ Atlas). Also Great Barrier I. (Bell 1976; NZ Atlas). Small flocks regularly recorded at scattered sites elsewhere in coastal regions farther S (CSN; NZ Atlas). Rare inland records, presumably on migration: L. Rotorua: single, mid-summer (Sibson 1963), two, 19 Jan. 1952 (CSN 5) 19 Jan. 1958 (Black 1958); 12, L. Hatuna, 5 Apr. 1968 (Waters 1969); inland Taranaki (Hay 1984).

SI Breed Wairau, Awatere, Clarence, Waiiau, Hurunui, Ashley, Waimakariri, Wilberforce, Rakaia, Cameron, Ashburton, Potts, Rangitata, Clyde, Havelock, Macauley, Godley, Cass, Tasman, Edwards, Tekapo, Pukaki, Dobson, Hopkins, Ohau, Ahuriri, Hakataramea, Waitaki, Hunter, Makaroro, Matukituki, Shotover and Clutha Rs and L. Ellesmere, Washdyke Lagoon and L. Wainono (Child 1973; Hay 1984; Hughey 1985, 1989; Bomford 1988; Falla *et al.* 1981; Oliver). Post-breeding flocks on e. coast, between n. Pegasus Bay and L. Wainono. Infrequent at Farewell Spit and Tasman Bay, probably on passage. Rarely recorded on W. Coast, e.g. Greymouth, Crowaiti Estuary (Grant 1967; CSN 35, 36). S of breeding range, small numbers recorded annually round Invercargill (Sutton 1968; Falla *et al.* 1981; CSN). Vagrants recorded: five, Inch Clutha, 5 Oct. 1988 (CSN 37); five, Stewart I., 18 Apr. 1974 (CSN 21); Eglinton Valley, Fiordland, 21 Nov. 1983 (Morrison & Morrison 1985); mouth of Upukurora R.,

Fiordland, singles, 10 Nov. 1985 (CSN 34), 23 Oct. 1987 (CSN 36).

Populations In late 1970s, total estimated between 5000 and 7000 birds (Hay 1979), with a mean of 5140 between 1975 and 1980 (Hay 1984); in 1961–62, c. 5000 (Sibson 1963). Average number of birds/ha during winter at Firth of Thames and Manukau Harbour was 0.39 and 0.06 (Veitch 1978). In breeding range, 1000–1500 breeding birds in Rakaia R. (O'Donnell & Moore 1983); c. 100 in Ahuriri R. (Robertson *et al.* 1983); and c. 100 in Cass R. (Pierce 1983).

Till 1940s, birds shot for sport (Veitch 1978). After shooting was stopped in 1940s, population expanded till c. 1960; by early 1960s, population had stabilized (Veitch 1978; Hughey 1985). Entire population may be at risk if breeding sites on braided rivers in Canterbury and Mackenzie Basin are developed for hydro-electric schemes (Hughey 1985).

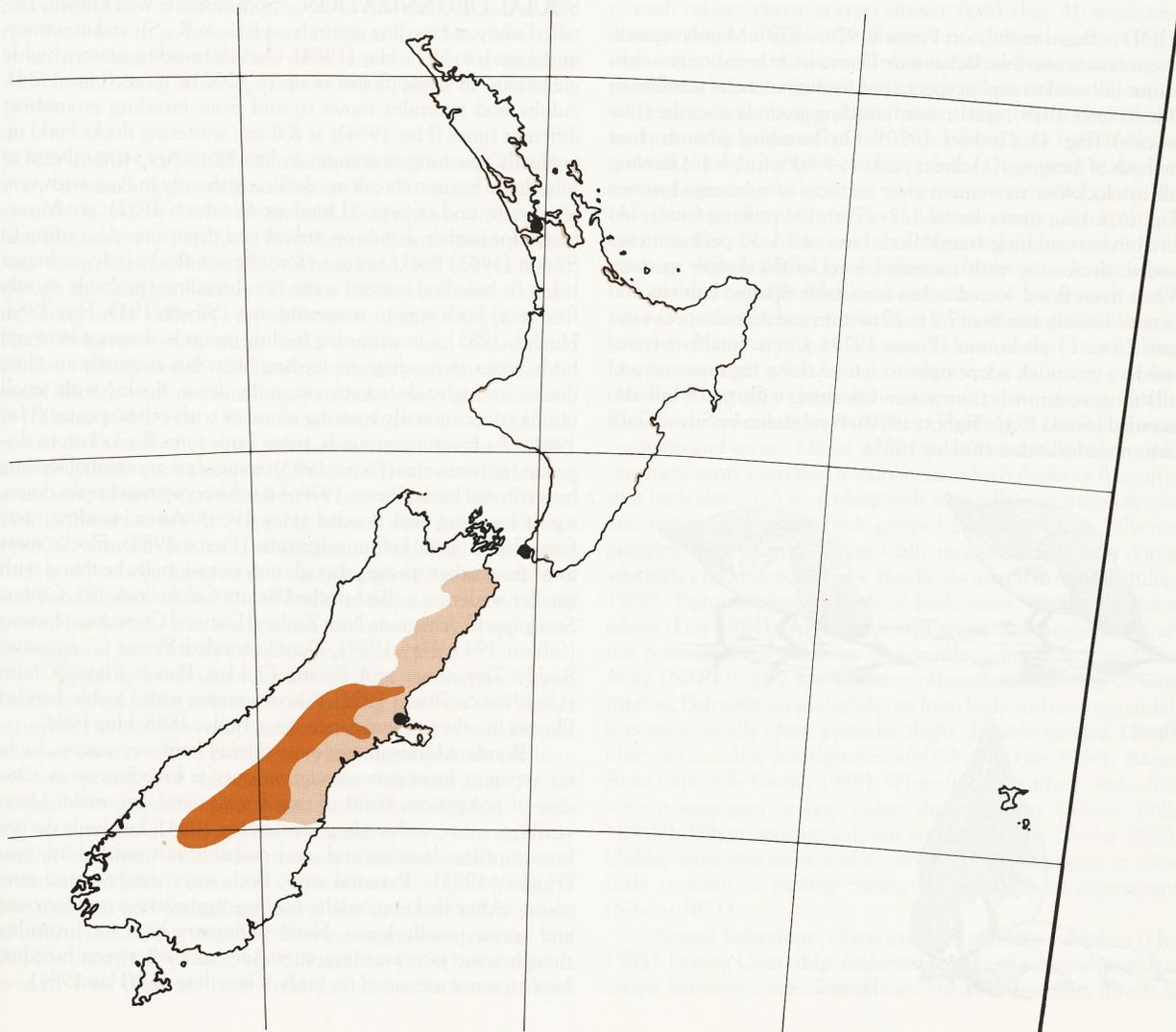
MOVEMENTS Migratory; breed central-e. SI, moving N to harbours of n. NI in non-breeding season.

Departure Stay on river for short period after breeding. In Cass R. Valley, leave late Dec. to early Feb. Adults and juveniles move N at different times, with juveniles seen in N well before end of breeding; juveniles from first nests leave before parents finish nesting for second time. Post-breeding flocks of 30 adults and juveniles at L. Ellesmere until 19 Feb. and up to 25 in Jan.–

Feb. at L. Tekapo, with a few remaining till about Mar., depending on availability of food (Pierce 1980). Migration mainly coastal, up e. coast of SI and w. coast of NI with few reports from W. Coast, SI; rarely inland (see Distribution; Grant 1967; CSN). Generally thought to travel directly between breeding and wintering sites (Hay 1984), but will stop off on way, e.g. Farewell Spit (Dennison & Robertson 1979); also two banding records: adult recorded Auckland on 6 Feb., Nelson on 15 Aug. and on Rakaia R. on 18 Aug.; and juvenile, banded Rakaia R., last seen on 15 Nov., seen L. Onoke, Wairarapa, 27 Dec.

Non-breeding In n. NI, with maximum numbers May–July (Veitch 1978). First juveniles arrive late Dec. to early Jan. Some unsuccessful adults may arrive from early Jan. with most arriving mid-Jan. to Feb. (Hay 1984). No correlation between sites of breeding and wintering, but high fidelity to roosting and wintering sites among adults. Juveniles inclined to be transient, but once settled at one wintering and roosting site, remain faithful to it (Hay 1984; Davies 1991). Birds very rarely over-winter at breeding sites (Pierce 1983). Some reverse migration to estuaries in S (Sutton 1968; Morrison & Morrison 1985; CSN). Some unusual records may be juveniles that were late leaving (Hay 1984).

Return About 90% leave n. NI harbours in Aug.; most remaining birds, thought to be second-year non-breeders, leave midway through breeding season (Hay 1983; Hughey 1985);



banding evidence suggests many first-year birds return to breeding grounds. Return indirect, with stops along way (Sagar 1976; Dennison & Robertson 1979; Pierce 1980; CSN). In Cass R. Valley, birds begin arriving second week of Aug. with most late Aug.–Sept. Early arrivals congregate at river mouth, but by mid-Sept. disperse upstream (Pierce 1983).

Breeding Mid-Sept. to Jan. Over-summering birds in n. NI are first- and second-year birds and some adults (Hay 1984), together making up less than 4% of wintering population (Veitch 1978). Fewer birds over-summer in years after spring floods that may seriously reduce breeding success, which suggests that most birds that over-summer are first-year birds (Hughey 1985). Adults generally return to within 500 m of area of river bed occupied previous season. Philopatry among immatures high, but some evidence of wandering. Returning immatures arrive at breeding site later, usually well after start of breeding (Hay 1984).

Banding Adult banded Miranda, 7 June 1980 recaptured 20 Apr. 1991, 10 years 10 months later, same site. Breeding bird, banded Lower Rakaia R., Sept. 1986, recaptured 19 Feb. 1988. Breeding bird, banded L. Tekapo, Oct. 1986, recaptured Kaipara Harbour, 1988 and 1991, 600–800 km distant (Davies 1991). Juvenile banded Rakaia R., sighted at Tabora, Kaipara Harbour; at Paua, Parengarenga Harbour; at Miranda, Firth of Thames; at Favona, Manukau Harbour and Miranda over its first 2 years; it then wintered at Miranda for next 3 years (Hay 1984).

FOOD Based mainly on Pierce (1976, 1979). Mainly aquatic invertebrates; also fish. **Behaviour** Diurnal. On breeding grounds, unique bill used to exploit specialized feeding niche of mayflies in riffles (Pierce 1979), and on non-breeding grounds as scythe (like avocets) (Fig. 1) (Turbott 1970). On breeding grounds, four methods of foraging: (1) direct pecks (54–60% freq.); (2) moving bill in clockwise movement over surfaces of submerged stones (Fig. 2), taking insect larvae (22–27%); (3) probing (rare); (4) aerial insect-catching (rare). Peck rates of 13–30 pecks/min recorded, decreasing with increased level of floodwater in river. When rivers flood, forced to less favourable riparian habitats and increase feeding area from 7.2 to 20 m²/min and decrease peck rates from 26 to 13 pecks/min (Pierce 1979). On n. mudflats (non-breeding grounds), adopt right-to-left scything (against curve of bill) to sieve animals from water. Gleaning with tip of bill also recorded (Stead 1932; Turbott 1970). Food stolen by Silver Gulls *Larus novaehollandiae* (Keeley 1985).

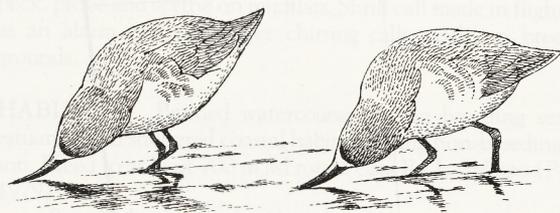


Figure 1

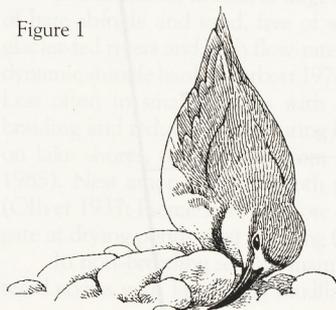


Figure 2

Adult Breeding On Rakaia and Cass Rs (inference from searches of foraging area, Pierce 1979): Platyhelminthes: *Dugesia montana*. Annelids: tubificids; oligochaetes: *Eiseniella teraedra*; leeches *Glossiphonia heterociliata*. Molluscs: gastropods: *Potomopyrgus antipodarum*. Arachnids: mites; spiders. Insects: Ephemeroptera: Leptophlebiidae: *Deleatidium* eggs, larv., sub-imagines and ads; Siphonuridae: *Nesamaletus* larv.; Dermaptera: Formicidae: *Siphicula auricularia*; Plecoptera: Eusteniidae: *Stenoperla prasina* larv.; Gripopterygidae: *Aucklandobius* larv.; Hemiptera: Saldidae; Pentatomidae; Cicadidae; Hymenoptera: Formicidae; Lepidoptera; Megaloptera: Corydalidae: *Archichauliodes diversum* larv.; Coleoptera: Carabidae; Elmidae: *Hydora* ad.; Trichoptera: Leptoceridae: larv.; Sericostomatidae: larv.; Hydrobiosinae: larv. and pupae; Hydropsychidae: larv. and pupae; Diptera: Simuliidae: *Austrosimulium* larv.; Therevidae: *Anabarhynchus*; Tachinidae; Muscidae; Tipulidae: pupae; Hymenoptera: Pompilidae: *Cryptocheilus* ad. Fish: *Gobiomorphus cotidianus* eggs, ads; *G. breviceps* ads.

Other records Aquatic insects (Potts 1871; Buller 1882, 1888; Soper 1963, 1972). **Non-breeding** Plant matter: Poaceae (Burton 1972). Marine-life (Buller 1882). Annelids (Turbott 1970; Keeley 1985); polychaetes (Burton 1972). Molluscs: small bivalves (NZRD). Crustaceans (Buller 1882). Insects: Coleoptera: Staphylinidae; Diptera: larv. Small stones (Burton 1972).

SOCIAL ORGANIZATION Some aspects well known. Detailed study at breeding grounds on Rakaia R., SI, and at wintering grounds in NI by Hay (1984). Outside breeding season, highly gregarious; in dense flocks of up to 4000 or more (Hay 1984). Adults and juveniles move to and from breeding grounds at different times (Hay 1984); at Kakara, wintering flocks build up gradually, reaching maximum in late Mar.–Apr.; toward end of July, flocks begin to break up, declining sharply in Aug. with very few left by end of Sept. (Urquhart & Sibson 1952); see Movements for further details on arrival and departure. According to Sibson (1963) flocks unite to form largest flocks only on bigger tides. In breeding season, some non-breeding (probably mostly first-year) birds stay in wintering sites (Sibson 1943; Hay 1984; Hughey 1985). On wintering feeding grounds, distance between birds varies depending on feeding area, but normally in close flocks; at high-tide roosts, occur in dense flocks, with small numbers occasionally roosting alone or with other species (Hay 1984). At breeding grounds, some birds form flocks before dispersing to territories (Pierce 1983); some semi-communal feeding by territorial birds (Pierce 1976a) if territory system breaks down, e.g. if breeding area flooded (Hay 1984). After breeding, may form flocks again before migration (Pierce 1983). Flocks roost away from other species, though may occasionally be found with smaller waders, e.g. Red-necked Stints *Calidris ruficollis*, Curlew Sandpiper *C. ferruginea*, New Zealand Dotterel *Charadrius obscurus* (Sibson 1943; Hay 1984), Double-banded Plover *C. bicinctus*, Ruddy Turnstone, and Pacific Golden Plover *Pluvialis fulva* (Urquhart & Sibson 1952). Also associates with Double-banded Plovers in other circumstances (e.g. Buller 1888; Hay 1984).

Bonds Monogamous; mate fidelity between seasons, high; no apparent intra-pair association outside breeding areas. One case of polygynous bond of two females and one male. Many yearlings move to breeding areas (Hay 1984), but birds do not breed until at least second, and probably not until third, year (Hughey 1985). **Parental care** Both sexes incubate and tend young. After fledging, adults become aggressive towards young and young usually leave. Natal philopatry high for juveniles, though some non-breeding immatures move between breeding localities; not measured for birds of breeding age (Hay 1984).

Breeding dispersion Single pairs breed in territories; nesting site or area often traditional. Usually well-spaced along river beds, even where territories contiguous. Density varies much (Hay 1984); occasionally nests as close as 40 m; usually 400 m or more apart (Soper 1972). **Territories** Maintained constantly during breeding. Nest-area normally vigorously defended; immatures often, and neighbours occasionally, trespass. If pair remains together, normally holds territory in same area each year; birds whose mates fail to return usually move territories. Mean size, 5.5 ha. Hay (1984) noted decrease in size over 3 years with corresponding increase in breeding density. On Rakaia R., breeding pairs mostly forage in territories centred round nests, but sometimes considerable overlap between pairs; some birds forage in non-defended areas away from territories (Hay 1984); on Cass R., often flew several hundred metres to forage semi-communally off territory (Pierce 1976a). Access to edge of stream appears to be important aspect of territories. In some cases, territory also defended against Double-banded Plovers who often have to move across Wrybill areas to forage at edges of stream (Hay 1984).

Roosting Outside breeding season roost in large flocks at traditional sites on edges of harbours and inlets (Sibson 1943), usually not far from water-line. Daily routine of winter seems to start only after enough birds have arrived in area; early arrivals may rest at sites other than traditional high-tide roosts. In winter spend much time resting or asleep; timing associated with tide but may return to roost-site during day while tide still low, and usually not in a hurry to start feeding after high tide (Sibson 1943). To roost, tuck head in scapulars; often rest on one leg and hop without untucking other leg (Sibson 1943; Falla *et al.* 1970; Hay 1984).

SOCIAL BEHAVIOUR Some aspects well known. Detailed study at breeding grounds on Rakaia R., SI, and at wintering grounds in NI by Hay (1984), and observations during early breeding season by Phillips (1980). Extraordinarily tame, particularly when nesting (Buller 1888; Sibson 1943, 1963; Soper 1963), though shy during courtship (Phillips 1980). Has habit of standing completely still, so very difficult to detect (Soper 1963). **Flock behaviour** On wing, flocks compact and co-ordinated (Buller 1888; Sibson 1943). In winter, flocks perform spectacular aerial displays with much calling, particularly just before moving S (Sibson 1943; Hay 1984); aerial displays seen at high-tide roosts, and usually just after tide has turned (Chambers 1989). Roosting flocks pack closely together, often with each bird facing same way; when disturbed, members may chatter softly (Sibson 1943; Chambers 1989). Some behaviours described by Phillips (1980). **NORMAL POSTURE:** when resting, walking, or running, body c. 45° above horizontal, with bill slightly below horizontal and head slightly above line of back; at faster paces tend to tip toward horizontal. **BOB:** seems much like other plovers; appears to be backward jerk of body round a pivot at hip joint.

Agonistic behaviour Common within roosting flocks, particularly soon after arriving from feeding grounds and before returning; ranges from simple adjustments of individual distance to overt attacks where bird runs in horizontal posture (without obvious spreading of feathers) at another bird and pecks it; run normally accompanied by aggressive call (Hay 1984). At breeding sites, territorial pairs aggressive towards conspecifics and show similar territorial behaviour towards Double-banded Plovers; conspecific conflicts often involve non-breeding birds (young of previous year and fledgelings) being displaced by resident adults (Phillips 1980; Hay 1984). Following aggressive postures and displays described by Phillips (1980) and Hay (1984): **HORIZONTAL SPREAD (HS)** (Fig. 3): body held just above horizontal, back

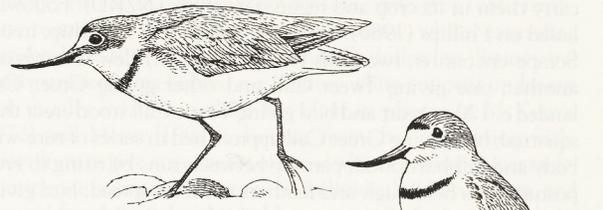


Figure 3 Horizontal Spread Posture (HS)

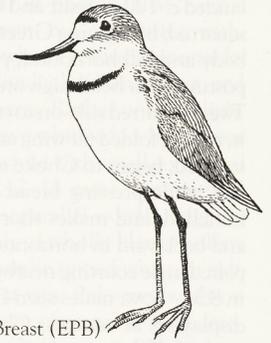


Figure 4 Erect Puffed Breast (EPB)

rounded, head withdrawn, and bill horizontal; feathers of breast and belly sleeked and those of flanks spread laterally; sometimes sleeking reduced or does not occur and ventral feathers fluffed instead. In more intense version, head lowered farther, throat bulged downward, and spread tail depressed; in most extreme form aggressor runs towards recipient, repeating agonistic call; at apparently lower levels of motivation, given quietly by birds close to each other. **ERECT PUFFED BREAST (EPB)** (Fig. 4): sometimes during pauses in aggressive chases or on alighting from flight, male assumes erect stance with breast-feathers spread at margins, presenting other birds with broader than normal frontal outline and particularly obvious white breast; breast often sleeked, and feathers of flanks spread laterally; head above back but withdrawn and bill below horizontal, resting on breast. **PARALLEL RUNS:** long curving runs by two birds (of either sex) on parallel paths, frequently often adjacent territory holders moving c. 1 m apart; run either in HS, sometimes with tail depressed and spread, or with plumage slightly fluffed, giving them cylindrical look; rise at end of each run to EPB. Usually, run continues for several metres before one bird reverses direction and other follows, distance between them varying in 'see-saw' fashion as they move along. Display sequence often lasts several minutes, ending in one bird chasing other off, in both moving apart, or in fighting. Parallel Runs occur repeatedly at some sites. **Fighting** At breeding areas, common and severe. Often, while two birds running side by side, one turns away then flies at opponent, which ducks or flies up so that birds rise c. 0.5 m, flailing with feet, bills, and wings; several encounters seen where birds grasped each other with bills and grappled for 2–3 min. Tweet Calls most common calls during agonistic encounters; Whee-Cheedle also given in fights (Phillips 1980). Fighting seen in birds of both sexes, usually territorial adults (Hay 1984). **Appeasement, Escape** Submissive birds, often non-territorial yearlings or juveniles, may crouch and turn away (NZRD); give few postures other than Bobbing; at most intense, Bob with wings slightly out from body and neck extended, a posture which often precedes flight. Double-banded Plovers observed avoiding feeding territorial Wrybill (Hay 1984). **Alarm** Reluctant to fly (Buller 1888). When flock disturbed, birds often remain stationary or hop rather than fly away (Sibson 1943; NZRD). When approached, run without calling (Buller 1888). Unlike some species of waders, flocks of Wrybills seem to show little concern at passing Swamp Harriers *Circus approximans* (Sibson 1943).

Sexual behaviour Often involves aggressive displays (Hay 1984). During **Courtship**, male said to hollow out sandy patch or scrape between stones with breast, then flick pebbles into it or

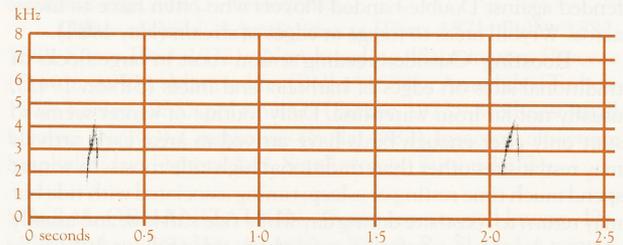
carry them in its crop and regurgitate them (NZRD). Following based on Phillips (1980): Scrape important in Courtship; in one Scrape-encounter, two birds (sexes unknown) flew towards one another, one giving Tweet Call and other giving Greet Call; landed c. 100 m apart and bird giving Tweet Call stood erect then squatted; bird giving Greet Call approached in series of runs with body and bill horizontal, pausing between runs by rising to erect posture with head high and feathers of breast spread; bird giving Tweet squatted side-on to oncoming bird and tilted dorsum toward it, raising folded far wing and Bowing; approaching bird passed by, stopped, began to Choke and to Scrape, alternately kicking with feet while pressing breast down in hollow. **CHOKE:** bird stands hunched, and makes short darting movements of head forward and backward in horizontal plane; typically in unpaired or newly paired male courting nearby female; one observation of ten Chokes in 8.5 s. **BOW:** males seen Bowing between series of Chokes while displaying at scrapes; Choking bird stops, dips head forward, points bill down and spreads tail. **TILT AND WING-RAISE:** scrape-exchange encounters seen where Scraping bird stood and tilted body so that dorsum turned to approaching bird; sometimes far wing raised (with wrist folded) and tail briefly spread. Tilting bird also Bows, pointing bill down and tipping slightly forward. **LEADING:** when female approaches and passes Scraping male, latter usually leaves scrape and glides in long smooth run past her then resumes Choking or Scraping or both in front of her; when Leading, male holds back c. 45° from horizontal with head forward and low, and tail depressed and spread. **Greeting** Pairs keep up series of low calls while feeding and moving about (Phillips 1980). During incubation one sitting bird, when approached by mate, assumed hunched attitude, and mate turned and went away (Soper 1963). **Copulation** Before mating, male runs with body horizontal or **PARADE-MARCHES** (Phillips 1980): gives exaggerated high-steps in erect stance with neck extended vertically, and bill horizontal or slightly below. If female receptive, she crouches (NZRD). In two observed copulations, body-plumage of both sexes relaxed or slightly fluffed; females crouched and held heads low but kept bills nearly horizontal; males did not grasp females' nape until moment of cloacal contact; one fell over on his back after copulation but other landed on his feet; as males fell off, pulled females slightly back; one male rapidly called Wheet during treading. After copulation, both birds stood in normal postures with heads hunched into shoulders and plumage slightly sleeked. Both times female ran to scrape in horizontal hunched posture and Scraped (Phillips 1980).

Relations within family group During incubation, adults not far from each other (Oliver). After hatching, lead young to nearby feeding area (NZRD). Young forage for themselves (Hay 1984). Swim well when only 1–2 days old (Oliver). **Anti-predator strategies of young** Freeze in response to adult calls (NZRD); if 'molested', run, giving piping alarm call; if pressed, take to water (Buller 1888). **Parental anti-predator strategies** Soper (1963) suggested male occasionally ordered female back to nest by running up to female and assuming erect stance. When aerial predators such as Kelp Gulls *Larus dominicanus* nearby, if adult brooding chicks, it quickly moves away from young (NZRD). **Distraction Displays:** during incubation partly extend wings, hold head low with bill just above ground, and give low purring sound (Oliver). In another display, lift and spread one or both wings, and fan and twist tail to one side; face, and may run toward, observer (Soper 1963).

VOICE Quite well known. Account based on Sibson (1943) and Phillips (1980); sonagrams in latter. Variety of calls described; synthesis difficult and classification given somewhat

speculative. Some calls similar to those of Double-banded Plover.

Adult COURTSHIP CALLS: *tweet* or *grtreet*, repeated before Bow, Scrape, Choke Display (Phillips 1980). Probably corresponds to *zwee-zwee-zweep*, almost a trill, thought to be beginning of courtship song (Sibson 1943). Subdued bubbling trill *quit-wiirr*, *quit-wiirr*, *quit-wiirr*, repeated three or four times, accompanied chases denoting some sexual excitement (Sibson 1943). Also rapid *wheet* uttered at c. 4/s, by male treading female during copulation (Phillips 1980). **THREAT CALLS:** rapid buzzy *towheetowheetowheet* (Phillips 1980), probably corresponds to *wee-ti-ti* of Sibson (1943); rhythmical chirring when challenging aggressor (NZRD). *Tweet* the most common call during agonistic encounters (Phillips 1980). **ALARM CALLS:** shrill *weet* or *peep* from single birds flying overhead after being disturbed at feeding grounds (Sibson 1943). *Wheet* (sonagram A), most common call, sometimes harsher and sounding more like *greet*, corresponds to *tic* and *tweet* of Double-banded Plover (Phillips 1980). *Skürr-skürr*, apparently in anger



A. L. McPherson; Upper Rakaia R., SI, NZ, Oct. 1977; P104

(Sibson 1943), and low purring (Oliver); possibly correspond to *weer* of Double-banded Plover. When flock excited or disturbed at high-tide roost, or until return and settle after flight, utter thin soft clear-cut chattering *wik-a-wik* or *chitter-chitter* (Sibson 1943); these probably describe sound of many birds calling. **FLIGHT CALL:** short clear *weet* as in alarm calls (NZRD). **CONTACT CALLS:** loud *whip* and *whee-whip* calls between members of pair feeding; low contact calls also given (Phillips 1980). **Other calls** Calls described as *gwheet* and *quoit*; sonagrams in Phillips (1980) but circumstances of use not stated.

Young Harsh high distress calls from chicks when handled; short high *peep* from fledgelings and juveniles, especially in flight (Buller 1888).

BREEDING Detailed study by Hay (1984), on which account based unless otherwise referenced, and anecdotal information in literature. Monogamous; one instance of polygyny.

Season First clutches laid from late Aug. or early Sept. to late Oct., occasionally mid-Nov.; re-laying after loss, from mid-Sept. to early Dec.; second clutches, late Oct. to late Dec. (Hay 1984; Oliver).



Site On braided streams, on shingle in river beds, not more than 250 m from running water; on high points on banks of shingle free of vegetation, spits or islands above fluctuating river-levels; usually located where individual stones 100–200 mm in diameter; often against protecting stone or piece of wood (Oliver 1937; Hay 1984; Bomford 1988; Davies 1991). High site-fidelity; pairs often return to within 500 m of previous year's site, sometimes using same scrape. Occasionally as close as 40 m from conspecifics but usually several hundred metres apart (NZRD). Nest in same sites as Double-banded Plovers.

Nest, Materials Scratching in sand, occasionally with a few small pebbles round edge (Oliver 1937); shallow scrape lined with several hundred small (less than 5 mm diameter) pebbles. During courtship, male hollows out sandy patch between two stones with his breast; flicks pebbles into it or said to carry them in his crop and regurgitate them (NZRD). **MEASUREMENTS:** diameter, generally 60–80 mm.

Eggs Pyriform; pale grey, faintly tinged blue or green, closely and evenly covered with minute dark and pale blotches, spots and lines (Oliver); occasionally brown because heavily blotched (NZRD). **MEASUREMENTS:** three eggs: 32.5 x 25.8, 33.8 x 25.2, 35 x 26.5 (Oliver); average, 35.2 x 26.4 (n=49). **WEIGHT:** 11.4 g (1.7; 49).

Clutch-size Invariably two eggs per clutch; possibly two instances of three eggs (Oliver 1937). Average, 1.95 (0.22; 115): C/1 x 6, C/2 x 109. Two clutches of four eggs resulted from two females laying in one nest, and two clutches apparently laid in same nest 14 days apart.

Laying Interval at one nest, at least 48 h, less in others. Usually re-lay after failure, almost immediately or not for several weeks; can raise two broods per season.

Incubation Both sexes incubate, female more than male; begins at or just before second egg laid (Oliver 1937; Hay 1984; NZRD). **INCUBATION PERIOD:** for three clutches: 30, 30 and 36 days. Infertile egg incubated for 54 days before nest destroyed, another for at least 62 days. Hatching synchronic, or up to 36 h apart.

Young Precocial, nidifugous. First chick remains in nest until second hatches; both led to suitable feeding area; able to swim well when 1–2 days old (Oliver). **Growth** Estimated from growth-curves in Hay (1984): weight (g), at 5, 10, 15, 20, 25 and 30 days, respectively: 10, 13, 26, 34 and 37; bill-length (mm), at hatching, 5, 10, 15, 20, 25 and 30 days, respectively: 9.4, 11.4, 13.4, 15.4, 17.4, 19.4 and 21.4. Tarsus (mm), from Fig. 6.8 in Hay (1984): at hatching, 21.2 (20.4–22; 4); 5 days, 22.9 (20.4–24.8; 6); 10 days, 21.1 (20.6–22; 3); 15 days, 24.8 (23.3–27.4; 4); 20 days, 27.0 (25.6–27.8; 4); 25 days, 27.2 (26.0–27.9; 4); 30 days, 30.5 (n=1). Both adults guard young; if intruder approaches, chicks freeze in response to loud adult calls (Oliver; NZRD).

Fledging to maturity **FLEDGING PERIOD:** three determinations: 35, 36 and 37 days. First breed in second or (more likely) third summer (Hay 1984; Hughey 1985).

Success From 254 eggs, 196 (77%) hatched, minimum 168 (66%) young survived first week, and 96 (38%) fledged; 0.79 young fledged per pair. Of eggs that failed: 25 (9.8%) flooded; 11 (4.3%) infertile; nine (3.5%) abandoned; eight (3.1%) broken by adults, died at hatching or through disturbance by observer; two (0.8%) taken by predators. A clutch apparently deserted after snowstorm. Average life expectancy, 5.4 years.

PLUMAGES Prepared by D.J.James. Hatch in natal down. Begin pre-juvenile moult at unknown age. Partial post-juvenile moult during first autumn introduces first immature; followed in first spring by partial pre-breeding moult to second immature. Each cycle thereafter, complete post-breeding moult in autumn and partial pre-breeding moult in spring produce alternating non-breeding and breeding plumages with distinct change in appearance.

Adult male breeding (Definitive alternate). Plumage appears worn toward end of breeding season and on arrival at wintering grounds (Sibson 1943). **Head and neck** Crown, nape, hindneck, and lores and ear-coverts, light grey (c85); concealed plumulaceous bases, grey (84). Narrow black frontal band between crown and forehead, apparently always sharp in fresh

plumage. Forehead, white except for some pale-grey (c86) feathering round base of bill. Supercilium, narrow, white, extending from forehead to just behind eye; generally duller, less distinct and faintly streaked grey behind eye. Diffuse white crescent under eye (not usually evident in skins but clear in photos in McKenzie [1972] and Moon [1992]); disjunct from, but combining with, supercilium to give appearance of broad white eye-ring or spectacle; prominence seems to vary between individuals. Chin, throat, and side and front of neck, white. **Upperparts** Rather uniform light grey (c85). Lateral upper tail-coverts have white edges but appear uniform in flight. **Underparts** Mostly white with small concealed grey (84) bases to feathers. Narrow (12–15 mm), symmetrical black breast-band, generally sharp, almost parallel-sided but slightly narrower towards centre; consists mostly of wholly black feathers but varies, and those at lower margin can be tipped white; at side of breast, feathers flecked with white at tips. Pale-grey wash on lower side of breast (where visible in front of carpal at rest), fore-flanks and axillary coverts; composed of light-grey (c85) feathers with white fringes. **Uppertail** Generally grey in centre, fading to slightly paler outwards with indistinct white tip. T1–t2, grey (c84); t3, light grey (c85) with white fringe at tips; t4–t5, light grey (c85) with white tips and thin white edges; t6, pale grey (c86) with broad white tip, thin white edges and narrow indistinct white shaft-streak. **Undertail** Pale grey (c86) with indistinct white tip. **Upperwing** Primaries, grey-black (82), with very slight brown tinge on outer webs, grading to faintly darker at tips; inner webs, similar at tips but grade to light brownish-grey (light 80) over most of web and paler greyish at base and inner edge; shafts, white; p2–p6 have broad white panel on basal third of inner webs forming short, broad outer wing-bar. Alula and primary coverts, grey-black (c82); lesser primary coverts have white tips, which at rest may show as a little white mottling at bend of wing if scapulars held tightly folded. Secondaries, light grey (c85) with thin white tips. Tertiaries and secondary coverts, light grey (c85); median and greater coverts have thin white tips (though these often worn), which form narrow white wing-bar across inner wing. Marginal coverts, light brownish-grey (light 80) broadly tipped white. **Underwing** Remiges, grey (c84), grading to light grey (85) or pale grey (86) along inner edge. Outer four primaries grade to dark grey (83) at tips. Greater primary coverts, pale grey (c86) with narrow white fringes, forming very faint crescent at base of primaries. Rest of coverts and subhumeral, white.

Adult female breeding As male except always lack sharp black frontal band; some entirely lack black on forecrown but others probably show some black mottling; degree of overlap, if any, between sexes, unknown and confounded by unreliable sexing of skins. Breast-band said to be narrower and less sharp on average (Oliver) though distinction very slight and may not be possible (Hay 1984; skins).

Adult non-breeding (Definitive basic). Sexes similar. Similar to breeding plumages, but differ by: **Head and neck** No black frontal band. **Underparts** Between Feb. and late Apr. or early May, no breast-band; by late May, usually show conspicuous traces of black mottling at sides of breast, forming partial band; formed by black or grey-black (82) feathers with broad white tips and concealed grey (84) bases. During June, breast-bands vary, but by mid-June, all show partial or complete breast-bands of breeding plumage. Most birds have complete bands by late July (Sibson 1943; skins). **Wing** Inner primaries have thin white tips that are quickly lost, before moult to breeding plumage.

Downy young General appearance of head and upperbody, pale and uniform (Jehl 1968; skins), off-white to pale grey (86) with fine, rather indistinct grey-black (82) flecking. Narrow grey-black (82) loreal stripe (not extending quite to bill) forks round

eye almost encircling it, remaining broken posteriorly. Underparts, white. Generally, slightly paler than adult.

Juvenile Very similar to adult non-breeding. No fresh skins examined; photos by B. Chudleigh (of birds in various stages of post-juvenile moult but all retaining some down) show feathers of upperparts and perhaps head with very narrow speckled whitish fringes and possibly narrow faint dark-grey (83) submarginal bars when fresh; one photo shows trace of very narrow but complete breast-band. Hay (1984) noted sole distinguishing feature of juveniles on breeding grounds was dark-grey mottling on forecrown between white forehead and grey crown, but this lost quickly after migration. Worn skins from NI after migration appear more uniform, with no evidence of submarginal marks, breast-band or forecrown mottling but with thin white fringes on crown, lower scapulars, and median secondary coverts that are distinct in early summer but subtle by late summer. Primaries, sometimes slightly narrower and more pointed than those of adults.

First immature (First basic). Extremely similar to adult non-breeding. Faint grey breast-band may be present, comprising one or a few rows of dark-grey (83) feathers, broadly tipped white. Juvenile remiges retained; should be worn in autumn, when plumage of adults is fresh or moulting. Do not retain white-fringed juvenile inner median secondary coverts (Davies 1991; *contra* Hayman *et al.* 1986).

Second immature (First alternate). Probably similar to immature non-breeding. Details of breast-bands and frontal bands, poorly known. Sibson (1943) reported that birds assumed to be immatures spending summer on NI lacked breast-bands or had scarcely to moderately developed ones with some individual variation; conversely, Oliver implied that young attain breast-bands during first spring; Hay (1984) stated that indistinguishable from adult breeding except that several males did not acquire frontal bands.

BARE PARTS Based on photos (McKenzie 1972; Pierce 1989; Chambers 1990; Moon 1992; NZRD; unpubl.: B. Chudleigh) and specimen record cards (NMNZ). **Adult** Bill, black. Orbital ring, narrow, off-white. Iris, dark brown. Legs, black with dark olive or green tinge. **Downy young** Bill, black. Orbital ring, off-white. Iris, black-brown or black. Legs, dark grey-green, or grey-olive. **Juvenile** Bill, black. Iris, dark brown. Legs, dark olive-grey.

MOULTS Based on banding data from Firth of Thames, NI (A. Reigen; S. Davies) and skins. **Adult post-breeding** (Pre-basic). Complete. Primaries, outwards. Moult on wintering grounds, which is atypical for short-distance migrant plovers (Snow 1967); moult of flight-feathers begins immediately after migration; breast- and frontal bands begin to fade and assumed to begin moulting in Jan. on breeding grounds (Hay 1984). Initially, four inner primaries active at once but in latter stages only one or two active. Primary moult-score (PMS) data from Firth of Thames (sexes combined): 31 Jan. 87, 22.5 (3–31; 4); 3 Feb. 91, 21.5 (15–34; 14); 17 Mar. 91, 44.5 (36–49; 24); 5 Apr. 92, 48 (35–50; 56). On 5 Apr. 1992, 14% had finished moult (PMS 50). On 20 Apr. 1991, most had finished but some had PMS 49. Four individuals trapped 3 Feb. and 17 Mar. showed median advance in PMS of 19. Of skins from Jan.–Apr., eight in primary-moult and two (both Mar.) finished; no skins Nov., Dec.; all 23 skins May–Oct., not in primary-moult. Sexes close in timing but males possibly about 3 weeks ahead (skins). Data do not give accurate indication of starting date but suggest mid-Dec. to early Jan. Duration of primary-moult roughly estimated at 100 days. Secondaries, from several centres more or less concurrently with each other; tentatively suggested from six records, inwards from s1–s4, outwards

from s8–s5, inwards from s8 and perhaps s11; begin slightly after primaries (sometimes possibly earlier) and finish at similar time. Tail, centrifugal, mostly a pair at a time, but possibly t2 and t3 together; roughly coincides with moult of primaries. **Adult pre-breeding** Partial moult of all head and body; flight-feathers retained; fate of wing-coverts unknown. Four skins from mid-Aug. in moult and two not so (no others examined critically). Sibson (1943) described development of breeding plumage (from field observations) from late May. to late July. **Pre-juvenile** Fledging period c. 36 days. **Post-juvenile** (First pre-basic). Partial. All head and body. Remiges, greater coverts and rectrices retained. Hayman *et al.* (1986) suggest inner median coverts sometimes retained. **Immature pre-breeding** (First pre-alternate; immatures do not breed). Partial moult of head and body. Timing similar to adult pre-breeding but details not known. **Immature post-breeding** First complete moult, in summer and autumn of second year, beginning when c. 1 year old. Timing probably similar to adults but details not known.

MEASUREMENTS NI and SI, skins (AWMM, CM, NMNZ): (1) adults (sexed by labels and confirmed by patterning of head when possible); (2) juveniles and immatures (sexing based on labels). (3) NI and SI, live; wing, minimum chord (Hay 1984).

	MALES	FEMALES	
WING	(1) 122.5 (2.33; 118–126; 13) (2) 120.0 (3.24; 116–125; 5) (3) 119.3 (2.0; 39)	123.0 (2.04; 121–128; 12) 117.0 (1.85; 114–120; 8) 119 (2.3; 67)	ns ns ns
8TH P	(1) 79.3 (4.67; 73–88; 14) (2) 77.5 (2.65; 75–81; 4)	79.6 (4.08; 74–87; 11) 75.5 (1.42; 74–78; 8)	ns ns
TAIL	(1) 45.9 (2.42; 41–50; 15) (2) 44.2 (2.68; 41–47; 5) (3) 44.9 (1.6; 31)	45.6 (2.66; 41–48; 11) 44.4 (2.37; 42–49; 7) 43.6 (1.5; 45)	ns ns **
BILL F	(1) 29.5 (1.15; 28.0–30.8; 13) (2) 27.8 (0.99; 26.2–28.9; 5) (3) 29.9 (0.8; 48)	29.1 (1.09; 26.9–30.9; 12) 27.7 (0.73; 27–29; 6) 28.8 (1.2; 75)	ns ns **
TARSUS	(1) 29.2 (0.79; 27.7–30.4; 14) (2) 29.1 (0.96; 29.0–29.2; 4) (3) 30.0 (1.1; 48)	29.0 (0.92; 27.0–30.7; 12) 28.8 (0.35; 28.4–29.4; 6) 29.3 (1.2; 74)	ns ns **
TOE	(1) 19.6 (0.67; 18.6–20.5; 13) (2) 19.5, 19.8	19.3 (0.55; 18.3–20.0; 10) 19.3 (0.33; 19.0–19.9; 6)	ns ns
TOE C	(3) 24.5 (0.9; 28)	23.8 (1.1; 41)	**

For female skins, juvenile wing and 8TH P significantly shorter than adult.

(4) Firth of Thames, NI, live, Mar.; ages combined (A. Reigen; S. Davies.).

	UNSEXED
WING	(4)120.2 (3.36; 112–127; 155)

WEIGHTS (1) Adults; data from record cards (NMNZ). (2) NI and SI, live; weighed with spring balance, sexed by plumage and behaviour (Hay 1984).

	MALES	FEMALES	
(1)	59.9 (5.7; 50.4–66.5; 7)	64.8	
(2)	58.6 (5.3; 46)	56.7 (3.7; 75)	**

(3) Firth of Thames, NI, live, Mar.; ages combined (A. Reigen; S. Davies.).

UNSEXED

(3) 52.5 (2.83; 43–60; 155)

Between trapping 3 Feb. and retrapping 17 Mar., weight increased by 2 g (n=3) and decreased by 1 g (n=1) (A. Reigen; S. Davies). At hatching, c. 8 g; growth sigmoidal to asymptote of c. 60 g, probably after fledging (Hay 1984).

STRUCTURE Wing, narrow pointed. Eleven primaries; p10 longest; p9 1–3 mm shorter, p8 6–9, p7 14–18, p6 23–27, p5 32–35, p4 41–44, p3 49–52, p2 54–58, p1 62–65, p11 minute. Fourteen secondaries including four tertials; longest tertial falls between p6 and p8 on folded wing. Tail, square; 12 rectrices. Bill, very long for plover, with diagnostic bend to right about two-thirds from base of bill: angle 18.3° (3.2; 12–26; 72) (Hay 1984); bend present in embryo and at hatching. Moderately broad at base; upper mandible tapers gradually to bend and rapidly from bend to rather fine tip; lower mandible tapers evenly along length. Nostril, slit-like, horizontal, very long (c. 10 mm). Tarsus, fairly short and light, similar to typical *Charadrius*; scales, reticulate. No hind-toe; toes have typical fleshy pads; semipalmations, quite large between middle and outer toes and small between middle and inner toes. Outer toe 84–90% of middle, inner 67–76%. Claws, fine, twisted slightly outwards.

GEOGRAPHICAL VARIATION Single population with no known geographical variation.

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Volume 2, Plate 64 [caption error corrected from original]

Double-banded Plover *Charadrius bicinctus* (page 847)

1 Adult breeding male; 2 Adult breeding female; 3 Adult non-breeding; 4, Downy young; 5 Juvenile; 6, 7 Adult non-breeding

Wrybill *Anarhynchus frontalis* (page 919)

8 Adult male breeding; 9 Adult female breeding; 10 Adult non-breeding; 11 Downy young; 12 Juvenile; 13, 14 Adult female breeding