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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 Limicolae or Laro-limicolae (e.g. Mayr & Amadon 1951); colloquially, the assemblage (excluding alcids, skuas, gulls, terns and skimmers) is often referred to as waders (especially in Britain) or shorebirds (especially in North America).

About 350 species in 19 families, though taxonomic treatments vary. Following families recognized (mostly based on

recent reviews of Order [Sibley et al. 1988; Sibley & Ahlquist 1990; Sibley & Monroe 1990]):

Thinocoridae seedsnipes; four species, S. America. Pedionomidae Plains-wanderer; monotypic, Aust.

Scolopacidae sandpipers, snipes and allies; c. 85 species, cosmopolitan. Rostratulidae painted snipes; two species, s. America and Old World.

Jacanidae jacanas; seven species, pantropical.

Chionididae sheathbills; two species, Antarctica and subantarctic islands.

Burhinidae thick-knees, stone-curlews; nine species, widespread in Old World and two in Neotropics.

Haematopodidae oystercatchers; c. 11 species, worldwide in tropics and temperate regions.

Recurvirostridae avocets and stilts; about seven species, worldwide in tropical and temperate regions.

Ibidiorhynchidae Ibisbill; monotypic, central Asia.

Charadriidae plovers and lapwings; c. 60 species, cosmopolitan.
Pluvianellidae Magellanic Plover; monotypic, S. America.
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, 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, Ibidorhyncidae, Charadriidae, Pluvianellidae, Dromadidae, Glareolidae, Stercorcariidae, 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 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 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, Stercorcariidae, 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 subfamilies: 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, holorhinal, 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 (tricollaris); 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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Charadrius obscurus Gmelin, 1789, Syst. Nat., ed. 13 1(2): 686 — New Zealand = Dusky Sound, South Island, ex Latham 1785, Gen. Syn. 3(1): 208.

The Latin obscurus (dusky) refers to the type-locality of this species.

OTHER ENGLISH NAMES Red-breasted Dotterel.

MONOTYPIC

FIELD IDENTIFICATION Length 26–28 cm; wingspan: 46– 50 cm; weight: 130-170 g. Large bulky plover with big head and heavy bill, tip of which often appears uptilted. Close in size and shape to Pacific Golden Plover Pluvialis fulva; noticeably bigger and much bulkier than Large Sand Plover Charadrius leschenaultii, with shorter legs and heavier bill. Sexes alike; male more brightly coloured than female at times. Marked seasonal variation. Juvenile usually separable.

Description Adult breeding Crown, brown with fine dark streaking. Forehead, anterior lores, supercilium, lower cheeks, chin and throat, white, with varying brown patch in front of and under eye, through ear-coverts to sides of nape; diffuse broad whitish arc under eye on many. Nape, hindneck and rest of upperparts, brown, finely streaked darker and fringed paler greybrown, with inner wing-coverts narrowly fringed white. In flight, upperparts uniform brown, except for white sides to rump and narrow white sides to tail, clear narrow white wing-bar on tips of greater coverts and bases of inner primaries, and narrow white trailing-edge to secondaries. Underbody, white with varying suffusion of orange-brown, mostly on belly, extending to lower breast and flanks; on some males, foreneck to lower belly and face and sides of neck, orange-brown. Underwing, whitish with dusky trailing-edge to primaries. Plumage much affected by wear and fading: crown and eye-patch often only dark areas on otherwise whitish head and neck; eye-patch can also be reduced to faint brown smudge; upperparts, slightly paler, rather scruffy, with dark streaking more prominent; orange-brown suffusion may be much reduced. Bill, black, typically with small pinkish-orange patch at base of lower mandible. Iris, black-brown. Legs and feet, grey with slight olive tinge. Adult non-breeding Rather nondescript: brown above and mostly white below, with no orange-brown in plumage and with brown smudging on flanks and brownish wash across breast; differs from adult breeding by: patch round eye larger, including whole of cheeks, ear-coverts and lores; slightly paler brown above; pale supercilium, narrower and duller; in fresh plumage, indistinct scaly pattern to upperparts with narrow white fringes on longest scapulars and tertials; underbody, white, with grey-brown smudges and spotting on upper breast, sides of breast and fore-flanks and some grey-brown streaking on mid-flanks. Juvenile Similar to adult breeding except: upperparts darker, blackish brown, with narrow paler fringes to feathers, which are reduced or lost with wear; nape and hindneck slightly paler than rest of upperparts, which, with pale sides of head and neck, create more capped appearance; tail, tipped buff-white when fresh; chin, throat, foreneck, vent and under tail-coverts, white, with pale orange-buff wash on breast, belly and flanks when fresh; sides of breast heavily spotted dark brown; flanks, sparsely spotted; narrow gorget of fine dark spots in some.

Similar species Adult breeding plumage distinctive. Nonbreeding birds and juveniles may be confused with corresponding plumages of Large Sand Plover (q.v.) and Oriental Plover Charadrius veredus, which is slightly smaller and less bulky, with markedly slimmer body, longer wings clearly projecting beyond tip of tail at rest (roughly level with tip on New Zealand Dotterel), finer and more pointed bill, much longer and paler, vellowish, legs; no wing-bar above; and distinctive all-dark underwing.

Generally coastal, on broad sandy beaches, particularly near estuaries; on Stewart I. only, nest on exposed mountain ridges. In pairs during breeding season; singly, in pairs, or in small flocks during winter. Gait, flight and feeding actions as other Charadrius plovers; toes do not project beyond tip of tail in flight. Feed in estuaries and on sandy beaches, by picking at surface of exposed wet sand or mud; as tide rises, shift to margins of streams or to dry sand at top of beach or in dunes; sometimes also forage in nearby grazed fields. In estuaries, roost on sandy spits, sandy or shelly islets, or on saltmarshes, typically in small loose groups not closely attached to other waders. Generally tame and approachable. Usual call short penetrating reedy chirp, often sharpening to disyllable in flight.

HABITAT Typically littoral and estuarine. Mainly broad ocean beaches with banks and spits of sand or shell, where often seen along tide-line or in sand-dunes; in estuaries and harbours with firm intertidal mudflats; often favour beaches where freshwater streams enter sea; on offshore islands with suitable sandy beaches (Watt 1947; Sibson 1967; Edgar 1969; Phillips 1980; Parrish 1987; Dowding 1989; Oliver). Rarely on narrow stony beaches with no hinterland of sand (Sibson 1953). Also on farmlands with grassy pasture paddocks (wet, marshy and lush, or dried out) or cereal crops; rarely hillsides with open scrub (Sibson 1967; Edgar 1969).

On Stewart I., on coastal sandy beaches, tidal mudflats, and at high altitude on bare hilltops with open tussocky or boggy ground (Watters 1958; Edgar 1969; Dowding & Murphy 1993). Formerly in SI up to 2400 m in Southern Alps, and on shores of inland lakes and in river beds (Oliver).

Usually feed on firm exposed mudflats, sand or stones; avoid soft sticky mud, e.g. near mangroves. Feed between tide-lines at falling tide: sometimes at upper tide-levels; along fresh tide-line, following water as substrate exposed; may feed ahead of rising tide. Also in shallow water in streams, rock pools, puddles or soaks; dry or wet grassland; exposed seagrass flats; mussel-covered rock platforms (Sibson 1967; Edgar 1969; Heather 1980; Phillips 1980; Latham 1987; Dowding 1989).

Roost on flat open areas with good visibility: exposed shell banks, sandspits or sandy islands in estuaries or harbour entrances; beaches and sandy flats, sometimes among tide-wrack; duneland; coastal farmland with grassy paddocks (Sibson 1967; Edgar 1969; Phillips 1980; Dowding 1989; Dowding & Murphy 1993). Also on rough earthworks of newly created airport runway (Sibson 1967) and occasionally on football ground at Maketu when tides very high (P.C.M. Latham).

In NI, breed mostly on broad or narrow coastal beaches, especially wide flat areas near estuaries with little or no vegetation; on sandbanks or shell banks; sometimes among debris or sparse vegetation; in sand-dunes; may nest on small offshore islets or reefs; also on stony beach at mouth of Motu R. (Watt 1947; Sibson 1953, 1967; Edgar 1969; Phillips 1980; Dowding 1989; Cumming 1991; P.C.M. Latham). Occasionally in pasture, e.g. next to Kaituna Cut Lagoon (P.C.M. Latham). Rarely on hillsides with open scrub (Watt 1947; Turbott 1951). Has nested on reclaimed land (Munro 1971), e.g. at Sulphur Pt, Tauranga, and on flood stop-bank of Kaituna R. (P.C.M. Latham). On Stewart I., breed well inland on bare hilltops between 300 and 980 m asl, always above the scrub line, where vegetation is low, commonly wet herbfields among rocks (Dowding & Murphy 1993); also in sand-dunes (Edgar 1969). Formerly nested at high altitudes in SI (Dowding 1989); in nineteenth century nest found in Southern Alps at c. 1450 m (Oliver); early records of breeding among tussock-grass, on grassy flats and terraces beside braided rivers and subalpine areas (Potts 1883).

Development of coastal regions has deprived birds of traditional breeding and roosting sites (Cumming 1991). Quickly use reclaimed land, such as rough earthworks (Sibson 1967; Munro 1971; P.C.M. Latham). Recorded breeding, roosting and feeding in farmland with short sparse pasture closely grazed by stock (Sibson 1967; Edgar 1969; Phillips 1980), and among crops of oats and winter fodder (Edgar 1969). May use artificial shell banks (Sibson 1967). Areas made unsuitable when overgrown with introduced weeds, e.g. lupins (Edgar 1969).

DISTRIBUTION AND POPULATION Endemic to NZ. Two distinct populations: in NI, N of 39°S, and on Stewart I. and adjacent coast of Southland, SI. Small numbers recorded sporadically between.

NI Widespread in n. half, in coastal regions from Taharoa, N through harbours of Auckland isthmus to North Cape, and SE, through Firth of Thames and Coromandel Pen. to e. Bay of Plenty. Also on many offshore islands, including Cavalli, Great Barrier, Great Mercury, Motuihe, Brown's, Ponui, Beehive, Waiheke, Motukorea, Whale Is and Rurima Rocks. Rare on e. coast S of East Cape; stragglers reach sw. coast between Wellington and Wanganui (Bell & Brathwaite 1964; Edgar 1969; McKenzie 1978; Falla et al. 1981; CSN; NZ Atlas; NZCL): s. records to 1968 summarized in Edgar (1969); recent records: Ahuriri Estuary, Hawke's Bay, 1989 (CSN 38); near Rahotu,



1988-89 (CSN 37); Manawatu, 1976, 1983 (CSN 24, 31); Waikanae, 1980-81 (CSN 29, 30, 37); Ohau R., 1982, 1987, 1991 (CSN 31, 35; H.A. Robertson); Pauatahanui, 1989 (CSN 37). SI Widespread on Stewart I. In Southland often round Awarua Bay; occasionally Fortrose Estuary, Waituna Lagoon and Oreti R. Estuary (Edgar 1969; Muller 1969; Barlow 1993; Dowding & Murphy 1993; CSN; NZ Atlas). Regular in small numbers on Farewell Spit and, less often, Tasman Bay (Bell 1966; Andrew 1967; Edgar 1969, 1974; Dennison & Robertson 1979; Dowding & Murphy 1993; CSN; NZ Atlas). Occasionally elsewhere; records to 1968 summarized in Edgar (1969). Recent records of vagrants include: Nelson Haven, 1978 (CSN 26); Wainui, 1987 (CSN 36), Westhaven Inlet, 1991 (J. Hawkins); L. Wainono, 1971–72 (CSN 19); Heathcote-Avon Estuary, 1973-74, 1989 (CSN 21,22,37); Marlborough, 1990 (CSN 38); Barrytown, West Coast, 1985 (Edgar 1969; CSN 34). Only recent inland record, Matukituki R. valley, 1969 (CSN 19 Suppl.).

Breeding Breed widely in NI, N of 38°S, from Taharoa South Beach (S of Kawhia), N to North Cape, and SE to e. Bay of Plenty, including offshore islands (see above); scarce S of East Cape. Isolated breeding records in n. Hawke's Bay at Oraka Estuary and Portland I., 1990 (Foreman 1991). Widespread breeding on Stewart I. Not recorded breeding Foveaux Str., Nelson or Marlborough (Barlow 1993; Dowding & Murphy 1993;

B.D. Heather contra Edgar 1969).

In nineteenth century, described as nowhere very plentiful but dispersed along whole coast (Turbott 1967). In the past 150 years, range has contracted and numbers have declined considerably (Dowding & Chamberlin 1991). Formerly occurred inland at Rotorua, Mt Taranaki, Spencer Ras, Southern Alps and Canterbury Plains; records from Mt Egmont probably erroneous (Hutton & Drummond 1904; Turbott 1967; Edgar 1969; Oliver; B.D. Heather). Still breeding in parts of SI in late nineteenth century but declined rapidly there by early twentieth century (J.E. Dowding). No confirmed breeding records from SI or inland NI for at least 50 years (J.E. Dowding). On e. coast NI, S of Te Araroa, rare before 1988; since then apparent s. expansion, a few pairs colonizing coast between East Cape and Portland I. (Foreman 1991); single birds recorded farther S at Napier and Porangahau (J.E. Dowding; B.D. Heather).

Endangered (Reed 1981), threatened (Bell 1986). In 1992, estimated NI population c. 1350 birds; estimated Stewart I. population c. 60 birds; NI population, vulnerable; Stewart I. population declining rapidly and endangered (Dowding & Murphy 1993). Total population estimated at c. 1500 birds (Dowding & Chamberlin 1991) and <1400 (Reed 1981). In 1968, estimated NI population 1114 (Edgar 1969); by 1979-81, c. 1024 (Reed 1981). Earlier, Stewart I. population probably c. 200 birds (Reed 1981). When disturbed by human activity, breeding birds leave eggs or young temporarily, which leaves them vulnerable to predation (McKenzie 1953; Reed 1981; Dowding & Chamberlin 1991). Nests sometimes robbed (Edgar 1969). Also disturbed by motorbikes, but birds have successfully nested within 100 m of busy highway (Reed 1981). Nests often trampled by stock (McKenzie 1952, 1953; Edgar 1969). Eggs and young taken by variety of introduced predators (see Breeding). Once considered an excellent gamebird (Hutton & Drummond 1904).

MOVEMENTS Information supplied by J.E. Dowding. Dispersive or sedentary; nature and timing of movements in the n. and s. populations different, with no evidence of mixing between the two. In n. population (detailed study by Dowding & Chamberlin 1991), some adults entirely sedentary while others move short distance annually between breeding site and flocking site after

breeding. In s. population, all adult birds move from breeding grounds to winter flock (Dowding & Murphy 1993). Post-fledging dispersal occurs until about 18 months old, with much variation in distance of movement, some remaining within small area and moving seldom, others moving hundreds of kilometres. In flock at Omaha, transient juveniles stayed from few days up to 4 months. Bereaved adults also wander beyond normal range but commonly return to usual flock (Dowding & Chamberlin 1991).

NI Timing of movements of adults to flocking sites apparently determined by breeding; first birds arrive in mid-Jan., most arrive by late Feb. Birds leave flocking site gradually, between Apr. (exceptionally late Mar.) and July; of those that bred away from flocking site, two-thirds had left by end of Apr. Members of pairs often arrive and depart together. Between July and Jan., most fed within 2 km of their territory; a few make short trips from breeding territories to favoured foraging areas and back, 15–25 km round trip, usually in a day (Dowding & Chamberlin 1991). Occasionally, birds seen well outside usual range, often juveniles or occasionally adults who have lost partner; possibly from Hawke's Bay, where breed occasionally (Edgar 1969; Foreman 1991; CSN 38), Wanganui (CSN 19), Waikanae (CSN 29,37), Marlborough (CSN 38), Heathcote-Avon Estuary (CSN 21,22,38), L. Wainono (CSN 19). May be some variation in timing of movements in different areas but little data (J.E. Dowding). Stewart I. Little information; probably arrive at breeding grounds Aug.—Sept.; most leave mid-Jan. to late Feb. (J.E. Dowding). Birds breeding on Table Hill and Mt Rakeahua, Stewart I., commonly fly to tidal flats in Paterson Inlet to forage at low water, returning within a few hours. Highly mobile wintering flock feeds in Paterson Inlet, Stewart I. but at high tide during daylight moves to Masons Bay on w. coast and roosts there until returning to inlet as tide falls. At high tide at night fly to e. coast and roost at The Neck: round trip of about 60 km every 24 h (Dowding & Murphy 1993). Former SI breeding population moved from inland breeding grounds to form winter flocks on e. coast SI in Jan., returned to breeding sites in spring (Potts 1872, 1883).

Banding NI Longest adult sight recovery: adult (probably bereaved) moved from Whatipu, Auckland w. coast, 400 km S to Ohau Estuary, Manawatu. Post-fledging dispersal: longest 260 km from Whale I., Bay of Plenty, to Omaha, N. Auckland (J.E. Dowding), also 133 km from Jordans, S. Kaipara, to Miranda in 10 months. On e. coast, N. Auckland, banded adults showed very strong fidelity to breeding and flocking sites (Dowding & Chamberlin 1991). SI Longest distances recorded for adults are annual movement by a few birds from breeding grounds on Stewart I. to wintering flocks at Awarua Bay, Southland, c. 70 km (Barlow 1993). Two juveniles from Stewart I. seen in n. SI; one at Motueka (770 km in 54 days), other at Farewell Spit (835 km in 13 days), the latter seen again at Westhaven Inlet (35 km) 3 months later and back on Stewart I. 7 months after that (Dowding & Murphy 1993). Adults have very strong fidelity to flocking sites; fidelity to breeding site appears high but few data (Dowding 1992b).

FOOD Molluscs, insects, amphipods, crabs and fish. Behaviour Feed by night and day; on tidal estuaries, feeding related to tide-cycle; on n. beaches, feed irrespective of state of tides (J.E. Dowding); no data on feeding times at breeding grounds on Stewart I. Solitary or in pairs; away from breeding territories, commonly in loose groups, especially on tidal estuaries; no evidence of co-operation by pairs or groups. Feed with walk- or runstop-peck manner typical of plovers (Phillips 1980); occasionally stand-wait-peck and sewing-machine search. Forage on sandy beaches, mudflats, tidal rock platforms (J.E. Dowding), saltmarsh,

wet pasture (Sibson 1967). Move between habitats depending on tide. In s. population during breeding season, use subalpine mountain tops, usually in moist herbfields but also among rocks. Turn dung and shells (e.g. cockle Chione stutchburyi) to capture sheltering prey. Stab fish with bill and pound against ground, then swallow them (Latham 1979). Pull small mussels from rocks, and swallow whole at rate of up to 15/min (Heather 1980). Pounce on crabs and dismember them by shaking them until limbs of crab break off; eat legs, then eat body whole (Parrish 1987; J.E. Dowding); eat small crabs whole, e.g. Hemigrapsis edwardsi (Latham 1987). Observed taking small crabs from beneath empty cockle Chione stutchburyi shells (P.C.M. Latham). Foot-tremble in soft sand to disturb prey (Searle 1984). To disturb sandhoppers (e.g. Talorchestia), rake small mounds of seaweed covered by windblown sand for 3-5 s, then pause (often with head cocked), and may peck or probe sand. Active foot usually extended well forwards: raking tends to be front to back rather than side to side (CSN 22; J.E. Dowding). At Cooks Arm, Stewart I., six birds fed in loose group, wading in water up to 60 mm deep, catching crabs, carrying them above water-line, bashing and eating them (I.E. Dowding: E.C. Murphy). Recorded running along tide-line, scavenging for beachcast mussels and other bivalves opened by other birds and stranded invertebrates (Latham 1987; J.E. Dowding). Seen feeding on small fish dropped by White-fronted Terns Stema striata returning to nearby colony (M.J. Taylor).

Adult No detailed studies (observations of n. population unless stated). Marine organisms (Edgar 1969; Searle 1984). Annelids (Powers 1971); oligochaetes: earthworm (s. population, J.E. Dowding). Molluscs (Buller 1888; Edgar 1969); bivalves: Xenostrobus pulex (<20 mm, Heather 1980); Atrina zelandica; Paphia subtriangulata (J.E. Dowding). Crustaceans (Buller 1888; Edgar 1969): amphipods: sandhoppers (Buller 1888; Searle 1984; CSN 22); Talorchestia quoyana (Dowding 1989); small crabs (Parrish 1987; n. and s. population, J.E. Dowding; E.C. Murphy): Helice crassa (n. and s. popn., M.L. Barlow; P.C.M. Latham); Hemigrapsus edwardsi (Latham 1987). Insects (Buller 1888; Edgar 1969): Orthoptera: grasshoppers (Hutton & Drummond 1904); Gryllidae: cricket (McKenzie & Sibson 1963); Coleoptera: Carabidae: Neocicindela (J.E. Dowding); Tenebrionidae: Chaerodes (Cumming 1991); Diptera: Tipulidae: crane-flies (Hutton & Drummond 1904); Lepidoptera: moths (McKenzie & Sibson 1963). Fish (c. 60 x 5–6 mm, Habraken 1980b): Eleotridae: Forstervgion (Latham 1979); Pleuronectidae: Rhombosolea (s. population, R.R. Sutton).

Young Small chicks accompanied by one or both parents, larger chicks may forage alone (J.E. Dowding). No data.

Intake No data.

SOCIAL ORGANIZATION Reasonably well known; detailed study at Omaha, NI, by Dowding & Chamberlin (1991); information supplied by J.E. Dowding. Statements refer to n. population, except where indicated. Breed as solitary pairs; gregarious at other times. During breeding season (from May on, but usually Aug.-Jan.), adults mostly in pairs and occupying territories, which may be defended; juveniles solitary or in small flocks (J.E. Dowding). A few adults remain on territories all year; 90% of population moves into post-breeding flocks, which start to form in Jan., reach maximum numbers in Feb.-Mar., and decline from Apr. as birds return to territories (though timing varies from year to year and between areas). Adults show strong fidelity to flocking site and spend between 2 weeks and 5 months in flock; time of arrival at and departure from flocks by individuals appears to be consistent. Birds that breed together also flock together. Juveniles appear to wander widely, as occasionally do single, mostly bereaved, adults. Flocks from 10 to c. 100 birds, commonly 20–60; in winter, size of flock influenced by arrival and departure of wandering juveniles (Dowding & Chamberlin 1991; CSN 37; J.E. Dowding); for further details of flock-sizes see Edgar (1969). In s. population, all adults join flock Feb.-Aug.; largest flock recorded, 218+ on Stewart I. (CSN 6); some juveniles join winter flocks, and some wander round coasts of Stewart I, and SI. In summer, in territorial pairs; unpaired adults and juveniles also on Table Hill breeding grounds (Dowding & Murphy 1993).

Bonds Long-term, probably life long; monogamous, with pair-bond held year-round; one pair bred together in at least 10 of 12 years; mate again on death of partner (Dowding & Chamberlin 1991). Members of pair often join and leave post-breeding flock simultaneously. Usually, pair and breed first in second year of life (I.E. Dowding); one inconclusive case of breeding in first year (McKenzie 1978). Parental care Both parents incubate (J.E. Dowding contra Phillips 1980) and guard chicks. Neighbouring pairs and non-breeding juveniles regularly assist in defence of chicks but not nests. Fledged young may remain with parents for weeks or months, or leave soon after fledging (J.E. Dowding). Little detail on s. population but both members of pair incubate and guard chicks, and co-operative defence by adults and juveniles occurs (J.E. Dowding).

Breeding dispersion Solitary pairs breed in territories but, at some favoured sites, groups, commonly 2-10 pairs, nest close together and territories may be small. Nest density: in NI, 11 breeding sites averaged 1.74 pairs/ha of potential habitat (0.6-3.6) (Cumming 1991). In some areas, densities higher, e.g. five pairs on 0.5 ha sandbar at Wade R. (I.E. Dowding). Lower densities occur on long stretches of beach without streams, e.g. one pair on 5 km at Pakiri Beach. Territories Usually occupied by both members of pair for much of year except when pair moves to post-breeding flock (see above); birds with high-quality territories may leave flocks early; some birds remain on territories all year. High site-fidelity between years (Dowding & Chamberlin 1991). In s. population, pairs on territories from about Sept.to Jan. Little feeding occurs inside small territories, off-duty birds moving to nearby feeding sites. Chicks very mobile, and poor indication of locations of territories. Home-ranges Move within predictable areas; in one area, distance between breeding and flocking sites, 0-16 km. During July-Jan. most feed within 2 km of territories; also see Movements (Dowding & Chamberlin 1991).

Roosting During breeding season, adults within territory. Post-breeding flocks normally on wide flat areas of sand, mud, shell bank or grass with good visibility (see Habitat); in very windy conditions individuals or whole flock may use more sheltered sites, e.g. pans among dunes, or behind rocks, vegetation, or similar wind breaks. Sites traditional but exact location varies, e.g. at Omaha, N. Auckland, always within 200 m of base of sand spit. At Omaha, in post-breeding flock, time spent at high-tide roost varies; some birds loaf at roost-site 3 h before high water, and others arrive only when tide covers last of feeding grounds; some leave immediately tide begins to fall, while others remain (J.E. Dowding; S.P. Chamberlin). At Mason Bay, Stewart I., birds of winter flock arrive in 1-3 groups, 1.5-2.5 h before high water covers feeding area at nearby Paterson Inlet; roost in one flock, then leave 1-2.5 h after high water (Dowding & Murphy 1993). Flocks sometimes roost with other species, particularly Doublebanded Plovers C. bicinctus and Bar-tailed Godwits Limosa lapponica. Commonly roost on one leg and move short distances by hopping; in undisturbed, resting flock, many birds close eyes (J.E. Dowding).

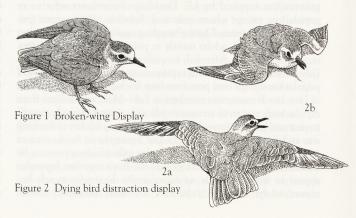
SOCIAL BEHAVIOUR No detailed studies; some information on n. population by I.E. Dowding, and during Nov. by Phillips (1980); based on contribution by J.E. Dowding. No obvious difficulties in observing displays. Many displays seem typical of *Charadrius* plovers; for comparison, see Phillips (1980). NORMAL POSTURE: when relaxed, stand with line of back 30–45° above horizontal, head held slightly above highest point of back; plumage relaxed, wing-tips folded over tail (Phillips 1980). Repeated vertical Head-bobbing, occasionally slow and exaggerated, common sign of concern, particularly in presence of potential threat; often accompanied by Chrp Call. When preparing for flight, birds commonly stretch wings, either both simultaneously vertically above body (UP-STRETCH) or singly sideways with leg (SIDE-STRETCH). At Stewart I., birds bathed after feeding on mudflats and before moving to high-water roost (J.E. Dowding).

Agonistic behaviour In flocks, some adults clearly dominant, often displacing juveniles and other adults from favoured (sheltered) roosting sites. During breeding, intruding juveniles or adults not tolerated on territory (J.E. Dowding). Observations of aggression in individuals and pairs in Nov. (Phillips 1980) of unknown function, possibly territorial. CHASE: resident holds head and body roughly horizontal, puffs out feathers of flanks and breast, and runs directly at intruder; often accompanied by Churr Call (J.E. Dowding). Birds attacking on foot usually run in Horizontal Spread but assumed Erect, Puffed Breast posture during pauses (see below); head of attacker always withdrawn whereas that of fleeing bird sometimes raised (Phillips 1980). If intruder returns or does not retreat sufficiently far, aerial chase often results. In air, chases often swift, twisting and low, accompanied by calls; wing-beats shallow and rapid; attacking approach often low, usually ending in soar near opponent, who ducks to avoid being hit; sometimes ends in glide with wings held over back in V (Phillips 1980). At territorial boundaries, chases may go back and forth (e.g. Heather 1980) with parallel running, some runs long and straight, others shorter and punctuated by rapid 180° turns (J.E. Dowding) or complete turns of 360° (Phillips 1980). Occasionally both members of neighbouring pairs may have STAND-OFFS, with birds facing each other, standing tall and calling; usually little ground given. Phillips (1980) also describes following aggressive postures and movements: ERECT, PUFFED BREAST: stand with body 45° from horizontal and head withdrawn, with feathers of breast and flanks puffed to ruffled; seen in either sex; occurs in pauses during approaches or chases, and assumed by birds about to attack or advance. HORIZONTAL SPREAD: horizontal posture with bill, head, body, and tail in line and parallel to ground; feathers of breast and belly usually sleeked but spread laterally, hiding edges of wing and showing white from behind; often with ventral feathers puffed; occurs in both sexes; used when chasing other birds; also used by retreating birds except that they often spread and depress tails, occasionally tilt exposing dorsum to pursuer, tend to be less fluffed, and hold carpals out from feathers of flank. STRETCHED ERECT: similar to Erect, Puffed Breast except neck extended vertically rather than withdrawn. Seen when bird retreats from antagonist and also when nesting birds approach observer near nests. Fighting Birds fly at one another kicking and flailing; short low attacks met thus or by ducking or by jumping up and letting attacker pass below. Birds may vigorously grasp feathers of back and circle violently (Phillips 1980). Once, in June, three birds (probably all males) alternately stood very tall then flew at opponent, pecking; attacked bird usually ducked and aggressor flew over; little physical contact, and much calling; incident lasted about 15 min (J.E. Dowding). Fighting only occasionally seen (J.E. Dowding) though physical attacks considered common (Phillips 1980).

Sexual behaviour Phillips (1980) saw individuals courting in Nov.; made following observations on breeding displays. SCRAPE:

similar to that of Double-banded Plover; performed by both sexes. Occurred in nest-making, courtship, and before copulation. CHOKE: some movements seen during Scrape encounters similar to Choking of Double-banded Plover but sometimes differ slightly, looking more like stabbing at ground rather than choking down morsel. Bow: sometimes associated with tail-spreading and Tilt and Wing-raise; unknown whether accompanied by calling; occurred during Advertising and Scrape encounters. TILT AND WING-RAISE: appeared similar to that of Double-banded Plover; seen during Scrape encounters, and occurred in same circumstances as Bowing. PICK-AND-TOSS: scraping birds often pick up and toss plant material. On several occasions in Nov., lone birds, claimed to be males, seen vigorously Scraping and then were displaced by another, claimed to be female; Scraping bird stepped out of scrape and stood, bowing forward and tipping dorsum toward the other; then Picked or Choked at sand or tilted even farther while raising wing and quickly spreading and folding tail. Displacing bird variously Scraped, squatted in scrape, then stood and Picked-and-Tossed, just stood, or even ran on and stopped. In any case, displaced birds glided away from displacing birds in horizontal runs with heads withdrawn and backs humped (contrasting to flat back during aggressive chases), and began to Scrape on another knoll. If displacing bird followed, whole sequence was repeated. Copulation Few records; male follows female with exaggerated high-stepping PARADE MARCH, mounts, and treads; in one case, treading lasted 60 s then male grasped feathers of nape of female and pulled female over backwards; birds lay momentarily on backs, wings flailing, then stood upright and fluffed with short necks (Phillips 1980); in another case, treading lasted 75-80 s then male dismounted and stood about 2 m away while female preened (J.E. Dowding).

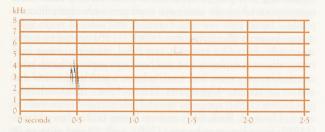
Relations with family group Anti-predator behaviour of young Small chicks (to c. 1 week) normally crouch to avoid detection, older chicks run to cover and crouch, and chicks close to fledging run very fast and often ignore available cover. Chicks of all ages readily take to water to escape. Parental anti-predator strategies Normally little or no defence of eggs until clutch complete. One of pair often stands guard while other incubates or broods; will call mate off nest or sound alarm while approaching and distracting intruder. DISTRACTION DISPLAYS: perform Rodentrun where head hunched, and head and body horizontal, and crouch-run, quickly or slowly, usually in straight line, away from nest or chicks; tail sometimes partly spread. May become Brokenwing Display (Fig. 1), where body tilted, tail spread downwards, and outerwing partly spread and dragging on or near ground; may be given slowly near nest, with bird weaving rhythmically back and forth ('waltzing'), upperbody always turned to intruder. Rodent-run and Broken-wing Display commonly given at right angles to line of approach to nest of intruder; if unsuccessful in



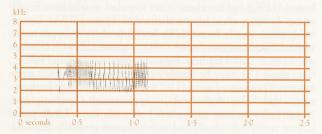
attracting intruder, bird may fly back in front of intruder and repeat run. At most intense, display resembles dying bird (Fig. 2a,b): lie on belly, usually in small hollow in sand but sometimes behind small piece of driftwood or similar; half-extend both wings and beat them rhythmically against ground; tail usually at least partly spread, sometimes tilted up and sometimes down; nearly always accompanied by loud agonized squealing; on some substrates (e.g. shells) wing-beats clearly audible; may attempt to perform display on water. Considerable individual variation in intensity of displays but normally more intense when with chicks than with eggs. Neighbouring pairs and non-breeding juveniles regularly join in Distraction Displays when parents defending chicks, but not nests (J.E. Dowding). Bar-tailed Godwits recorded being attracted by Broken-wing Displays (Habraken 1980a). Adults will fly directly at Kelp Gulls Larus dominicanus and head them off, particularly when chicks present. False-feeding common, especially when bird returning to nest after disturbance. When chicks released after banding, usually escorted away by one parent, on ground or in air, calling repeatedly, while other gives prominent displays away from chick. Displays often continue for some days after loss of nest or chicks (J.E. Dowding).

VOICE No detailed studies; account based on Phillips (1980) and contribution from J.E. Dowding. At least five distinct adult calls recognized, all quite loud and penetrating. No sexual, individual or regional differences known. Normally silent when handled.

Adult CHRP (sonagram A): probably composed of several tic syllables (Phillips 1980); variously described as cricket-like krik (Falla et al. 1981), reedy trrt (Hayman et al. 1986), short penetrating trrt or prrp (NZRD), a single prip (Moon 1992). Most common call. Slow or infrequent use associated with alertness and mild alarm. Often accompanies head-bobbing. Sometimes given as double call chrp-chrp, used more rapidly and often when given as warning to family, or when defending nest or chicks. TSEEP: a thinner-sounding, rising call; sounds considerably more high-pitched than chrp but sonagrams (Phillips 1980) show little difference in frequency; presumably tweet (Phillips 1980; Hayman et al. 1986), and high-pitched pweep (Moon 1992). Commonly given (often alternately with chrp) to keep chicks in hiding when dogs or people nearby (J.E. Dowding); may have other functions.



A L. McPherson; Mangawai Beach, Northland, NZ, Sept. 1981



B L. McPherson; Mangawai Beach, Northland, NZ, Sept. 1981

CHURR: longer buzzing call (sonagram B), probably same as che-weewrrr (NZRD), shweeerr (Heather 1980) and rolling turr (Hayman et al. 1986). Mainly agonistic, associated with territorial chases on ground and in air. SQUEAL: used with highest level of defensive action at nests or with chicks, commonly associated with Dyingbird Distraction Display, also sometimes given by birds standing a few metres away while eggs being measured (I.E. Dowding). WEER-WHIT: loud, assertive buzzing call, fluctuating in pitch, same as wheeerwhreet of Phillips (1980). Associated with stand-offs, fights and territorial defence. Often given with bird standing very tall. Other calls more complex, less well defined, may be combinations of some of the above.

Young Thin high-pitched monosyllabic call given by recently hatched chicks; similar sound heard from pipping eggs 24 h before hatching (J.E. Dowding).

BREEDING Not well known. Studied in Clevedon, NI by McKenzie (1950, 1952, 1953) and by Cumming (1991). Account based on review of literature and account by I.E. Dowding. Breed in simple pairs, solitarily.

Season NI Eggs, late Aug. to early Jan.; first clutches usually laid late Aug.-Sept.; up to three replacement clutches in season; eggs rarely laid after mid-Jan. (McKenzie 1950, 1952, 1953; Edgar 1969; Oliver; J.E. Dowding). Laying probably a month later on Stewart I. (Oliver). Fledging, early Nov.-Feb. or Mar.



Site NI On beaches and sea-fronts, banks of shells and sand, sand spits at mouths of tidal estuaries or streams, occasionally on shingle or stony beaches; once, on hillside of open scrub in Te Kao Valley. On Stewart I., in stunted subalpine vegetation, often in rocky areas, sometimes close to scrub-line; formerly on sanddrift and stone-strewn plain (Guthrie-Smith 1914; Oliver). In grass on beach, on mound of wind-blown sand against piece of driftwood, vegetation or grass tussock, sometimes among thicker vegetation in dunes, in lee of rock or thicket of prostrate manuka on mountain tops, among stunted subalpine vegetation (Guthrie-Smith 1914; Watt 1947; McKenzie 1952; Dowding & Chamberlin 1991; Foreman 1991; Barlow 1993; Dowding & Murphy 1993; Oliver). Nests may be 7 m from nests of conspecifics (J.E. Dowding). High site-fidelity, most pairs occupying same or similar territories in consecutive years; nearly all nests < 200 m from previous nests (Dowding & Chamberlin 1991).

Nest, Materials NI Scrape in sand or ground, sometimes lined with a few pieces of grass, seaweed or shell, one nest decorated with dried pine needles. Often make numerous scrapes before laying (McKenzie 1952; McKenzie 1967). Scrapes often need scraping out as they can rapidly fill with wind-blown sand (Oliver). Stewart I. In depressions between cushion plants, sometimes in lee of a small tussock or rock, lined, often deeply, with dry vegetation, usually tillers of snow-tussock, lichen sometimes added as insulation or, possibly, decoration (Oliver; J.E. Dowding).

Eggs Pyriform, or ovoid, sharply pointed; ground-colour varies from pale olive to buff-brown, with small to large blackishbrown and pale-brown blotches all over, sometimes concentrated near larger end (Oliver; J.E. Dowding). MEASUREMENTS: e. coast NI: 44.2 (1.39; 41.5–46.5; 20) x 31.3 (0.58; 30.3–32.3) (J.E. Dowding); 44.3 (0.81; 43.4-45; 3) x 31.2 (0.52; 30.6-31.5) (Oliver). WEIGHT: e. coast NI: 21.7 (0.97; 20.0–23.7; 20) (J.E. Dowding).

Clutch-size Usually three eggs per clutch; of completed clutches from NI: average 2.8: C/2 x 9, C/3 x 33 (Cumming 1991); average 2.8: C/1 x 3, C/2 x 8, C/3 x 48 (NZ NRS). Clutches of four, five or six exceptional and, at least some, from two females laying in same nest (McKenzie 1967; Foreman 1991; NZ NRS; R. Butcher; J.E. Dowding; R. Morris; S.M. Reed); single-egg clutches sometimes result of predation of other eggs (J.E. Dowding).

Laying Synchronized at each site but timing varies between sites (Cumming 1991). Clutch of three eggs probably laid over c. 7 days, third egg of clutch laid 4 days after second (McKenzie 1953). Will re-lay after failure, up to three times; clutches can be replaced in 3 weeks (J.E. Dowding); one pair re-laid only 4.9 m from previous site (McKenzie 1952; Edgar 1969). No double-broading granted d. L. Dowding.

brooding recorded (J.E. Dowding).

Incubation Begins 1–2 days after clutch complete; both sexes sit on eggs before laying complete but female seems to do most incubation by day after clutch complete (McKenzie 1952, 1953) (see Fig. 3). Males probably incubate at night; occasionally sit on nest when female has been disturbed (J.E. Dowding). Eggs may pip up to 4 days before hatching; young all hatch within 24 h (McKenzie 1950, 1952). INCUBATION PERIOD: 28–32 days (McKenzie 1950, 1953). After a clutch of five eggs was washed out by a high tide, new nests were made for two eggs, 1.2 m apart, and one egg continued to be incubated (McKenzie 1967).



Figure 3 Turning eggs

Young Precocial, nidifugous. Hatch in buffy-white down with black, brown and yellowish speckles and blotches above, white on underparts and on forehead and sides of face (Oliver). Young leave nest soon after hatching and remain nearby for some time (Edgar 1969); chicks found away from parents at 31 days old (McKenzie 1952). Growth Weight of four chicks at hatching, 16–18.4 g; weight of six fledged but still dependent young averaged 106 g (83–120) (J.E. Dowding). FLEDGING PERIOD: varies from c. 28 to 52 days (McKenzie et al. 1977), 35–40 days (Cumming 1991). Parental care, Role of sexes Young guarded and brooded by both parents; if intruder, such as grazing animal, approaches nest, adults try to distract it by making aggressive passes, feigning injury or fluttering close to its face (McKenzie 1953; Edgar 1969; J.E. Dowding).

Fledging to maturity Fledged young stay with parents for varying period: some young leave soon after fledging, others remain for weeks or months (J.E. Dowding). Usually, pairing and

breeding occurs in second year (J.E. Dowding).

Success At protected sites, 0.62 young fledged per breeding pair; at unprotected sites, 0.31 per pair; difference not significant (Cumming 1991); at Omaha, commonly only one or two young fledged by eight or nine pairs (J.E. Dowding; S.P. Chamberlin). Hatching success of nests, where sites were much and little disturbed, respectively: 37 and 60% (Cumming 1991); survival of chicks in a season, at sites where much and little disturbance respectively: 67 and 84%, but may not be typical (Cumming 1991). From 21 eggs, five young fledged (McKenzie 1952, 1953); at Wade R., near Auckland, 22 eggs laid, five hatched, one chick fledged (J.E. Dowding). Nests washed out by high tides, buried by wind-blown sand, trampled by stock, robbed (Edgar 1969); known

predators of eggs include Silver and Kelp Gulls; chicks taken by Kelp Gulls and dogs; other potential predators include Swamp Harriers Circus approximans, cats, rodents, hedgehogs, and mustelids (Dowding 1992a). One egg of clutch often fails to hatch or produces a weakling that dies (Edgar 1969). On Stewart I., predation of adults almost certainly by feral cats (Dowding & Murphy 1993). Banding studies from N. Auckland suggest average annual mortality of adults about 7–8% (J.E. Dowding; S.P. Chamberlin); on Stewart I., 23% (Dowding & Murphy 1993). In NI, some birds live to 15–19 years old (J.E. Dowding). Believed to hold longevity record for Charadriiform: 41 years 1 month (male, banded as pullus at Mataitai, e. coast Auckland; last sight-record, Jan. 1991, Seagrove, Manukau Harbour, South Auckland) (McKenzie 1978; Goodwin 1991).

PLUMAGES Prepared by D.J.James. Hatch in natal down. Begin pre-juvenile moult at unknown age; fly at 28–52 days. Partial post-juvenile moult to first immature plumage followed by partial pre-breeding moult to second immature in first spring. 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 seasonal variation; ageing of first and second immatures, difficult. Sexes sometimes differ. Normally first breed at end of second year, but sometimes first year (McKenzie 1978). Two allopatric populations: population breeding NI all or mostly light-plumaged; on Stewart I., all or mostly dark-plumaged.

Light-plumaged birds All birds in extant NI population: see Geographical Variation. Adult male breeding (Definitive alternate). Head and neck Forehead, lores, chin and throat, white, though brightest birds may have slight orange tinge; sometimes faint grey mottling on lores. Crown and nape, grey-brown (c91), streaked by pale-brown (c223D) fringes to feathers; feathers have light grey-brown bases. Hindneck, light grey-brown (119C), with concealed white bases to feathers; tips and edges of feathers washed pale orange-brown, forming faint pale collar. Ear-coverts, light grey-brown (119C), fading to pale grey-brown (119D) at basal edges of feathers; grey-brown (119B) centres at tips of feathers give lightly streaked appearance; prominence of earpatch varies, usually separated from side of neck. Fairly broad, illdefined, off-white supercilium extends from side of forehead, broadening into pale patch above and behind eye. Sometimes conspicuous white arc under eye combines with supercilium to produce broad pale eye-ring. Foreneck and sides of neck, light orange-brown with varying grey-brown (119B) centres to feathers on sides. From Oct. onwards, very faded and worn; orange-buff tinges almost completely lost and head can appear whitish with mottled brown crown and faint indistinct smudging round eye and on ear-coverts. Upperparts Mantle, brown (c28) with light grey-brown (119D) fringes at tips and pale orange-brown wash at edges of feathers. Back, fairly uniform brown (c28) to grey-brown (119B). Scapulars, grey-brown (119B), with varying mixture of light orange-brown wash at tips of some feathers and light greybrown (119D) tips to others; outer scapulars usually have broad orange-brown wash at fringes; shafts, dark brown (119A). Upper tail-coverts, mostly brown (28); lateral feathers in upper rows, white; longest row, grey-brown (c91) to brown (28) with mottled white tips to lateral feathers. Subject to extreme wear and fading: from about Oct. may be untidy light grey-brown (c119C) with indistinct paler grey-brown (119D) to whitish fringes to feathers; narrow dark-brown shaft-streaks, more prominent. Outer scapulars in particular become pale when buff wash lost. Underparts Colour varies individually and with freshness; generally acquired Apr.-May or, in some, as late as June (J.E. Dowding). When fresh,

some mostly rich orange-brown. Feathers of breast, light orangebrown at tips, with large concealed white bases; intensity of orange wash fades slightly toward tips, giving uneven coloursaturation or slight frosty appearance. Belly, richer, deeper orange-brown with thin pale fringes. Sides of breast, light greybrown (119C-119D) with pale orange-brown wash to tips of feathers; here, appearance is of grubby orange-brown feathering. Some feathers on fore-flanks, grey-brown (119B) with thin whitish fringes; rest of flanks and axillaries, white. Thighs, vent and under tail-coverts, white; tail-coverts sometimes have very faint buff tinge. Some males, paler and more orange when fresh with weaker and less extensive wash on breast and flanks, and broader fringes on belly; some have scattered whitish feathers, giving mottled or blotched effect and suggesting that not all feathers of breast replaced in pre-alternate moult; impression is of much paler and less evenly toned underparts. With wear, orange-brown fades, especially on breast, and whole of underparts, paler with large whitish areas, especially on breast; after about Oct., may be mostly white with only slight orange wash on belly. Uppertail Central rectrices, dull brown (28), grading to light grey-brown (119C) at bases with thin whitish fringe at tip, which is often worn away. T2, similar but with broader fringes; t3-t4 have increasingly broad white tips. T5, light grey-brown (119C) at base grading to grey-brown (119B) subterminally, with broad white tips and narrow white edges. T6, light grey-brown (119C) with white tip, inner edge and most of outer web. Undertail Appears grey-brown (c119B) with diffuse whitish tip and sides. Upperwing Mostly grey-brown, with moderate white wing-bar on innerwing and broad white patch at base of inner primaries. Outer primaries (p6-p10), dark brown (121) on outer webs and tips; light grey-brown (119C) on inner webs grading to white along inner edges; shafts, white. P5, light grey-brown (119C), faintly darker towards tip with large white base and broad white inner edge and white basal two-thirds to outer web. P2-p4, light grey-brown (119C), with white basal quarter of inner web and basal half to three-quarters of outer web; on outer web, white extends along outer edge and beside shaft in forked tongue and forms white flash at base of inner primaries. Shafts of primaries, white, grading to grey-brown (119B) near tips. Secondaries and inner primary (p1), light grey-brown (119C), with moderate white fringe at tips (forming conspicuous pale trailing-edge), white basal quarter, broad white inner edge and white wedge extending half way along shaft from base. Shafts, white, grading to light grey-brown (119C) at tip. Inner few secondaries, mostly white, with grey-brown (119B) speckling distally along centre of outer web and faintly over inner web, and with white shaft and broad white tip. Inner greater primary coverts, dull brown (c28) with thin white fringe at tips; lesser and outer greater primary coverts and alula, dark brown (c121). Greater secondary coverts, grey-brown (119B) with broad neat white tips and narrow edges; together with white patch on inner primaries, form moderate white wing-bar. Median secondary coverts, grey-brown (119B) and lesser secondary coverts, brown (28), both tracts with thin whitish to light grey-brown (119C) fringes and brown (28) shafts. Tertials, grey-brown (119B) with thin whitish to pale-buff outer edges when fresh (but usually worn in this plumage); shafts, dark brown (121). Underwing Coverts and subhumerals, mostly white. Greater primary coverts sometimes very pale grey with broad white fringes, contrasting only slightly with rest of coverts and not producing darker crescent at base of primaries. Remiges, mostly reflective brownish grey (c80) or pale grey (c86), with broad darker brownish-grey (79) tips to primaries and outer secondaries. Inner primaries, mostly white.

Adult female breeding (Definitive alternate). When fresh,

similar to dullest males; face and underparts always duller than those of brightest males. If one bird of mated pair is noticeably brighter than other, female is the duller; however, in some pairs distinction cannot be made; by about Oct. both sexes usually sufficiently worn and faded that no difference apparent (J.E. Dowding).

Adult non-breeding (Definitive basic). Sexes similar. Head and neck Forehead, mostly white, usually with brown (28) tips, which give scaly appearance; width of pale forehead varies. Crown and nape, brown (28), with thin pale grey-brown (119D) fringes. Lores, brown (28), speckled white. Ear-coverts, brown (28), faintly streaked whitish; form much larger patch than in breeding plumage. Supercilium, white or off-white as in breeding, but narrower, tapering behind eye. Chin, throat and foreneck, white. Hindneck, grey-brown (91), slightly paler and more uniform than nape. forming pale, though somewhat obscure, hindcollar. Upperparts Feathers have concealed pale-grey (86) bases. Mantle, brown (28) to dark brown (119A) and scapulars, brown (28), both with very thin pale grey-brown (119D) fringes to feathers. Back, brown (28) with pale-brown (223D), moderately wide fringes to feathers; rump and shortest (most anterior) upper tail-coverts, similar but slightly darker. Longest tail-coverts, light grey-brown (119C), with broad whitish fringes. Underparts Generally white with mottled breast-band of varying width. Breast-band formed by white feathers with rounded brown (28) centres; sometimes narrow, obscure or incomplete across centre of breast but often up to 30 mm wide; sides of breast, similarly, though more densely. patterned to almost uniformly brown (28); variation strong but cause unknown. Anterior flanks, white with broad light-brown (223D) streaks along shafts and outer webs of feathers, producing mottled appearance; sometimes faint streaking extends to sides of lower breast, visible on standing bird. Tail As breeding plumage, but worn. Upperwing Remiges, alula and primary coverts, as breeding. Greater secondary coverts, brown (28), with white to off-white fringes, similar to breeding. Median and lesser secondary coverts, brown (29) with narrow pale grey-brown (119D) fringes. Underwing As breeding plumage.

Downy young Down, short, woolly, dense. Above, light brown (c223D) with dark-brown (121) bases, giving speckled appearance. Top of head has faint irregular median stripe from base of bill to about centre of crown, where it breaks up into line of blotches. No break between pattern of upperparts and top of head (Jehl 1968). Upperside of wing, light brown (c223D) with dark-brown (121) stripe on radius. Underparts and underside of wing, off-white to cream (92) with buff wash across breast.

Juvenile Head and neck Forehead, lores, chin, throat and foreneck, white. Crown and nape, dark brown (119A), with untidy narrow pale grey-brown (119D) fringes to feathers. Hindneck and sides of neck, light grey-brown (119C), with slightly paler (119D) fringes and large, white, often partly exposed, bases to feathers; form faint pale collar. Ear-coverts, greybrown (119B) with concealed white bases; lower ear-coverts washed pale brown (223D) on tips of feathers. Supercilium, broad, white, widening behind eye. Upperparts Mantle and back, dark brown (119A) with conspicuous cream (54) to pale-buff fringes to feathers. Scapulars, dark brown (119A) with broad buff (124) fringes and dark-brown (121) shafts; feathers distinctly smaller than in other plumages. Rump, dark brown (121) with pale-brown (223D) fringes. Central rows of short upper tailcoverts, as rump; lateral coverts, white; central rows of longest coverts, brownish grey with diffuse whitish tips. In general, fringes quickly wear and fade to pale grey-brown (119D) and become narrower. Underparts Breast and belly, white, washed pale orange-buff, brightest on belly; feathers, white with narrow orange-

buff wash at tips. Sides of breast and some feathers of fore-flanks, grey-brown (119B) with orange-buff tips and dark-brown (121) shafts. Rest of flanks, thighs, vent and under tail-coverts, white. With wear, buff wash quickly fades to cream. Uppertail Similar to adult, though with better defined white sides and darker centre. T6, white with grey-brown (119B) spot near tip of inner web. T5, white with broad grey-brown (119B) edges that gradually darken distally, and broad white tip. Central four pairs, dark brown (121) with broad white tips. Tips of rectrices more pointed than those of adult. Undertail Appears dark brownish-grey (dark 79) with white edges and tip. Upperwing As adult except as follows: leading few rows of lesser secondary coverts have broad white fringes that become slightly more buff towards rear; rest of lesser and median secondary coverts have broad buff (124) fringes; greater primary and secondary coverts have broader white tips, though these still narrow on outer primary coverts; primaries have pointed white tips; tertials, shorter and median coverts, smaller. Underwing Like that of adult. Greater primary coverts, less well formed, somewhat flimsy.

First immature (First basic). Very similar to adult non-breeding. Juvenile remiges and greater coverts, and inner median secondary coverts, retained. Inner primaries have broader white tips (c. 2–3 mm on p1–p4) and thin, very white fringes on p5–p7; fringes tend to be worn away on outer three primaries. In contrast, adults have fringes 1–2 mm wide on p1–p3, very thin on p4–p6 and no fringes on outer four primaries. Median upper secondary coverts have indistinct whitish fringes slightly paler than adult, but affected by wear. Lesser coverts have distinct but untidy cream (92) fringes.

Second immature (First alternate). Similar to immature non-breeding. Retained juvenile remiges rather worn. Most birds stay in dull plumage like non-breeding, but a few colour-up, generally in Sept. (J.E. Dowding).

Dark-plumaged birds Adult male breeding (Definitive alternate). Darker dorsally and more uniformly orange-rufous ventrally than light-plumaged birds; little, if any, overlap between them. Head and neck Ground-colour of top of head and hindneck, darker brown (119A-129), with narrower and darker but richer orange-rufous fringes to feathers. Forehead, lores and chin, varyingly washed orange-rufous. Supercilium, possibly slightly narrower and less distinct. Throat and foreneck, uniformly orange-rufous, darker and with stronger rufous component than light form; orange wash extends up sides of face to below earcoverts. Patch on ear-coverts, larger and continuous with sides of neck. Sides of neck, dark brown (119A) with broad orange-rufous fringes to feathers. Upperparts General ground-colour of feathers, slightly darker, dark brown (119A-129) with richer orangerufous to light rufous-brown (between 38 and 39) fringes to feathers. Underparts Breast and belly, fairly uniform orangerufous, richer, darker and more rufous than light-plumaged birds; feathers grade to orange-buff but not white at bases; some brown (c28) mottling often obvious in narrow band across upper breast. Feathers at sides of breast have darker (dark brown [119A]), more conspicuous centres, giving strongly streaked or mottled appearance. Vent, white, mottled or streaked with orange-rufous wash. Extent of variation in brightness between individuals not known. Tail Similar to light-plumaged birds; outer rectrices may be slightly darker. Upperwing Remiges, similar to light-plumaged birds. Underwing Probably as light-plumaged birds.

Adult female breeding Similar to male but with less even and intense rufous-orange wash to face and underparts; can be confidently sexed only when mated to brighter male.

Adult non-breeding (Definitive basic). Similar to lightplumaged birds but slightly darker, greyer brown. Head and neck

Forehead and lores, brown (28), with bold white fringes producing scaly pattern. Crown, dark brown (119A-121), with slightly darker indistinct shaft-streaks. Ear-coverts, rather dark, brown (28) with light grey-brown (119C) edges to feathers, producing streaky appearance. Supercilium, sometimes narrower than lightplumaged birds, indistinct. Broad diffuse white eve-ring often forms conspicuous spectacle. Upperparts Mantle and scapulars, dark brown (119A) with thin indistinct light grey-brown (119A) fringes when fresh; become paler and drab when worn. Underparts Mostly whitish. More prominent brown-mottled or streaked band on breast; feathers, brown in centre with broad diffuse whitish edges or fringes. Flanks, white, with brown (28) mottling and streaking visible below folded wing. Feathers near base of thighs, white, with light grey-brown (119C), wedge-shaped central streaks. Upperwing Very similar to light-plumaged birds, but ground-colour of feathers slightly darker when fresh.

Downy young Undescribed. Probably very similar or identical to light-plumaged birds. Faded mount (CM) from unknown locality (probably SI) has dark-brown (121) tips to some down,

giving increased speckled appearance.

Juvenile No skins examined. Probably differs from juvenile light-plumaged birds in parallel manner to adults: photos (DOC Slide Library) indicate ground-colour of upperparts and top of head, slightly darker brown. Underparts and fringes to crown, scapulars and wing-coverts, deeper orange-buff with slight rufous tinge. Sides of breast and flanks, heavily mottled brown (c28).

Aberrant plumages Albino seen, Sept. 1953, Paua, ne. NI (Edgar 1969).

BARE PARTS Based on photos (McKenzie 1972; Moon 1992; Moon & Lockley 1982; NZRD; DOC Slide Library). Few differences known between populations. Adult Little seasonal variation. Bill, black, usually with very narrow pinkish-orange or dullpink base to lower mandible when in breeding plumage. Orbital ring, narrow, white. Iris, dark brown to blackish. Legs, grey (84) to dark grey (83), with slight olive tinge. Downy young Bill, dark grey (83) with pinkish tinge, particularly at base. Orbital ring, dark grey (83). Iris, dark. Legs, grey (84) with pinkish tinge. Juvenile, Immatures Apparently similar to adult.

MOULTS About 60 skins examined, but only c. 25 with reliable data (AWMM, CM, NMNZ). Adult post-breeding (Pre-basic). Complete. Primaries outwards; about two primaries active at a time. Generally moult over summer; two skins in primary-moult, Feb. Adult pre-breeding (Pre-alternate). Partial, involving feathers of head and body, lesser and probably median wing-coverts. Begins July, usually complete by Sept. Pre-juvenile Details unknown; fly at 28–52 days (McKenzie 1952; McKenzie et al. 1977). Post-juvenile (First pre-basic). Partial, involving feathers of head and body, lesser and outer median wing-coverts. Begins about Jan. and finishes Mar.—Apr. Immature pre-breeding (First pre-alternate). Partial. Similar in extent to adult pre-breeding. Details, unknown. Immature post-breeding (Second pre-basic). First complete moult. Similar to adult post-breeding, but possibly begins earlier. Single skin with primary-moult score of 30 in Feb.

**MEASUREMENTS** (1–2) NI, skins; sexing based on labels (AM, AWMM, CM, NMNZ): (1) adults; (2) juveniles.

dyeme	MALES	FEMALES	301
WING	(1) 159.3 (5.33; 149–166; 10) (2)	159.1 (4.10; 152–166; 10) 153.4 (9.29; 143–163; 5)	ns
8TH P	(1) 101.3 (5.33; 94–109; 10)	101.8 (4.19; 93–107; 10)	ns

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(3) SI, adults, skins; sexing based on labels (AM, AWMM, CM, NMNZ).

MALES			FEMALES	
WING 8TH P TAIL BILL F TARSUS TOE	(3) (3) (3) (3)	167.2 (2.71; 163–171; 6) 103.2 (3.43; 97–107; 6) 67.3 (2.07; 65–71; 6) 28.0 (2.62; 24.1–30.7; 6) 39.7 (2.27; 35.9–42.9; 6) 23.7 (1.33; 21.1–24.7; 6)	163, 166 101, 102 63, 67, 67 26.4, 28.2, 29.8 38.0, 42.5 23.9, 24.2	rewnord redsliged rodw yn reange li rea exe

Wing of males, significantly larger (P<0.05) for SI (3) than for NI (1).

(4) Skins (mostly with no collection data or sex); ages and sexes combined. Where possible skins assigned, strictly on basis of plumage, to light form or dark form for analysis. Data show that dark birds are significantly larger. The population on Stewart I. appears to be entirely dark birds and the population in NI light birds, though many of the skins are old enough to have come from now extinct breeding populations in mountains of Canterbury and Wellington.

smilnode	es d	LIGHT FORM	DARK FORM	h
WING	(4)	158.0 (6.00; 143–166; 27)	166.2 (4.26; 156–174; 24)	*
TAIL	(4)	62.9 (3.53; 56–69; 28)	66.8 (2.37; 63–72; 24)	*
BILL F	(4)	27.7 (2.21; 22.1–30.9; 28)	28.8 (1.91; 24.1–32.4; 26)	ns
TARSUS	(4)	37.9 (1.87; 34.1–41.4; 25)	40.1 (2.15; 35.9-43.8; 26)	*
TOE	(4)	22.4 (1.13; 20.4–24.5; 25)	23.2 (1.07; 21.1–24.7; 21)	ns

WEIGHTS E. coast N. Auckland, NI, adults, live, unsexed (J.E. Dowding): 146 (10.41; 129-168; 23). Stewart I.: adult male, 156 g; adult female, 124 g; NI: juvenile female, 92; second year, unsexed, 123 g (museum labels: AWMM, NMNZ).

STRUCTURE Large, rather squat and plump plover. Wing, long, narrow. Eleven primaries; p10 longest; p9 1-4 mm shorter, p8 6–11, p7 16–21, p6 27–32, p5 39–43, p4 49–54, p3 60–66, p2 68–77, p1 76–84, p11 minute. Fifteen secondaries, including four tertials; longest tertial falls between p6 and p8 on folded wing; possibly differs between populations. Tail, square; 12 rectrices. Bill, heavy like Pluvialis plovers and intermediate between P. fulva and P. squatarola, but more attenuated than either. Culmen, bulged at tip; slight gonydeal angle, half-way along lower mandible, more pronounced than in Pluvialis plovers; slightly heavier in dark form. Nasal groove, deep and wide. Eye, large, prominent. Tarsus, moderately long and slim; slightly heavier in dark form. Scales, reticulate. Outer toe 82-88% of middle, inner 64-71%, no hind toe. Moderate semipalmation between middle and outer toes. Claws, typical of plover, slightly twisted outwards.

GEOGRAPHICAL VARIATION Considerable and complicated. No subspecies described. Two isolated populations, one breeding n. NI, the other on Stewart I. Plumage differences between populations covered above, under light- and darkplumaged birds. Historically, ranges of both populations much broader and possibly overlapping, with breeding reports from several montane localities in Canterbury, Nelson and Wellington districts (Buller 1873, 1888). No information on genetic isolation; populations may have interbred freely until recently or been long isolated by differences in breeding habitat (Dowding 1989); morphology suggests latter, but few skins with adequate data.

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Volume 2, Plate 61

New Zealand Dotterel Charadrius obscurus (page 818)

1 Adult breeding, s. population; 2 Adult breeding, n. population; 3 Adult non-breeding; 4 Downy young; 5 Juvenile; 6, 7 Adult non-breeding

Shore Plover *Thinornis novaeseelandiae* (page 912) 8 Adult male; **9** Adult female; **10** Downy young; **11** Juvenile; **12, 13** Adult male