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Order GRUIFORMES

Diverse assemblage of small to very large wading and terrestrial birds. Morphologically diverse, with few unifying characters within the Order. Anatomical details are summarized by Sibley & Ahlquist (1990). Possibly polyphyletic, though DNA comparisons indicate that the Order is monophyletic, composed of highly divergent groups that are more closely related to one another than to members of any other order (Sibley & Ahlquist 1990). The boundaries of the Order and relationships with other Orders and between families in this Order are uncertain (Sibley 1960; Sibley & Ahlquist 1972, 1990; Cracraft 1973; G.F. van Tets).

Peters, Wetmore (1960) and Storer (1971) recognized 12 families: Eurypygidae (monotypic Sun-bittern of tropical America); Otididae (bustards); Gruidae (cranes); Heliornithidae (finfoots of tropical Old and New World; three monotypic species); Aramididae (monotypic Limpkin of tropical and subtropical America); Psophiidae (trumpeters of tropical America; three species in single genus); Cariamidae (seriemas of central S. America; two monotypic genera); Rhynochetidae (monotypic Kagu of New Caledonia); Rallidae (crakes and rails); Mesitornithidae (mesites of Madagascar; three species in two genera); Pedionomidae (monotypic Plains-wanderer of Aust.); and Turnicidae (button-quails).

The Plains-wanderer is now recognized as being a charadriiform on evidence of morphology (Olson & Steadman 1981) and DNA-DNA hybridization (Sibley *et al.* 1988). Sibley *et al.* (1988) and Sibley & Ahlquist (1990) placed the Turnicidae in a separate Order, the Turniciformes *incertae sedis* (which we follow here; q.v.) and included Aramididae within the Heliornithidae but otherwise retained a similar arrangement of families. The Mesitornithidae, Rhynochetidae and Otididae have also been regarded as separate Orders.

Only Gruidae, Rallidae and Otididae occur in our region; other families are not considered further here.

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Family RALLIDAE rails, crakes and gallinules

A group of small to medium-sized (12–65 cm long), generally slender, terrestrial birds, usually of wetlands, often very secretive and skulking. Almost cosmopolitan, not occurring in polar regions and waterless deserts. In our region, 17 breeding species in 11 genera, five accidentals (one doubtful) and three extinct. Relation to other Gruiformes not fully resolved; skeletal morphology suggests close alliance to Psophiidae (trumpeters) and Heliornithidae (sungrebes) (Cracraft 1973); Aramididae, Eurypygididae and Cariamididae of S. America, and Rhynochetidae of New Caledonia and the extinct Aptornithidae of NZ also closely related; some or all of these families could be included as sub-families in Rallidae (G.F. van Tets). DNA–DNA hybridization evidence shows Rallidae form a distinct cluster separate from cranes and their allies (Sibley & Ahlquist 1990). Olson (1973b) recognized two sub-families: the monotypic Himantornithinae and the Rallinae, with Himantornithinae intermediate between Rallinae and Psophiidae. The Jacanidae (Charadriiformes; q.v.) may be derived as aquatic specialists from *Gallinula*-like stock and more appropriately placed within the Rallidae (G.F. van Tets).

Arrangements within the Rallidae have varied: Peters recognized 52 genera; Thomson (1964), 45; Olson (1973b), 35; Ripley (1977) 17; BWP, 32–39; Campbell & Lack (1985), 18; and Sibley & Ahlquist (1990) 34 (142 species). Rallidae vary anatomically in relation to diet and habitat. Olson (1973b) suggested they evolved from terrestrial to aquatic but admits evolution may have occurred several times. For practical purposes, broad division often made into (1) rails, crakes and wood-rails, most of which are terrestrial (in HANZAB region: *Rallina*, *Gallirallus*, *Dryolimnas*, *Porzana*, *Eulabeornis*, *Crex*); and (2) coots and gallinules (including swamphens, native-hens and waterhens), which tend to be more aquatic (in HANZAB region: *Amauornis*, *Gallinula*, *Porphyrio*, *Fulica*, *Gallicrex*). The affinities of the genera and, in brackets, the number of volant and flightless species recorded in HANZAB region given below. *Rallina* (2, 0): one species occurring Aust. and New Guinea and another vagrant to Aust.; close relatives are *Canirallus* and *Sarothrura* of Africa, *Mentocrex* of Madagascar and *Rallacula* of New Guinea (Olson 1973b). *Gallirallus* (1, 4): widespread in Indo-Pacific region; one or more species of volant *Gallirallus* are thought to be ancestral to several insular species in the sw. Pacific, including *lafresnayanus* of New Caledonia and *sylvestris* of Lord Howe I. (Olson 1973b; Fullagar & Disney 1981; Schodde & de Naurois 1982; Diamond 1991). *Dryolimnas* (1, 0): one species (*pectoralis*) occurring Aust. and Auckland Is; closely related to *Gallirallus* and *Rallus*; *pectoralis* often placed in *Rallus*. *Amauornis* (1, 0): one species occurring Aust., New Guinea, Philippines and Moluccas. *Porzana* (5, 0): worldwide, with four species native to our region and one vagrant; we follow Mees (1982) by including *Poliolimnas* in *Porzana*; Olson (1973b) thought *Porzana* may have evolved from *Amauornis*. *Eulabeornis* (1, 0) endemic to n. Aust. and Aru Is, and according to Olson (1973b), an allopatric close relative of *Habroptila* (1, 1) of Wallacea and New Guinea. *Crex* (1, 0) breeds in Eurasia and migrates S, mainly to Africa; vagrant to Aust. and, doubtfully, to NZ. *Gallicrex* (1, 0): vagrant from se. Asia to Christmas I. (Ind.); may also have derived from *Amauornis*. *Gallinula* (2, 1) worldwide distribution, with three species in our area; also an *Amauornis* derivative; sub-genus *Tribonyx* is endemic to Aust. with a fossil record going back to Pliocene (Olson 1975); differ from *Gallinula* in broad bill, long tail and short toes. *Porphyrio* (2, 2) appears to be a *Gallinula* derivative, with sub-genus *Porphyryla* intermediate in shape and plumage between *Gallinula* and nominate *Porphyrio* of Africa, Asia and Aust.; the sub-genus *Notornis* of Lord Howe I. and NZ consists of obvious derivatives of the nominate, but are terrestrial with an exceptionally deep bill and short toes. *Fulica* (1, 0): worldwide distribution, with one species in our region, and two flightless extinct species in NZ; probably derived from *Gallinula*-like stock (Olson 1973b).

Bodies, short, often laterally compressed for ease of movement in dense vegetation. Neck, short or moderately long; 14–15 cervical vertebrae. Males, often slightly larger than females. Wings, short, broad, rounded; in volant species, flight appears low, weak and generally not sustained though some species capable of long-distance movements, occurring on or colonizing oceanic islands (e.g. Purple Gallinule *Porphyrio martinica*, Watercock *Gallicrex cinerea* in HANZAB region). Some island species are flightless, yet many others migrate or disperse over long distances. In HANZAB region, all species have 11 primaries (p11 minute) and 10–12 secondaries; in Family, 10–20 secondaries, smaller species have ten and some flightless species have fewer primaries (BWP); diastataxic. Short sharp curved claw on alula. Tail, short, square to rounded, soft; often raised or flicked up to signal colours of under tail-coverts; normally 12 (6–16) rectrices. Bill varies: often rather slender, straight and slightly longer than head, and in some species, slightly decurved; or quite short and laterally compressed (crakes, most gallinules, coots); or massive and laterally compressed (some species of *Porphyrio*). Gallinules and coots have smooth, plate-like horny frontal shield (continuous with ramphotheca) on forehead. Nostrils usually in large depression (not in *Porphyrio*), pervious and perforate in some species. Sense of smell said to be well developed (Ripley 1977). Legs, well developed, usually strong, long to quite short, often laterally compressed. Toes, long and slender but may be rather short and heavy; hind toe, large, slightly raised. In most gallinules (not native-hens *Gallinula*, Takahe *Porphyrio mantelli* and White Gallinule *P. alba*) and some crakes, toes greatly elongated and legs modified for walking on floating vegetation; in coots, toes have enlarged lateral lobes to aid swimming, and pelvis and legs modified for diving. All species can swim; dive easily and can sink, using wings under water if necessary. Many species climb easily among thick vegetation; downy young of some (and

possibly adults) use wing-claw to assist climbing. Oil-gland bi-lobed, feathered in most species. Caeca, long. Syrinx, simple; tracho-bronchial. Feathers, fairly loose and soft, frayed and even hair-like in some; small after-feather usual.

Plumage, generally sombre browns, chestnut, black, or greys; iridescent purplish-blue and green in *Porphyrio*. Barring on flanks common. Vent and under tail-coverts may contrast with rest of plumage. Upperparts, spotted, barred, streaked, or plain. Bare parts often brightly coloured and forehead shield conspicuous. Sexes usually similar or nearly so (except in *Sarothrura* and *Gallixrex*). Pre-breeding moults restricted or absent, with no seasonal changes in appearance (except in *Gallixrex*) but colours of bare parts change in some species, coinciding with moults. Post-breeding moult, complete. Remiges may be moulted irregularly, or simultaneously, with consequent flightless period. Post-juvenile moult partial; can be followed by partial pre-alternate moult or by complete second pre-basic. Young, downy, and unlike other precocial birds, black (sometimes iridescent) or dark brown, which may be an adaptation for hiding in dense vegetation; evidently a derived condition (Olson 1973b). In some species, downy young have brightly coloured bills or skin on head or both, which may function for signalling (Fjeldså 1977). Downy young of *Gallinula*, *Porphyrio* and *Fulica* also have white or yellow terminal bristles on down. Post-natal development slower than in some other precocial birds, such as Galliformes and Turniciformes, with initial emphasis on development of legs and feet and not wings; flight-feathers develop last. Juveniles generally similar to but duller than adults.

Numerous flightless forms; incidence of flightlessness perhaps greater than in any other group except ratites and penguins. Flightlessness has evolved many times within the Rallidae, often and repeatedly on islands without predators and probably independently each time; appears to evolve rapidly and so probably of little phylogenetic significance above the level of species (Olson 1973a). Selection reduces flight-muscle and pectoral girdle, possibly through neoteny (Olson 1973a); usually corresponding increase in development of leg muscles. Frequency of flightlessness suggests that rails are predisposed to it; they are certainly pre-adapted for coping with some of the restrictions it imposes: many volant species are behaviourally flightless, e.g. avoiding predators by running away; many are temporarily flightless during wing-moult (a feature shared with several other groups containing flightless forms), when secretive and elusive; and post-natal development of flight is slow. In many species, populations of insular flightless species exterminated by introduced predators (e.g. Chatham Island Rail *Gallirallus modestus*, Dieffenbach's Rail *Gallirallus dieffenbachi*). Subfossils from our region have been reviewed (Olson 1977) and include flightless and often large species of coot, waterhen, rail and wood-rail and the distinctive snipe-rail *Capellirallus*. For discussion of biogeography of *Gallirallus* see Olson (1973b), Fullagar *et al.* (1982), Schodde & de Naurois (1982), and Diamond (1991).

Most inhabit all sorts of terrestrial, estuarine and littoral wetlands, from sea-level to mountain highlands. Some genera found in lowland and montane forests; others in wet grasslands; still others, e.g. Takahe *Porphyrio mantelli*, *Crex*, tussock grasslands, hay-fields and similar places, not necessarily with wet areas. Some species migratory; many dispersive; others apparently sedentary. Patterns of movements in HANZAB region generally not known, perhaps because they appear to take place at night and perhaps because the birds are so secretive and silent when not breeding that absences may be more supposed than real. Gallinules and coots appear to be more sedentary than crakes and rails, though at least the Black-tailed Native-hen *Gallinula ventralis* is notably irruptive, in response to floods and droughts of inland Aust.

Omnivorous, or in some species mostly vegetarian. Species with long thin bills probe for invertebrates in soft ground and litter. Eat all sorts of plants and submerged vegetation, insects, molluscs, crustaceans, eggs and young of other birds, small fish and carrion. Some gallinules graze, e.g. Tasmanian Native-hen *Gallinula mortierii* and coots. Only *Fulica* dives for food; they and *Gallinula* will up-end. Often wash food in water.

Mostly solitary or in small groups, though densities can be very high in some wetlands; *Gallinula* (e.g. Black-tailed Native-hen *Gallinula ventralis*) and *Fulica* form large flocks, especially in winter; after onset of inland droughts, irruptions may involve thousands of birds. Roost solitarily except in species that flock; generally at night on ground in cover; occasionally in bushes and trees. Some species nocturnal or crepuscular. Most species nest solitarily; some strongly territorial, advertising territories with loud persistent calling and chasing of intruders. Dense vegetation and apparently secretive habits make it hard to study social organization and behaviour in most species. Agonistic and sexual behaviour often conspicuous with wing-spreading, tail-flicking, fighting with use of bill and feet and other ritualized features of display. Pair-bond usually monogamous and only for one season but may be sustained. Polygyny known in captivity and suspected in wild, e.g. in *C. crex*; polyandry occurs in Tasmanian Native-hen *Gallinula mortierii* and possibly Weka *Gallirallus australis*. Co-operative breeding in some gallinules, e.g. Dusky Moorhen *Gallinula tenebrosa*. Pair-formation and courtship little known except in some gallinules and coots, in which a variety of chasing, bowing, nibbling, mock-preening and feeding, and courtship feeding takes place; no elaborate ceremonies at time of nest-relief. Copulation and other activities take place out of water or on specially built platforms. Most species very vocal, with screams, trills, whistles, booms, rattles, trumpets, grunts or barks; can be ventriloquial; mostly silent when not breeding but social species have loud rallying cries. Stand at rest (sometimes on one leg) in hunched posture with head sunk on shoulders, or lie down; sleep with head on back and bill among feathers. Bathe in shallow water, alternately ducking head in water and flipping water over back or by beating half-open wings in water; coots may bathe while swimming. Leave water to oil and preen after bathing. Sun themselves after preening. Allopeening common. Scratch head directly. Some species (e.g. *Porphyrio porphyrio*, *P. alba*, *P. mantelli*) recorded manipulating and grasping food in foot or holding down large items with feet.

Breed seasonally and protractedly. Nest fairly deep and cup-shaped; in some rails, domed; in wetlands, often with ramps up to nests. In thick vegetation, often near or on surface of water but some species nest high in trees; use old nests of other birds or nest on ground far from water; materials from any available plants; built by both sexes. Horned Coot *F. cornuta* of S. America builds islands of small stones. Some build nests that float or are attached to aquatic vegetation; nests on water may be built up rapidly if water-level rises. Non-functional nests often found in gallinules and *Gallinula*, which also build nursery nests after young hatch. Eggs, blunt oval; smooth and fairly glossy; dull white to tan ground-colour, blotched and spotted red-brown to black; unspotted in *Rallina*. Clutch-size, 5–10 (1–18) but dump-laying or laying by more than one female in same nest may complicate estimation of size of clutch laid by an individual. Usually one or two broods and replacement layings up to three times. Lay at intervals of 24 or 48 h. Incubation usually by both sexes but in some by female alone or with only small share by male. Incubation period, 14–24 days per egg; start of incubation varies from first to last egg and so hatching synchronic or asynchronic. Egg-shells left in nest or removed. Generally have two large lateral and one small median brood-patches. Young hatch in down, precocial, nidifugous; at first fed bill to bill, becoming self-feeding within few days or not until 8 weeks old. Normally tended by both parents and, in a few species, offspring of previous broods may help to feed young, e.g. *Gallinula*, occasionally *Porphyrio*. Fledging period, 30–60 days (20–70) and then independent except in co-operative breeders. First breeding usually when 1 year old or less.

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Gallirallus australis Weka

COLOUR PLATE FACING PAGE 520

Rallus australis Sparrman, 1786, *Mus. Carls.* fasc. 1: text for Pl. 14 — New Zealand.

Australis is Latin for southern.

OTHER ENGLISH NAMES Maori or Kelp Hen; Troglodyte or Weka Rail; Black, Brown, North Island and South Island Woodhen or Weka; Stewart Island, Buff, Eastern, and Western Weka.

Weka is a Maori name.

POLYTYPIC Nominate *australis*, n. and w. SI, from n. Marlborough to Fiordland; introduced Kapiti, Chatham and Macquarie Is (extirpated on latter); *greyi* (Buller, 1888), NI, formerly throughout but now mainly Poverty Bay area; introduced Kapiti, Rakitu, Mokoia, and Kawau Is and Bay of Islands; *hectori* (Hutton, 1874), e. coast and interior of SI, NZ, from Marlborough to Southland, now restricted to Chatham Is, where introduced; *scotti* (Ogilvie-Grant, 1905) Stewart I.; introduced to Solander and other outlying islands off Stewart I. and also Kapiti and Macquarie Is (extirpated on latter).

FIELD IDENTIFICATION Length: male 50–60 cm, female 46–50 cm; wingspan: male 50–60 cm; weight: male 520–1400 g, female 370–950 g. Large thicket flightless rail with stout bill, legs and feet; slightly smaller than Purple Swamphen *Porphyrio porphyrio* and larger than Buff-banded Rail *Gallirallus philippensis*. General colour and pattern of underparts varies much. Sexes similar; females smaller, bill and legs differ. No seasonal variation. Juvenile separable. Marked geographical variation: four subspecies: *australis* and *scotti* have chestnut, grey and black morphs; *greyi* and *hectori* similar to chestnut morphs of *australis* and *scotti*.

Description **Adult male** Forehead, crown, nape and hindneck, rufous-brown narrowly streaked blackish; supercilium,

chin and throat, dark grey, with broad rufous-brown stripe from bill to hind ear-coverts. Rest of upperbody, rufous-brown to yellowish buff with broad blackish-brown streaking; tail, rufous-brown to buffish brown with blackish barring. Wing-coverts, as upperbody but edged and notched rufous-brown or yellowish buff; remiges, chestnut with black barring. Broad rufous-brown breast-band, boldly streaked blackish, across foreneck and upper breast (lacking or inconspicuous in *greyi*); fore-flanks and upper belly, dark grey with faint darker barring; rest of flanks, belly, vent and under tail-coverts, rufous-brown, with broad dark barring grading to narrow black barring on under tail-coverts; in *hectori*, flanks, vent, under tail-coverts and undertail, yellowish brown with narrow

black barring; barring on flanks generally lacking in *greyi*. Bill, dull pink to grey at base, cream to grey distally; entirely pinkish grey in *scotti*. Iris, red to reddish brown, brown, light chestnut; thin white arc under eye. Legs and feet, dull red, brownish red or orange, some with darker hind-edge of tarsus. **Adult female** As male except: bill, paler, dull pinkish, darker pink basally and paler at tip; legs and feet, generally paler pink or orange-brown. **Black morphs** Like other morphs and subspecies but with broader black streaking and richer dark-chestnut margins to feathers, giving overall darker, more blackish appearance; legs and feet, darker brown. **Juvenile** Generally darker than adult (though lighter in subspecies *hectori*); dark markings less distinct and plumage generally more drab; bill, darker, grey-black; iris, darker, brown, lightening to tan; legs, grey-brown.

Similar species Normally unmistakable; superficially similar **Buff-banded Rail** can fly, is smaller, slimmer with bolder whitish supercilium and generally brighter chestnut eye-stripe extending to sides of neck and round hindneck; brownish-olive upperparts spotted white; underparts, finely barred black and white with narrow buff breast-band; different habitat. Spacing call of Weka sometimes confused with whistling territorial call of male Brown *Apteryx australis* and Little Spotted *A. owenii* Kiwis, but call of male Brown Kiwi more constant, repetitive and guttural, with resonant rolled 'r' sound; call of male Little Spotted Kiwi more constant, repetitive and each call lasts longer than that of Wekas. Advertising call of male Weka sometimes confused with Crowing of Purple Swamphen (q.v.).

Singly, in pairs or family groups in many habitats ranging from rocky shorelines to alpine tussock grasslands and settled districts. Generally secretive and wary but can be tame and inquisitive, especially round habitations. Semi-nocturnal, keeping to dense cover during day and becoming active in late afternoon and into night; active in open habitat at night. Gait, a slow deliberate walk with flicking tail, fast deliberate walk while foraging and fast run with head lowered; swim readily and well. Most commonly heard call, a shrill whistle, rising in pitch and repeated many times, often given by pair in duet; most often at dawn or dusk; also, resonating boom given by territorial birds, sometimes preceding main call but also while feeding or during disputes.

HABITAT Margins of marine, littoral, estuarine and terrestrial wetlands as well as woodlands, forest and grasslands; from sea-level to c. 1500 m asl, though apparently prefer lower altitudes in central Westland (<300 m asl) and avoid intermediate altitudes (400–800 m asl) (Falla *et al.* 1981; Child 1982; Coleman *et al.* 1983; NZCL). Prefer low vegetation that offers cover but does not hinder movement; require water (Carroll 1963a). Inhabit hills, mountains, sand-dunes and urban environments; gullies, valleys, moraines, sandy and rocky shores, cliffs (Fleming 1939b; Gee 1956; Coleman *et al.* 1983; Brothers & Skira 1984; CSN 21, 31). Forest, woodland, scrub and grassland usually with some cover; in some areas, prefer margins of forest; avoid forests lacking suitably dense understorey and enough food (e.g. pure open Beech *Nothofagus* and young pine *Pinus radiata* forests) (Johnson 1954; Carroll 1963a; Coleman *et al.* 1983; Brothers & Skira 1984; Beauchamp 1987b, 1988a). Also in subalpine tussock grassland (Child 1982; Coleman *et al.* 1983). Occur on beaches, particularly with rotting seaweed, and tidal creeks and bays (Edgar 1962; Blackburn 1968; Robertson 1976; Brothers & Skira 1984; Cooper & Morrison 1984; CSN 20; Oliver). Also occur in modified habitats, such as lawns, rough pastures, cultivated land, plantations (Johnson 1954; Gee 1956; Lindsay *et al.* 1959; Carroll 1963a; MacMillan 1990; Oliver; CSN 20).

Climb to c. 2 m in vegetation (St Clair & St Clair 1992).

Roost under logs, among rocks and in open (Beauchamp 1987a; Oliver). Nest in dry sheltered situations in or under vegetation, under logs, rock overhangs, in burrows and even outbuildings (Carroll 1963a; NZRD); occasionally in open (Beauchamp 1987a).

Modification of habitats by introduced mammals, especially browsers, may affect populations of Weka (A.J. Beauchamp). In broadleaf forests, possums may compete for native fruits that are part of Weka diet, thus leading to reduction in Weka population (Beauchamp 1987b). Few recorded in forests being logged (Onley 1983); nests destroyed by tree-felling (Guthrie-Smith 1910). Claimed that agricultural development and introduced predators caused decline in Weka numbers in parts of NI and SI late in nineteenth century (NZRD). Wekas may alter vegetational succession (St Clair & St Claire 1992). Wekas adversely affect native fauna on some offshore islands to which they have been introduced; in some areas eradication has been undertaken (Blackburn 1968; Brothers & Skira 1984; Veitch & Bell 1990), though need to do so on some islands is disputed (Atkinson & Daniel 1985; Jolly 1985).

DISTRIBUTION AND POPULATION NZ; formerly throughout NI, SI, D'Urville and Stewart Is and some inshore islands; now mainly moist upland areas of Poverty Bay and Bay of Plenty, and n. and w. SI. A few scattered populations elsewhere on NI and SI. Introduced to many offshore and outlying islands, including Chatham and Macquarie Is.

NZ NI Small numbers Gisborne and moist areas in Raukumara Ras–Wairoa district, from Tikitiki to L. Waikaremoana, S to 39°S; small numbers at Opuia and Parekura Bay of Islands. In 1993, birds found on Rakitu, Makoia and Kawau Is, and being liberated in the Karangahake Gorge (A.J. Beauchamp). **SI** Marlborough, Nelson and n. Westland, W of line from near Picton to L. Sumner and Hokitika; scattered locations S to Okuru and Open Bay islands; w. Southland, from about Milford Sound, S to West Cape, and inland to the Murchison Mts; Stewart I. and adjacent islands; also Solander I. (Cooper & Morrison 1984; NZ Atlas).

Formerly throughout NI and much of SI; range contracted in many areas. Found in most of NI until 1915–25; extinct in most areas by 1940 (Gee 1956; McKenzie 1979; Coleman *et al.* 1983; MacMillan 1990; Oliver; CSN 5). Extinct e. SI by 1924 (Coleman *et al.* 1983). In nw. Nelson and central Westland, 1980–90, recolonizing previous range (A.J. Beauchamp). No evidence that avian epidemic most likely cause of reduction of population and range (A.J. Beauchamp *contra* Williams 1960).

Introductions NI Transferred from Gisborne to several NI sites, 1960s–1980s; only two successful: (1) birds released Rawhiti, Bay of Islands; total of 149 birds released in six groups between 1966 and 1971 (Robertson 1976); by Feb. 1987, population increased to ≤ 400 , and spread throughout Rawhiti–C. Brett district (Beauchamp 1988a) and declined 1989–91 to c. 40 (A.J. Beauchamp); (2) birds from successful Rawhiti population liberated Opuia, Bay of Islands (A.J. Beauchamp). Successfully re-established Mokoia I., L. Rotorua, 1958. Unsuccessful releases at numerous sites in Auckland, Bay of Plenty, Hawke's Bay, Northland, Waikato, Wanganui and Wairarapa. **SI** In 1962, 16 birds from Chatham Is (of Canterbury descent) reintroduced unsuccessfully to Arthur's Pass NP after extinction in Canterbury in about 1917 (Long 1981; Oliver; NZCL; A.J. Beauchamp). Also Taramakau and Ottra Valleys, Oct. 1965 (CSN 19); unsuccessful (A.J. Beauchamp). **Offshore islands** Rakitu Is, 13 birds, Oct. 1951; in 1960, up to 100 present; in 1993, up to 135 (Bell & Brathwaite 1964; A.J. Beauchamp); D'Urville I., 1936, 1942 (Elliott 1983); Chetwode I. 1928, (NZCL; B.D. Bell); Kawau I.,

1863 (Oliver), 1976 (A.J. Beauchamp); Open Bay Islands, about 1905, 1912 (Stirling & Johns 1969); three birds (male from Stewart I.; female and young from Waikanae, NI), Kapiti I., c. 1895 (Wilkinson 1927), another liberation from 'Western Sounds', SI, early this century (Cowan 1907); islands round Stewart I.: introduced by Maori to provide food (Miskelly 1987; Oliver); Green I.; Jacky Lee I., after 1901; reintroduced Herekopare I., early 1920s, after extinction or removal in 1912; Big South Cape I., between 1913 and 1923; Solomon I., before 1913; Big Mogygy I., before 1918; Kundy I., 1947; Codfish I.; Big Solander I. before 1837 (Miskelly 1987). **Removals** Removed from Awaiti, Codfish, Herekopare, Kundy, Rabbit, Tawhitinui and Middle Trio Is because nesting seabirds and other wildlife were said to be threatened (Miskelly 1987; West & Imber 1989; Veitch & Bell 1990). Attempts to remove birds from Maud I., Marlborough Sounds, in 1978 failed when birds kept returning (Wright 1981). Other attempts at removal unsuccessful (Veitch & Bell 1990).

Chatham Is Introduced Chatham and Pitt Is from Canterbury, 1905 (Fleming 1939a).

Auckland Is Unsuccessfully introduced, 1864 (Oliver).

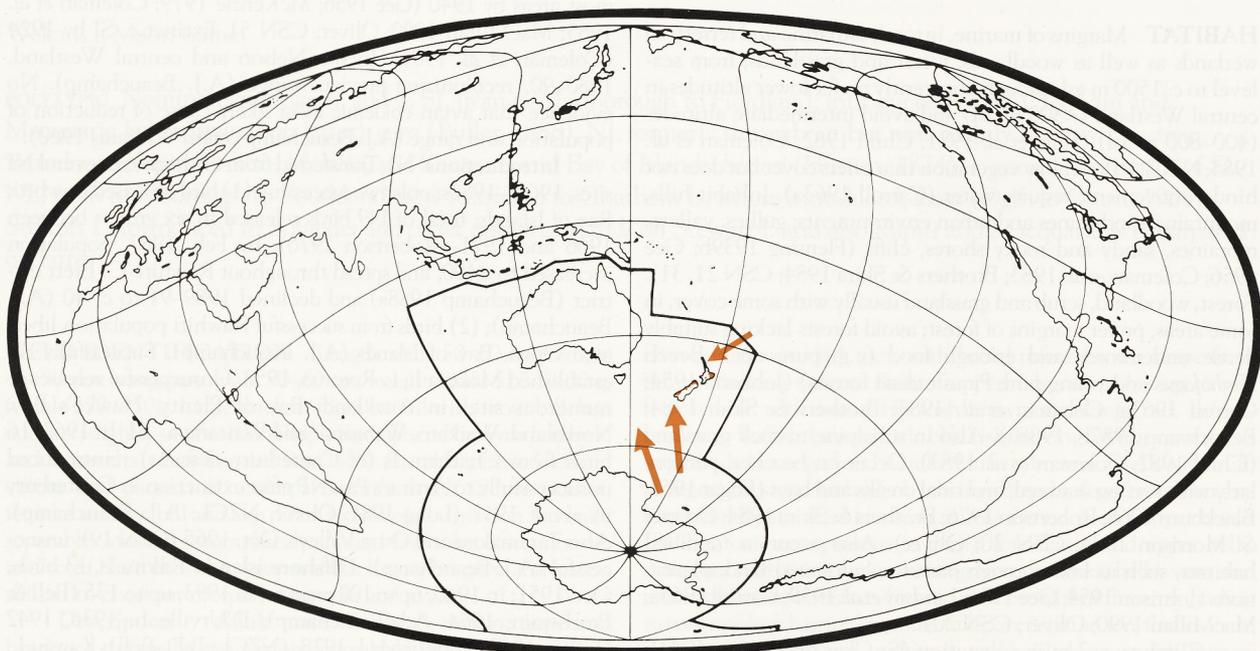
Macquarie I. Introduced but now extirpated (K. Green). Once numerous. Unknown number brought from Stewart I.; introduced c. 1830(?), 1867, 1874, 1879, 1886 by sealers and various sailors (Crowther 1933; Jones 1980; Brothers & Skira 1984; Oliver); were numerous and widespread in coastal regions of n. half of island (Brothers & Skira 1984).

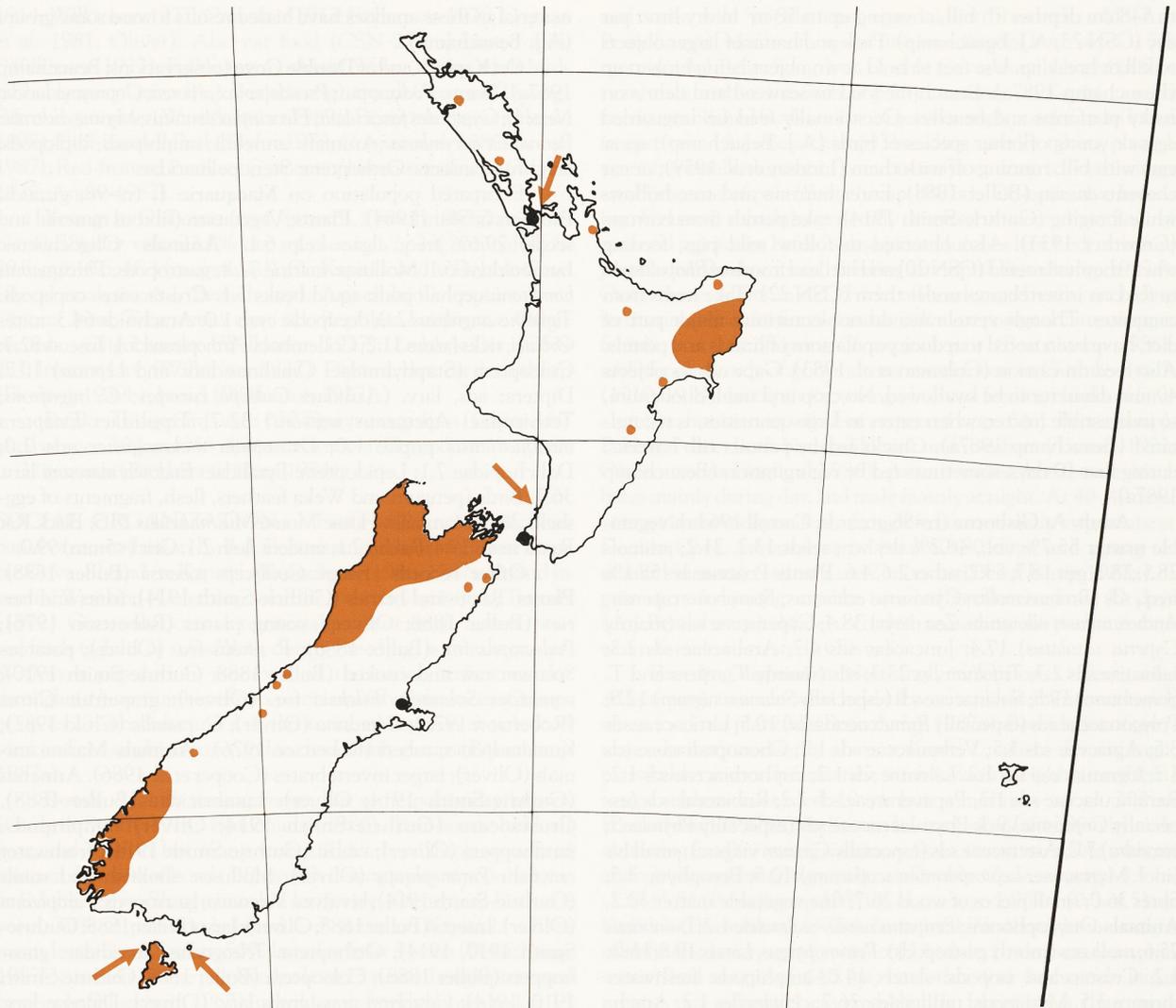
Generally rare; Gisborne, Northland and Bay of Plenty; common Marlborough Sounds, Nelson, n. Westland and Fiordland; also on some offshore islands (NZRD). Few measures of abundance. On Kapiti I., 1986, 0.8 birds/ha; Double Cove, Marlborough Sounds, 0.3 birds/ha; Bay of Islands, 1993, 0.05 birds/ha; Rakitu I., 1993, 0.8 birds/ha; Kawrau I., 1993, 0.65 birds/ha; Motu Valley, 1987, 0.3 birds/ha; Rakauora, 1986, 0.4 birds/ha; Allports I., SI, 1986, 0.75 birds/ha (Beauchamp 1987b; A.J. Beauchamp). In Rawhiti-C. Brett district, ≤ 400 birds, 1987 (Beauchamp 1988a). In 1970s, estimated up to 500 individuals on Macquarie I. (Brothers & Skira 1984). Populations can fluctuate markedly, possibly in response to climate or availability of food (Beauchamp 1987a),

e.g. Gouland Downs (Williams 1960). Local irruptions occur and Weka readily recolonize areas (Davenport 1950; Wright 1981; Coleman *et al.* 1983; Beauchamp 1988a; NZRD; Oliver).

Used by Maori and early settlers for food, oil and medicinal purposes (Oliver). Currently protected in most places except Chatham Is, where hunting parties took one hundred at a time during 1950s (Fleming 1939a; Bell 1955; Lindsay *et al.* 1959; NZRD), and islands of Foveaux Str. and round Stewart I. (A.J. Beauchamp). Sometimes considered a pest because birds pull up seedling crops, kill poultry and eat eggs (Johnson 1954; Lindsay *et al.* 1959; Carroll 1963a; Oliver). Eat grubs and pest insects (Carroll 1963a; Oliver). Often caught in possum traps (Secker 1964; Robertson 1976; Coleman *et al.* 1983). Cyanide baits laid for possums have reduced local populations in Marlborough Sounds (Beauchamp 1987b). Introduced predators were thought to have been main cause of local declines or extinctions (Stuart-Sutherland 1919; Pracy 1969; Oliver) but now thought unlikely (Robertson 1976; Coleman *et al.* 1983). Recolonizations may be hindered by predators (Pracy 1969; A.J. Beauchamp). Seen on side of roads, where many killed when population densities are high (Carroll 1963a).

MOVEMENTS Sedentary, flightless. Greatest natural movements 9 km by subadult and 35 km by adult male, both of which meant crossing major rivers or lakes (Coleman *et al.* 1983; Beauchamp 1987b). Adults generally confined to territories or core areas of home-range throughout year (Beauchamp 1987a); in Westland, adults moved on average 189 ± 80 m and subadults 170 ± 94 m between sightings on successive days (Coleman *et al.* 1983); can walk up to 1 km from territory to profitable feeding areas (A.J. Beauchamp). When subadults leave parental territories, establish core areas where they stay for life or move round different core areas until they die or establish a territory (Beauchamp 1987a). When adults displaced from territories, either established core areas near former territories or moved away and died soon after (Beauchamp 1987a). Mass migrations reported from 1890 to 1930s (Philpott 1914; Myers 1923; Guthrie-Smith 1910; Moncrieff 1928; Turbott 1967); associated with





disappearance of many populations in NI (Myers 1923; Moncrieff 1928), but reasons for movements not known (A.J. Beauchamp). Rapid increases in populations recorded (Guthrie-Smith 1910); one due to movement in SI associated with plagues of mice (Moncrieff 1928); others possibly due to short-term changes in food supply (A.J. Beauchamp). In some populations numbers fluctuate; in Westland, considerable flux of birds through area apparent (Coleman *et al.* 1983; Oliver). Sudden disappearances may be due to disease (McKenzie 1979). Guthrie-Smith (1910) reported seasonal movement from hill-country in summer to lowland grass plains in winter at Tutira (Hawke Bay); birds also recorded leaving forest for more open habitat in summer (Turbott 1967). Most dispersal undertaken by subadults in first 6 months after independence; dispersal of young was principle movement in five well-studied populations (Beauchamp 1987a,b; A.J. Beauchamp); in study of 22 months on SI, one population raised 23 chicks, only two of which remained more than a year after fledging (Beauchamp 1987b). Dispersal usually occurred in two phases: (1) move to just outside parental territory, normally followed within 4 months by (2) longer movement to region where likely to establish territories. On Kapiti I., distance of latter movements from parental territory averaged 1.3 km with maximum 5 km (Beauchamp 1987a); on mainland, maximum exceeds 5 km

in Marlborough Sounds and 9 km in Westland (Coleman *et al.* 1983; Beauchamp 1987b). On Bravo I., dispersing subadults swam or waded at low tide to Stewart I. (Traill 1951). Subadults can walk at least 4 km per day (Beauchamp 1987a); in Westland one young adult moved 2 km overnight (Coleman *et al.* 1983).

Homing ability demonstrated by various recoveries. Three birds removed from Maud I. returned by walking at least 2.5 km and swimming at least 914 m; one of these birds returned twice (Wright 1981); another bird returned 130 km when relocated from Gisborne to Hawke's Bay (NZRD). One bird (I. Robertson) that escaped in Auckland during transfer was reported 72 km S, 6 weeks later (Robertson 1976). Dispersal after relocation: about half the birds released at Huia Bay, Waitakene Ras, stayed near site of release for up to 5 years; others recorded to have moved and re-established territories up to 18 km away (MacMillan 1990). In another relocation, birds established territories 8 km from site of release (Pracy 1969).

FOOD Omnivorous, opportunistic; mainly native fruit and invertebrates; also sometimes vertebrates. **Behaviour** Diurnal and nocturnal. Feed on ground. Scratch in litter with bill; do not use feet (A.J. Beauchamp; H.A. Robertson); occasionally pull apart bark and wood to extract food (Carroll 1963a), loosen leaf litter

to 5–8 cm depth with bill, covering up to 50 m² in dry litter per day (CSN 23; A.J. Beauchamp). Peck and hammer larger objects to kill or break up. Use feet to hold down object being broken up (Beauchamp 1987a). Search for food in seaweed and debris on rocky platforms and beaches. Occasionally feed on unguarded eggs or young of other species of birds (A.J. Beauchamp); spear eggs with bill, running off with them (Lindsay *et al.* 1959); or eat contents *in situ* (Buller 1888). Enter burrows and tree-hollows while foraging (Guthrie-Smith 1914); take petrels from burrows (Crowther 1933). Also observed to follow wild pigs, feeding where they had rooted (CSN 20) and lift dead fronds of *Rhopalostylis* to feed on invertebrates under them (CSN 22). Take items from campsites. Though vertebrates do not constitute major part of diet, have been noted to reduce populations of lizards and petrels. Also feed on carrion (Coleman *et al.* 1983). Gape allows objects 40 mm diameter to be swallowed. No crop and small duodenum, so indigestible matter, when eaten in large quantities, is regurgitated (Beauchamp 1987a). Chicks fed by parents till 7 weeks; during first 10 days, sometimes fed by regurgitation (Beauchamp 1987a).

Adult At Gisborne (n=86 gizzards, Carroll 1963a): vegetable matter 55.7% vol., 46.2% dry wt.; seeds 13.2, 21.2; animals 28.5, 28.1; grit 18.7, 53.2; other 2.6, 4.6. **Plants** Poaceae: lvs 58.1% freq., sds (*Bromus mollis*, *Cynosurus echinatus*, *Sporobolus capensis*, *Anthoxanthum odoratum*, *Zea mays*) 38.4; Cyperaceae sds (mainly *Cyperus ustulatus*) 17.4; Juncaceae sds 4.7; Araliaceae sds 2.3; Liliaceae sds 2.3; *Trifolium* lvs 23.3; sds (mainly *T. repens* and *T. glomeratum*) 19.8; Solanaceae sds (especially *Solanum nigrum*) 12.8; Polygonaceae sds (especially *Rumex acetosella*) 10.5; Urticaceae sds 3.5; Apiaceae sds 3.5; Verbenaceae sds 1.2; Chenopodiaceae sds 1.2; Geraniaceae sds 1.2; Labiatae sds 1.2; Euphorbiaceae sds 1.2; Ranunculaceae sds 1.2; Papaveraceae sds 1.2; Rubiaceae sds (especially *Coprosma*) 9.3; Phytolaccaceae sds (especially *Phytolacca octandra*) 7.0; Asteraceae sds (especially *Cirsium vulgare*); small lvs (incl. Myrtaceae: *Leptospermum scoparium*) 10.5; Bryophyta: 3.5; fibres 36.0; small pieces of wood 26.7; fine vegetable matter 30.2. **Animals** Onychophorans: *Peripatus novae-zealandiae* 1.2; *Lumbricus* 75.6; molluscs (mostly gastropods): *Potomopyrgus*, *Limax* 19.8; *Helix* 1.2. Crustaceans: isopods: slaters 14.0; amphipods: freshwater shrimps 3.5. Myriapods: millipedes: 26.7; centipedes 1.2. Arachnids: 7.0. Insects: eggs 26.7; Blattellidae: 3.5; Pentatomidae: 3.5; Coleoptera: larv. 14.0, pupae 1.2, ad 75.6 (incl. Carabidae 26.7; Elatridae 28.0; Cerambycidae: 23.3; Scarabaeidae); Orthoptera: eggs 4.7, ads 40.7 (re-analysed to exclude Blattodea); *Deinacrida megacephala* 38.4; Acridiidae/Tettigoniidae 15.1; Hymenoptera 20.9: hymenopterous galls 2.3; Formicidae 11.6; Ichneumonidae 2.3; *Porina* pupae/larv. 8.1; Calliphoridae: pupae 3.5. Amphibians: frogs *Litoria aurea* 1.2. Birds: egg-shell 8.1. Fragments of sheep hoof; piece of wire; sand and organic matter. Higher proportion (% volume) of vegetable matter in winter; animals in summer.

In Westland (n=35, gizzards; Coleman *et al.* 1983). **Plants** Fern foliage 28.6% freq.; monocotyledon foliage 17.1; dictyotyledon foliage 65.7; gymnosperms: *Podocarpus* (*P. ferrugimus*, *P. totara*) 1.4, 20.0; *Dacrydium* 5.1, 2.9; Poaceae: 0.36% no., 8.6% freq.; *Carex* 1.3, 14.3; *Coprosma* (especially *C. pseudocuneata*, *C. parviflora*, *C. rigida*, *C. rhamnoides*) 76.6, 85.7; *Nertera* 10.2, 25.7; other plants (incl. *Carpodetus serratus*, *Myrsine divaricata*, *Pennantia corymbosa*) 2.5, 20.0. **Animals** Annelids –, 80.0. Molluscs 0.20, 5.7. Crustaceans: 0.04, 2.9. Myriapods: 0.04, 2.9. Arachnids: 0.33, 22.9. Insects: unident. –, 51.4; Coleoptera: 0.82, 8.6; Diptera: 0.57, 11.4; others: 0.16, 11.4. Amphibians: frogs *Litoria* 0.04, 2.9. Reptiles: Scincidae: 0.04, 2.9. Mammals: Brush-tailed Possum *Trichosaurus vulpecula* –, 14.3; rodents 0.08, 5.7; Brown Hare *Lepus capensis* tr., –; unident. –, 22.9. High level of unidentified

material in these analyses have biased results toward some groups (A.J. Beauchamp).

On **Kapiti I.** and at **Double Cove** (observations; Beauchamp 1987a). **Plants**: *Podocarpus*; *Pseudopanax arborea*; *Coprosma lucida*; *Nertera*; *Cyathodes fasciculata*; *Eleocarpus dentatus*; *Myrsine australis*; *Pennantia corymbosa*. **Animals**: annelids; amphipods; diplopods; arachnids; insects: Orthoptera: Stenopelmatidae.

Extirpated population on **Macquarie I.** (n=98, gizzards, Brothers & Skira 1984). **Plants** Vegetation (fibrous material and seeds) 79.6% freq; algae: kelp 6.1. **Animals** Oligochaetes: Lumbricidae 6.1. Molluscs: marine 72.4; gastropods: *Phrixgnathus hamiltoni*; cephalopods: squid beaks 1.1. Crustaceans: copepods: *Tigriopus angulatus* 2.0; decapods: crab 1.0. Arachnids 64.3: mites *Orbatei*, ticks *Ixodes* 11.2; Collembola: *Arthrolepta* 5.1. Insects 82.7: Coleoptera (Staphylinidae: Omalinæ larv. and *Leptusa*) 10.2; Diptera: ads, larv. (Asilidae: *Coleopa curvipes*, *C. nigrifrons*; Tethinidae: *Apetaenus watsoni*) 32.7; Tipulidae: *Erioptera macquariensis* pupae 1.0; *Drosophila melanogaster* ads 2.0; Dolichopidae 7.1; Lepidoptera: Pyralidae: *Eudonia mawsoni* larv. 36.7. Birds (penguin and Weka feathers, flesh, fragments of egg-shell) 28.6. Mammals: House Mouse *Mus musculus* 23.5; Black Rat *Rattus rattus* 19.4; Rabbit 2.1; unident flesh 2.1. Grit (<5mm) 99.0.

Other records Fungi: *Cordyceps robertsii* (Buller 1888). **Plants** Roots and berries (Guthrie-Smith 1914); fruits and berries (Buller 1888; Oliver); young plants (Robertson 1976); *Podocarpus* fru. (Buller 1888); *P. nivalis* fru. (Oliver); potatoes *Solanum* raw and cooked (Buller 1888; Guthrie-Smith 1910); tomatoes *Solanum*; *Fuchsia* fru. (Oliver); grapefruit *Citrus* (Robertson 1976); *Coprosma* (Oliver); *C. pumilla* (Child 1982); Kumara *Ipomea* tubers (Robertson 1976). **Animals** Marine animals (Oliver); larger invertebrates (Cooper *et al.* 1986). Annelids (Guthrie-Smith 1914; Oliver); Lumbricidae (Buller 1888). Crustaceans (Guthrie-Smith 1914; Oliver); amphipods: sandhoppers (Oliver); crabs (Guthrie-Smith 1914); freshwater crayfish: *Paranephrops* (Oliver). Molluscs: shellfish and snails (Guthrie-Smith 1914); bivalves: *Velesunium*; gastropods: *Paraphanta* (Oliver). Insects (Buller 1888; Oliver): larv. (Buller 1888; Guthrie-Smith 1910, 1914); Orthoptera: *Teleogryllus*; Acrididae: grasshoppers (Buller 1888); Coleoptera (Buller 1888; Guthrie-Smith 1910, 1914); *Costelytra* grass grubs larv. (Oliver); Diptera: larv. (Guthrie-Smith 1910); 'Phycodromidae' (Oliver); fish (Oliver): dead fish (Buller 1888; Oliver). Amphibians: *Leiopelma hochstetteri* (MacMillan 1990), though questioned (A.J. Beauchamp). Reptiles: Scincidae (Buller 1888; Beauchamp 1987a; Oliver). Birds: eggs, young (Buller 1888; Guthrie-Smith 1914; Oliver); Little Spotted Kiwi *Apteryx owenii* eggs (Jolly 1989); Brown Kiwi *A. australis* egg; Fiordland Penguin *Eudyptes pachyrhynchus*; Yellow-eyed Penguin *Megadyptes antipodes* egg (Henry 1898; Guthrie-Smith 1914); Sooty Shearwater *Puffinus griseus* eggs (Fleming 1939b); small petrels: ad., eggs, young (Crowther 1933; Falla 1948; Blackburn 1968; Cooper *et al.* 1986); Mottled Petrel *Pterodroma inexpectata*; Cook's Petrel *P. cooki* (Blackburn 1968); Common Diving-Petrel *Pelecanoides urimatrix*; Spotted Shag *Phalacrocorax punctatus* eggs (Stirling & Johns 1969); duck *Anas* young, eggs (Lindsay *et al.* 1959); California Quail *Lophortyx californica* young (Wilkinson 1927); Domestic Chicken *Gallus gallus* ad., young, eggs (Buller 1888; Lindsay *et al.* 1959); Song Thrush *Turdus philomelos* ad. (CSN 19); House Sparrow *Passer domesticus* ad. (Wilkinson 1927); New Zealand Robin *Petroica australis* young (Wilkinson 1927); European Goldfinch *Carduelis carduelis* (Henry 1898). Mammals: carcasses (Stirling & Johns 1969); once, after-birth of New Zealand Fur Seal *Arctocephalus forsteri* (Falla 1948); rarely, kill Stoats *Mustela erminea* (Morrison 1980; MacMillan 1990); rodents and young rabbits (Buller 1888; Guthrie-Smith

1914; Wilkinson 1927; Crowther 1933; Robertson 1976; Copson *et al.* 1981; Oliver). Also cat food (CSN 22); skimmed milk (Wilkinson 1927). Following records of Wekas eating adult birds probably speculation (A.J. Beauchamp): South Georgian Diving-Petrel *P. georgicus* (West & Imber 1989); Domestic Goose (Henry 1898); Buff-banded Rail (Taylor 1979; Cooper *et al.* 1986; Anon. 1987); Red-fronted Parakeet *Cyanoramphus novaezelandiae* (Taylor 1979; Anon. 1987).

Young In **Gisborne** (n=6, gizzards, Carroll 1963a): vegetable 41.5% dry vol., 22.0% dry wt.; seeds 1.2, 2.4; animal 46.8, 29.3; grit 10.5, 46.3 (re-analysed). On **Kapiti I.** and at **Double Cove** (faecal analysis; A.J. Beauchamp): Annelids; Coleoptera larv.; Diptera larv.; *Trioxycanus ensyi* ad. Reptiles: *Leiopisma*. **Other records** Oligochaetes (Wilkinson 1927); Lumbricidae (CSN 23); Insects: larv. (Wilkinson 1927); Diptera: larv. on dead sheep (Fleming 1939b); bread (Wilkinson 1927).

Intake Two gizzards with <50 *Tigriopus angulatus* (Copepoda) and between 100 and 358 *Apetaenus watsoni* (Phycodromidae) larv. in 32 gizzards (Brothers & Skira 1984).

SOCIAL ORGANIZATION Fairly well known; account based on contribution by A.J. Beauchamp; major studies at Double Cove, SI, and on Kapiti I. (Beauchamp 1986, 1987a,b), and in central Westland (Coleman *et al.* 1983); also in captivity by Timmis (1972). Generally occur as territorial pairs, or single non-territorial birds (adults or subadults); during breeding, as family groups. Within a population, numbers of territorial birds constant throughout year; number of non-territorial subadults varies. Groups of up to 13 subadults and 2–6 territorial adults seen at rich food sources. Feed singly, in pairs, and in close family groups (Beauchamp 1987a).

Bonds Mainly monogamous, but some polyandry known (Guthrie-Smith 1914; Beauchamp 1986). Pair-bonds held all year, and tend to last many years till death or displacement of partner; duration of bonds differs with demography of populations; at Double Cove, SI, where mean longevity of territorial birds is 4 years, 50% of pair-bonds lasted 2–3 years; on Kapiti I., where mean longevity 6.5 years, 50% lasted at least 5 years (Beauchamp 1987b); one semi-tame pair lived at least 18 years, though protected by people (Blackburn 1967); in wild, pair-bonds known to last 13 years (A.J. Beauchamp). Non-monogamous associations twice noted, each involving one male and two females (Guthrie-Smith 1910, 1914; Beauchamp 1986); in one trio, younger female temporarily joined established pair, and helped raise young for at least part of one season (Beauchamp 1987a). Male tolerates second female in territory provided appropriate postures and calls given; generally female does not tolerate other females, though one pair-bond between two females lasted at least 2.5 years when no males available (Beauchamp 1987a). Disproportionate sex-ratios occur in all populations at various times of population cycle; some sex-biases recorded in population counts may be because male more readily seen in the field (A.J. Beauchamp). On Macquarie I., 70:26 in favour of males (Brothers & Skira 1984); male-biased ratio suggested by capture data in Westland, SI (Coleman *et al.* 1983). Age of pair-formation depends on rates of mortality of adults, and interactions between territorial and non-territorial birds; at Double Cove, where high turnover in population, all pair-bonds formed and territories established before 18 months old (Beauchamp 1987b); on Kapiti I., where lower mortality, pair-bonds formed average 2 years old, but up to 4 years old. Non-territorial birds may bond with territorial Weka that has lost mate or another non-territorial bird, or challenge to gain territory and mate (Beauchamp 1987a); at Double Cove in 1 year, 38% of territorial Wekas died or were displaced (Beauchamp 1987b). In captivity

and some wild populations, eggs laid at 5 months old (A.J. Beauchamp). Minimum age of first breeding for both sexes is 5–9 months (A.J. Beauchamp); at Double Cove, usually breed in first year, once within 1 month of pair-formation; on Kapiti I., most newly established birds are not in good enough condition to breed in first year (A.J. Beauchamp), breeding usually taking place 1 year after establishment of pair, but may occur up to 5 years after establishment of pair (Beauchamp 1987a). **Co-operative breeding** Unusual; subadults generally deserted or were chased out of parental territories before subsequent clutches hatched, or before parents made subsequent breeding attempts (Beauchamp 1987a). Once three adults raised chick; all exchanged calls, including territorial call; older female undertook most parental care; younger female was not offspring of original pair (Beauchamp 1986); additional records of polyandrous associations in Guthrie-Smith (1910, 1914). In captivity, young observed feeding chicks of later clutches; not seen in wild but suspected once (A.J. Beauchamp). **Parental care** Both birds build nest and incubate (Timmis 1972; Oliver; *contra* Fingland 1986); pattern varies, but female incubates mainly during day, and male mainly at night. At 40–49 days, young almost independent, though fed occasionally by parents; at Double Cove, parental care lasted 60–80 days, and young remained in natal territory for 2 months (Beauchamp 1987a). If pair re-nest, young can be evicted or deserted at 40 days (A.J. Beauchamp). Male recorded providing all parental care when female re-nested (Oliver).

Breeding dispersion Nest singly in territories. **Territories** All-purpose; in some areas held all year, and not abandoned even when food not plentiful (Beauchamp 1987a). Boundaries of territories do not necessarily abut; at Kapiti I., where density high, pairs held common boundaries; intrusion into neighbouring territories seldom exceeded 10 m but sometimes up to 200 m (Beauchamp 1987a). On Kawau Is., incursions of >300m by male obtaining food for young common. Size of territory stable with no change during breeding cycle; at Double Cove, average 4.5 ha (2.6–15.8) (Beauchamp 1987b), cf. average 1.96 ha (0.7–4.5) on Kapiti I. (Beauchamp 1987a). In central Westland, home-ranges of individuals vary greatly; nine of 13 adults (unknown territorial status) had ranges of ≤4.5 ha, but other four had much larger ranges; two subadults covered slightly larger areas than most adults, 5.5 and 6.0 ha (Coleman *et al.* 1983). Non-territorials ranged over c. 70 ha at Double Cove and 1.6 ha on Kapiti I.; these ranges always overlapped territorial boundaries (Beauchamp 1986, 1987a,b). Changes in members of territorial pairs can influence territories and boundaries; if territorial male killed, another male or pair obtains territory; if territorial female killed, male takes new mate, or could be displaced by a pair (Beauchamp 1987a). Non-territorial pairs may establish territories along existing territorial boundaries. One record of territorial male displaced by non-territorial subadult (Beauchamp 1987a). Birds can obtain territories when 10 months old, usually away from natal territory (Beauchamp 1987a,b). Relocated territorial birds recorded swimming almost 1 km to return to territory after release (Wright 1981).

Roosting Nocturnal. Specific sites used in some territories (Beauchamp 1987a). Roost in open, under objects, in burrows, or nests. Non-incubating partner roosts beside or near partner (Timmis 1972; Beauchamp 1987a). In afternoon, often roost in thickets and occasionally seen in vegetation c. 2 m above ground (Robertson 1976). Evidence that birds become particularly active in the late afternoon and in open habitats on clear moonlit nights (Beauchamp 1987a). Brood-nests are modified incubation nests formed into platform 370±40 mm wide. Young usually led to same brood-nest at dusk and brooded under wing or beside parent (Beauchamp 1987a).

SOCIAL BEHAVIOUR Quite well known; based on contribution by A.J. Beauchamp; studied in wild (Beauchamp 1986, 1987b) and in captivity (Timmis 1972); much behaviour observed in captivity not observed in detailed studies in wild (A.J. Beauchamp) and not described fully here. Generally timid and difficult to observe in non-breeding and incubation periods; in some populations and when with chicks more curious and tame (A.J. Beauchamp). Carry off bright objects to inspect as potential item of food (Timmis 1972; Atkinson & Daniel 1985; Beauchamp 1987b). Displays conspicuous (Oliver). **SUNNING POSTURE:** with wings spread, adopted by adults after bathing; sometimes accompanied by flapping wings (Timmis 1972).

Agonistic behaviour Aggressive, particularly adult males (Ripley 1977; Fingland 1986). Employ calls, Threat postures, Fights, and Chases to maintain territory. More conflicts where densities high, and birds defend food supplies (Beauchamp 1987b). Parents occasionally attack young to drive them from territory at end of period of parental care (A.J. Beauchamp). Spacing Call given in response to similar call from neighbour, or after territorial encounter (also see Sexual Behaviour); Boom Call given by territorial owner when intruder suspected to be in territory, after chases, during fights, and occasionally when foraging; spacing calls heard night and day, either as duet by pair or singly. On Kapiti I., Boom Calls heard in 64% of daylight hours, Spacing Calls in 25%, and both in 11% (Beauchamp 1987a). **Threat** Face-to-face interactions between territorial and non-territorial birds generally involve wing-arching, feather-ruffling, posturing, often followed by chases; continue until intruder retreats. Territorial chases and fights undertaken by both sexes; on Kapiti I., chases 15 times more common than fights. In longer chases, up to 300 m, pursuing bird attempts to catch tail of intruder; if it manages to do so, Intruder may give Distress Call; females chase males as often as males chase females (Beauchamp 1987a). **Fighting** Occurs on territorial boundaries; usually ritualized face-to-face movements and parallel walking, sometimes with calls, along boundaries. More intense fighting occurs less often, causing loss of opponent's plumage by use of bill and feet; use of wing-spur insignificant (Andersen 1926); usually occurs only when establishing territory, or when pair tries to gain additional space (Beauchamp 1987a). Fights between territorial female and a challenging female for the territorial position may last up to 1 h; territorial male not involved, though late in fight he may drive challenging female away (Beauchamp 1987a). Death from challenge-fight recorded (Beauchamp 1987a). When non-territorial bird attacked, often gives Submissive Call as it flees, then turns side-on to attacking bird (Beauchamp 1987a). **Dominance** Pecking orders reported at sources of food (Miskelly 1981; Beauchamp 1987a). **Alarm** Run rapidly into and through cover

(Robertson 1976; Fingland 1986; Oliver), with wings spread, giving high-pitched shriek (Guthrie-Smith 1914; Beauchamp 1987a). Give Alarm Call when disturbed suddenly or on seeing threat while with dependent young; given more often by female (A.J. Beauchamp). Seem to flick tail when unsure or threatened, as with other rails (Robertson 1976; Falla *et al.* 1981).

Sexual behaviour In populations that breed all year, some pairs nearly always ready to breed; in populations with shorter breeding period, sexual behaviour only occurs before breeding attempts; on Kapiti I., this period usually <14 days but up to 32 days (Beauchamp 1987a). **Courtship** Initiated by either sex; when female initiates, she usually gives Courtship Growl and occasionally adopts **PRE-COPULATORY STANCE:** stands or crouches with bill very near or touching ground, but female preened on nape by male instead of being mounted; when male initiates, he chases female. Pair moves round territory together visiting potential nesting sites. Courtship usually consists of one bird Courtship Growling and nest-sitting while partner continues normal activity; Courtship Growling given by one or both members of pair throughout 90% of each hour. During this time Allopreening, Courtship feeding and Copulations occur (Beauchamp 1987a). **Courtship feeding** Male feeds female; Food Calls sometimes given by male. Not all pairs Courtship feed; on Kapiti I., only 60% do so (Beauchamp 1987a). **Greeting** Spacing Call given when pairs meet after long period of separation, and when one member of pair is trying to locate other (Beauchamp 1987a). In captivity, pair called during nest-building: female called loudly, and male rushed to her; both held heads low and called for c. 30 s (Fig. 1); then begged and neck-preened; at change-over during incubation, approaching bird brings food or nest material; sometimes sitting bird unwilling to leave and nudged off by mate (Timmis 1972). **Allopreening** Mutual preening by pair and adults with young; preen head and back (Timmis 1972). **Copulation** Pre-copulatory behaviour: utter Booming call and walk stiffly with necks stretched and curved downward; copulation followed intense Courtship and Boom calling; male did not feed female before copulations (Beauchamp 1987a). Copulation may occur every hour. Female adopts Pre-copulatory Stance (see Courtship above); male mounts from behind by stepping on female's back; he maintains grip using feet, and balances by flapping wings (Fig. 2); with neck arched, male depresses tail and moves it vigorously side to side while copulating for 3–4 s; male may grab female's neck feathers in bill, or peck female's nape; dismounts either to side or backwards, as female moves from under him. During dismount male, and occasionally female, uttered Dismount Call (Beauchamp 1987a; CSN 21; A.J. Beauchamp; H.A. Robertson).

Relations within family group Both parents brood chicks almost continuously on nest for 2–3 days; then off nest by males

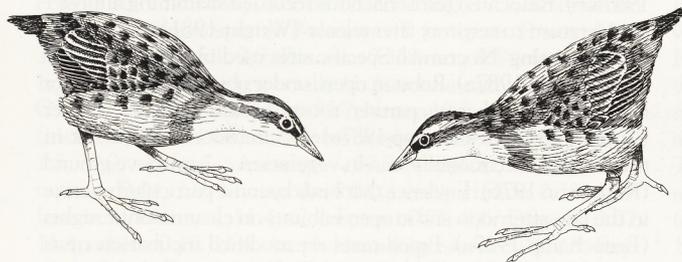


Fig. 1 Greeting (in captivity)

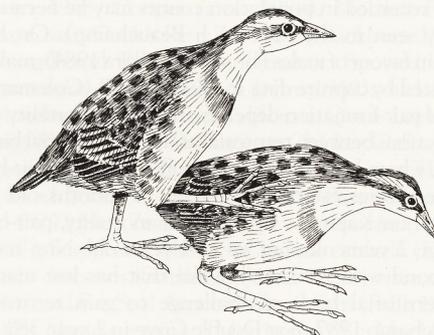
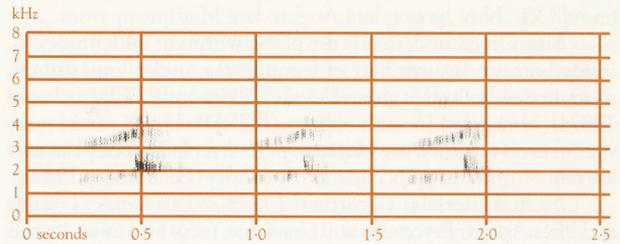


Fig. 2 Copulation

during cold weather for the first 4–10 days; in nest, under wing of parent; parent usually remains brooding till mate arrives with food. When feeding young chicks, one parent feeds near young while other forages farther away; may change over when food delivered to young; sometimes food passed to attendant parent to feed to young, so other can continue foraging away from group (Beauchamp 1987a). After feeding, young may be left in safe place while parents feed (NZRD). For first few days, parent either directly feeds chicks on soft foods, or regurgitates food for chick; to feed young, parent will carry food in base of bill from anywhere in territory. Parent gives Food Calls which induces Begging in chicks (Beauchamp 1987a). **BEGGING:** chick crouches (Timmis 1972); or stands in upright wing-flapping posture, chick pecks at food or tip of parent's bill. If chicks do not beg, parents often swallow food (Beauchamp 1987a). Parents also noted placing food on ground for older young (20+ days old) (Wilkinson 1927; Beauchamp 1987a). When 10–15 days old, young move with parent; stand nearby and approach when they see food or are called; during following week, begin to feed themselves (Beauchamp 1987a). Parents give Contact Calls to nearby young, from day of hatching till near end of parental care. When 24–45 days old, young become more curious and may ignore Distress Calls of parents. Towards end of parental care some parents feed and then attack young (Trial 1951; Beauchamp 1987a); young may crouch on haunches, beside or under breast of parent; if chick still young enough to give chick calls, seldom seriously attacked by parents or by other territorial Wekas (Beauchamp 1987a). Some young feed independently at 21 days; on Kapiti I., parental care did not stop until between 40 and 108 days old; at Double Cove, young remained in natal territory for up to 2 months after independence, however most had dispersed by 4 months, though in summer, young birds constantly passed through area (Beauchamp 1987b). If pair re-nest, young evicted earlier (NZRD). **Anti-predator responses of young** Four hours after hatching, young able to leave nest and hide; while still in intact egg, stop calling in response to Distress Call; when feeding, crouch or run to cover (Timmis 1972). **Parental anti-predator strategies** Incubating bird usually refuses to leave nest (*contra* Fingland 1986), and, if forced off, may peck own eggs (Wilkinson 1927), or may return to nest and eat own eggs (A.J. Beauchamp). If young captured, parents attempt to rescue it; peck vigorously at captor (Fleming 1939b) or look on in agitation, with fluffed body-feathers, fanned drooped wings and open probing bill (Coleman *et al.* 1983; A.J. Beauchamp). Hawk Calls given to young when shadows cast from birds passing overhead; Distress Calls given when young in danger of being located or when young are caught (Beauchamp 1987a).

VOICE No detailed studies but calls reasonably well known from work of A.J. Beauchamp, on which account based. Most noticeable call, repeated shrill whistle *coo-eet*, most often heard at dawn and dusk and in early evening (Gee 1956; NZRD) but given at any hour; and throughout year. Given solitarily or as duet. Calls of female more rapid than those of male (A.J. Beauchamp). When one bird calls, others nearby are likely to join in (Falla *et al.* 1981). On Stewart I., birds said to whistle more rapidly than on NI (Guthrie-Smith 1914).

Adult Spacing and fighting calls. **SPACING CALL:** shrill whistle *coo-eet*, rising in pitch (sonagram A) and repeated up to 25 times. Usually given when members of pair meet after separation, when one member tries to locate other, after territorial encounter, or in response to similar call from neighbour. **BOOM:** *doon-doon-doon*. Usually given during fight, after chase or when a bird suspects an intruder is in its territory but cannot see it



A C. & L. Weisman; Kapiti I., NZ, Oct. 1956; P106

(Beauchamp 1987a). Where territories large, seldom given while foraging (Beauchamp 1987b). Given only by birds holding a territory. **DISTRESS GROWL:** given when tail of chased bird caught, or by bird in the hand. **Close contact and courtship calls** **CONTACT CALL:** *ih-ih-ih*. Given by members of pair close together and with more intensity just before copulation. Occasionally takes place of soft calls during chick-rearing. **COURTSHIP GROWL:** repeated *guuuuurra*. **DISMOUNT CALL:** *uhahhuah*. Given by males while following females, during pre-copulatory manoeuvring, or while dismounting after copulation. **LEAD CALL:** *put-put-put*. Given by either sex while directing partner in courtship, while directing dependent young between feeding stations or away from danger. Also during and after fights, together with Boom and Spacing Calls, to locate partner. **Parental calls** **FOOD CALL:** repeated *uuurra-uuurra*; varies in duration and intensity. Given by males when Courtship feeding and by both parents when feeding chicks; while food held in bill and also before regurgitation. Longer and more shrill if chicks do not respond with begging posture or are not located; becomes similar to call of Purple Swamphen. **SOFT CONTACT CALL:** *im-im-im*. Most often heard when chicks and parents in close contact. Repeated every 3 s when chicks close. Occasionally given by lone bird. Also given while parallel-walking during boundary disputes (see Social Behaviour). **DISTRESS CALL:** *uh-uh-uh*. Given to young in danger of being located or when young are caught. **DISTRESS SQUEAK:** *uhhreek*. Replaces Distress Call when highly agitated. **HAWK CALL:** undescribed; given in response to raptor passing overhead; not heard often. **Other calls** In captivity, Timmis (1972) reports soft murmuring *kuck-kuck-kuck* given when pausing, after having fled a few metres when attacked; in wild, Contact Calls given in this situation (A.J. Beauchamp).

Young Chick heard chirping in egg before and during hatching, even before shell broken. Chicks ceased chirping immediately parents called in alarm or anxiety (Timmis 1972). Chirping *ieep* from chicks while with parents from hatching until near end of parental care; louder and more intense when searching for parents. Wavering call, initially given in presence of feeding adult, becomes almost continuous by end of fourth week while parent present (Beauchamp 1987a).

BREEDING Detailed study on Kapiti I., s. NI (Beauchamp 1987a) and Double Cove, n. SI (Beauchamp 1987b); also studied on Macquarie I. (Brothers & Skira 1984) and in captivity (Gorgas 1968; Timmis 1972). Additional unreferenced material supplied by A.J. Beauchamp.

Season Highly varying; start and duration influenced by climate, food supply, and size of population. At Gisborne, NI, in 1960s, one semi-tame pair recorded raising up to four broods, in Mar., June–July, Aug.–Sept. and Nov.–Dec. (Carroll 1963b). On Kapiti I., in 1980s with all available territories occupied, began Aug.–Nov., ended Nov.–Mar.; in 1920s–1930s when population was expanding, breeding recorded most of year (Wilkinson 1927). On Macquarie I., female with well-formed egg, early Aug.; nests

found Oct., Nov.; young late Aug. to late May.

Site On ground, in any dry place; within or under tussocks, inside burrows, against butt of leaning tree, under logs, stumps, rocks, in tree-hollows at ground level (Wilkinson 1927; Beauchamp 1987a); concealed in outbuildings (NZRD). Up to seven nest-sites in each territory, used for many years; replacement pairs may use nest-sites of former occupants of territory (Beauchamp 1987a).

Nest, Materials Constructed from sedges *Carex*, *Uncinia* and lilies *Astelia*, *Erycynetia* and *Cordolone*; twigs and moss, if grass not available; lined with finer grasses, sometimes feathers, wool, hair and leaves (NZRD) or leaf-litter surrounding nest. On Kapiti I., only male seen carrying nesting material (Beauchamp 1987a). In captivity, both sexes brought material; nest shaped by sitting on nest, prodding with bill and stamping feet; towards end of construction male brought most material and female did most sitting and shaping. In captivity, material added during incubation (Timmis 1972), but not in wild (Beauchamp 1987a).

Eggs Ovate; glossy when fresh, becomes duller during incubation; pinkish to creamy white, variously blotched light chestnut or pale and dark brown, chiefly at larger end, and streaked all over with purplish and reddish brown. Blotches fade and eggs become creamier before hatching (Wilkinson 1927; Oliver). **MEASUREMENTS:** Kapiti I., 57.7 (3.00; 53.1–61.2; 9) x 39.9 (1.18; 38.2–41.8) (Beauchamp 1987a); NI, 60.4 (2.29; 57.5–63; 4) x 41.7 (1.39; 40.5–43.2); SI, 59 x 41.5 (Oliver); Macquarie I., 58.3 (55.4–61.0; 6) x 38.5 (38.1–39.0).

Clutch-size Varies through range. On Kapiti I., 2.3 (1–5; 24) C/1 x 2, C/2 x 16, C/3 x 4, C/4 x 1, C/5 x 1 (Beauchamp 1987a); can average three eggs in populations of lower density (A.J. Beauchamp); 3–4, occasionally six (Carroll 1963b).

Laying In captivity, laying started within few days of completion of nest; clutch of three eggs laid in 5 days (Timmis 1974). On Kapiti I., eggs laid 2.5 days apart, possibly longer in large clutches. Possible dump-nesting reported (Guthrie-Smith 1910), perhaps as result of polygynous behaviour or long laying period (Beauchamp 1987a). Raise up to four broods per year in Poverty and Parekura Bays (Carroll 1963b; A.J. Beauchamp). In captivity, one pair re-laid within 5 days of losing newly hatched young (Timmis 1972).

Incubation By both sexes, female generally during day, and male at night; in shifts usually exceeding 4 h; on Kapiti I., male generally relieved female in last 90 min of daylight; female in turn relieved male in first 180 min after dawn (Beauchamp 1987a). Nest constantly attended; chase intruders from nest area (Beauchamp 1987a). **INCUBATION PERIOD:** 20 days (Smith 1886); 26–27 days (Timmis 1972); 28 days (Gorgas 1968); on Kapiti I., 26–28 days from end of laying. Hatching asynchronous, first two eggs of one clutch hatched within 4 h, two eggs in another clutch hatched c. 24 h apart (Timmis 1972). Egg-shells and viteline membrane carried away from nest (Timmis 1972); on Kapiti I., egg-shell eaten and viteline membrane left beside nest.

Young Precocial, semi-nidifugous. On Stewart I., most chicks covered in brown-black down (NZRD); some chicks on Bravo I. occasionally black (Traill 1951). At 4 weeks, feathered and beginning to resemble adults (Timmis 1972). **Growth** Tarsometatarsi fully developed at 56 days; bill-depth at 50 days, width of leg at 60 days, bill-length >100 days (Beauchamp 1987a). Attain adult size by independence; adult weight at 6–9 months in Westland (Coleman *et al.* 1983). **Parental care, Role of sexes** In wild, young leave nest after 2–3 days (Beauchamp 1987a). Chicks fed by brooding adult; other adult supplies food, collected within 30 m of nest. For first 8 days after young leave nest, brooded during cold periods (Beauchamp 1987a); brood sometimes left in sun or in hiding place while parents forage; call young when food

found (NZRD). Chicks fed bill to bill or by regurgitation when small (Timmis 1972; Beauchamp 1987a); fed till nearly fully grown; late in period of parental care, male generally more attentive to young than female (Wilkinson 1927; Beauchamp 1987a). Placing of food on ground for chicks, by adults, does not necessarily indicate that adults about to re-nest (A.J. Beauchamp *contra* Wilkinson 1927). Once two females (4-year-old and 2-year-old), and one 6-year-old male attended a chick 18±3 days old; older female contributed most care (Beauchamp 1986).

Fledging to maturity Some young feed independently at 21–40 days; parental care stops between 40 and 108 days (Beauchamp 1987a); at Double Cove, young remain in parental territory up to 2 months; most dispersed 4 months after independence (Beauchamp 1987b). Can breed in first year (Coleman *et al.* 1983); at Double Cove, female first bred at 18 months, male at 12 months.

Success On Kapiti I., over 5-year period: 44.8% pairs tried to breed, 27.1% successful; 0.3 young raised per pair (Beauchamp 1987a), 2.8 young raised per pair at Double Cove, success rate related to supply of food (Beauchamp 1987b). At Gisborne, from 15 young hatched, 14 reared (Carroll 1963b). In Westland, average brood-size of young weighing 500–800 g (just before independence), 2.1: 6 x 1 young, 3 x 2 young, 5 x 3 young, 1 x 4 young (Coleman *et al.* 1983). Predators of young and adults include: skuas *Catharacta*, Stoats, Weasels *Mustela nivalis*, Ferrets *Putorius putorius*, dogs and feral cats (Moncrieff 1928; Adams 1960; Brothers & Skira 1984; MacMillan 1990). Unusual record of chick found strangled in wool of dead sheep (Fleming 1939b).

PLUMAGES Prepared by D.J. James. Four allopatric subspecies. Nominate *australis* and subspecies *scotti* share three morphs: grey, chestnut and black (grey and chestnut morphs have usually been viewed as a single highly varying morph, e.g. NZRD); each morph varies greatly though most birds readily categorized and intergrades uncommon; there are also slight differences within morphs between the two subspecies. Subspecies *hectori* and *greyi* have no morphs but differ from other subspecies. Sexes similar at all ages. No known change in appearance produced by alternating plumages.

Adult non-breeding and breeding Definitive basic and alternate. First attained at beginning of second year.

Subspecies *australis* and *scotti* Grey morph **Head and neck** Crown, nape and hindneck, black, with broad rufous-brown (340) edges to feathers, giving streaked appearance; edges, broadest anteriorly narrowing towards hindneck. Sides of neck, dull rufous-brown (37) with dark-brown streaks or spots at tips of feathers giving speckled appearance. Prominent light-grey (85) supercilium almost from base of bill to side of nape, narrow and tinged pale buff in front of eye (especially along lower margin), broadening posteriorly. Broad dark band (facial stripe) from base of bill through and broadly under eye (but not over it), widens on ear-coverts and peters out behind ear or merges into side of neck; darkest on lores, dark brown (121) with rufous-brown (340) tips to feathers (darkest birds have almost blackish lores); slightly paler behind eye where rufous-brown (340) with black-brown (119) centres to feathers. Partial cream (56) to buff-grey eye-ring round underside of eye. Chin, off-white, grading to light grey (c85) on throat and cheeks below facial stripe. Base of foreneck, continuous with breast-band (see Underparts). **Upperparts** Vary in darkness. Mantle and scapulars, black to black-brown (119), with rather narrow rufous-brown (340) to light-brown (c123A) edges to feathers. Back and rump, brown (c121C–223B), generally uniform, though sometimes with indistinct dark-brown (121) centres to feathers; grey-brown (c91) bars sometimes evident,

giving faintly mottled appearance and duller tone. Upper tail-coverts, vary from black-brown (119) with rich-brown (121C) edges, to rich brown (121C) with rufous-brown (c37) edges, notches or barring, to all black. **Underparts** Upper breast has varying, though usually broad and indistinct, rich rufous-brown to duller olive-brown band fairly sharply, though untidily, cut off from grey of throat and lower breast; feathers of breast-band, brown (32) grading to rufous-brown (37) at edges, giving streaky appearance; or brown (123) with indistinct buff-brown (24) spots on each web, giving mottled appearance. Lower breast, brownish grey (c79, 80), usually forming distinct clean patch below breast-band and emphasizing it; sometimes lower breast, grey-brown, merging with belly. Belly and vent, grey-brown (c91) with faint olive tinge. Anterior flanks, as belly; sometimes washed brown (123). Posterior flanks, dark olive-brown (129) with very faint red-brown tint, varying barred brown (123) to light brown (123A) on tips of feathers; feathers often barred black-brown (119) and brown (123) with tips as above, though extremely varied. Under tail-coverts, rich brown (121C) to rufous-brown (340), boldly barred with black. **Tail** Rectrices, rufous-brown (340) with black centres and bold broad black barring (black notched rufous-brown); tips often uniformly rufous-brown; generally black bars well defined, equal in width to intervening rufous bars. **Upperwing** Remiges vary; generally black with red-brown (32) to rufous-brown (340) barring, similar to rectrices; centres usually broadly black; bars may peter out before reaching edges, producing pattern almost of black centre with irregular rufous edges; secondaries, usually less distinctly barred, often black mottled or blotched red-brown (32) to rufous-brown (340) along edges; inner secondaries and tertials tend to be like other remiges at bases but like scapulars at tips, thus not visibly contrasting with upperparts when wing folded. Greater, median and rear rows of lesser coverts, black-brown (119) barred rufous-brown (340) with brown (123) mottled tip. Leading rows of lesser coverts, as scapulars. **Underwing** Remiges, rufous-brown (340) with subdued black-brown (119) barring. Coverts and subhumeral, grey-black (82) with two rather narrow, pale olive-buff bars at tip and pale olive-buff fringe.

Chestnut morph Differs from other morphs and subspecies in mottled red-brown underparts similar in tone to upperparts. **Head and neck** Similar in pattern to other forms. Feathers of top of head and hindneck, black with red-brown (32) edges of varying width; generally appear strongly streaked. Supercilium, typically narrower than on grey morph; usually pale rufous-brown (pale 139), palest in front of eye; never very prominent behind eye and often obscured. Facial stripe like that of grey morph but tends to be broadest in front of eye, narrowing posteriorly; lores, mostly black with very fine rufous-brown (340) streaking; behind eye, narrow rufous-brown (340) edges to black feathers give indistinct streaked appearance. Chin, throat and lower cheeks, brownish grey (c79) or washed pale dirty-brown, providing less contrast with facial stripe than in grey morph. **Upperparts** Mantle and scapulars, black with rich-brown (121C) to rufous-brown (340) edges to feathers (about one-eighth width of feather on each web); general appearance usually distinctly richer than grey morph. Back and rump, dark rufous-brown (dark 340 to rufous 132) with partly exposed grey-black (82) bases giving dark mottled appearance. Upper tail-coverts, similar to rump but with black wedge-shaped shaft-streaks, usually narrow but sometimes rather broad; some have largely black centres with dark rufous-brown (c340) notches along edges of feathers giving impression of indistinct barring. **Underparts** Breast, rufous-brown, mottled, not streaked, black; feathers, rufous-brown (340), sometimes fading to orange-rufous (orange 340) at edges, with black centres that do not reach

tips, most prominent towards foreneck and sides. Belly and anterior flanks, uniform dark brown (121A) with warm rufous or reddish tint. Posterior flanks, may be uniform, as breast, or rufous-brown (340) with blotchy black barring. Vent, dark brownish-grey (dark 79). Under tail-coverts, rufous-brown (340) boldly barred black. **Tail** Like grey morph: rectrices black varying barred or notched rufous-brown (340). **Upperwing** Pattern of the remiges varies, like other morphs, but generally with duller rufous-brown (340–37) (not red-brown) barring, edging or notching; tertials, black with broad rufous-brown (340) to red-brown (32) edges, blending inconspicuously with upperparts. Coverts generally as upperparts; leading coverts have broad blackish centres to feathers and poorly defined rufous-brown (340) to red-brown (132) edges; rear coverts become progressively more distinctly barred along edges; greater coverts have pattern like remiges basally with tips like upperparts. **Underwing** Greater and median coverts, grey-black (82) tipped and distally barred rufous-brown (340). Lesser coverts, grey-black (82) mottled rufous-brown (340).

Black morph Much darker than other morphs: mostly black with dark reddish-brown streaking above. Birds from Stewart I. and former population on Macquarie I. can be as black as those from Fiordland (*contra* Falla *et al.* 1981; NZRD). **Head and neck** Crown and nape, black with narrow russet-brown (34) edges to feathers; neck, similar or uniform black. Lores, black. Rest of face, black with very faint russet-brown (34) edges to feathers giving speckled appearance; no trace of typical facial pattern. Chin and throat, very dark brownish-grey (very dark 79). **Upperparts** Mantle and scapulars, black with varying, usually very thin, russet-brown (34 or reddish 34) edges to feathers; on some, russet-brown edges almost absent. Back to upper tail-coverts, similar but with slightly broader edges, becoming broader towards tail. **Underparts** Breast and anterior flanks, black to black-brown (119) with varying russet-brown edges like upperparts; edges very thin and obscure to broader and conspicuous. Some have more extensive russet-brown flecking on feathers of upper breast forming indistinct breast-band. Centre of lower breast often dark olive-brown (dark 129) or faintly greyer than rest of underparts. Posterior flanks, black with extremely thin russet-brown (34) to rufous-brown (340) fringes to feathers. Belly, vent and thighs, black-brown (sooty 19). Under tail-coverts, black, narrowly and indistinctly barred rufous-brown (340). **Tail** Normally uniform black; palest birds may have narrow russet-brown (34) or rufous-brown (340) edges to rectrices, especially basally. **Upperwing** Coverts and tertials, as scapulars. Remiges, black-brown (119) with narrow to broad irregular russet-brown (34) edges; usually not barred but some have red-brown (32) notches along inner webs. **Underwing** Coverts, black; greater coverts, narrowly tipped russet-brown (34). Remiges, as upperwing.

Within black morph, some paler birds appear intermediate between grey and black morphs though intergradation not complete; such birds typically very dark above but with olive-brown (29) or olive-grey breast-band and barring on flanks, and some trace of red-brown (32) barring through remiges; rectrices, never barred; barring on tail seemingly correlated with pale plumage in nominate *australis* and subspecies *scotti*; intergrades with chestnut morph also occur but rare; characterized by intermediate upperparts and dark reddish-brown underparts.

Subspecies hectori Pale; only form with yellow-brown or buff edges to feathers of upperparts. However, this character not present on all birds from Chatham Is (A.J. Beauchamp). Differs from palest *australis* by: upperparts, more olive-buff; underparts, more olive; more prominent barring on flanks and spotting in breast-band; olive-buff edges to remiges. **Head and neck** General

pattern similar to grey morph. Crown, nape and hindneck, black with fairly narrow and indistinct yellow-brown (123–123a) edges giving profusely and finely streaked appearance; sides of neck, similar though with broader yellow-brown edges. Supercilium, from upper lores to side of nape, light grey (85) with some faint light-brown (123A) flecking in front of eye; on average, more distinct posteriorly than other forms. Typical facial stripe, brown (c121B) faintly flecked black (short black streaks at tips of feathers); paler, less distinct posteriorly, sometimes petering out. Chin, off-white to pale grey (86), grading to light-grey (85) throat and lower cheeks; foreneck, yellow-brown streaked black; feathers, brown (123) and becoming straw-yellow (56) along edges with black centres; often a hint of reddish brown on centre of foreneck.

Upperparts Feathers have large, usually concealed, grey-black (82) bases. Mantle and scapulars, black with fairly narrow (one-eighth width of feathers) pale yellow-brown (pale 24 or brown 56) edges to feathers giving buffy streaking; sometimes, edges have faint olive tinge. Back and rump, brownish olive (brown 51) grading to straw-yellow (56) edges of varying width, with narrow black-brown (119) central streaks. Upper tail-coverts, similar to rump but faintly barred dark-brown (121). **Underparts** Breast, like foreneck; black streaks more prominent towards side of breast; feathers, brown (123) with olive (48) tinge down centres and yellow-brown (123A) tinge along edges, often with scattered olive (c48) spots; palest birds may have more yellow-brown or buff-brown (123B) tinge generally. Lower breast, clean greyish-brown (c79–80). Anterior flanks, olive-brown (olive 123). Belly, olive-brown (olive 30), darker and greyer than anterior flanks; tips of feathers, slightly paler than bases, giving faintly mottled or untidy impression. Posterior flanks and thighs, brown-olive (c29) on bases of feathers, barred black-brown (119) and pale brown (223D) towards tips; flanks more boldly and consistently barred than other forms. Under tail-coverts, rufous-brown (340) boldly barred black. **Tail** Rectrices, black, broadly edged and barred rufous-brown (340) basally and edged brown (123) distally; can be narrowly barred brown (123) distally. Basal barring generally more obvious below. **Upperwing** Remiges, rufous-brown (340) to red-brown (32), with bold black to black-brown (119) barring, which breaks up to form mottling on feathers towards body; tertials, blackish, broadly tipped and edged olive-buff. Greater coverts, red-brown (32) at bases of feathers, grading to yellow-brown (24) at edges with olive (c48) tips, and barred black-brown (119). Median and rear lesser coverts, black-brown (119) in centre of feathers with broad notches that are light brown (123A) towards centre fading to straw yellow (56) towards edges. Leading lesser coverts, as scapulars. **Underwing** Greater and median coverts, grey-black (82) with rufous-brown (340) barring at tips of feathers. Lesser coverts, dirty olive-buff. Remiges, generally rufous-brown (340), paler towards tip with subdued black-brown (119) barring.

Subspecies greyi Little variation. Closest to grey morph from n. populations of nominate *australis* but greyer below, usually with no barring on flanks and less clearly defined and narrower breast-band without spotting; pattern of head more distinct. **Head and neck** Top of head, and hindneck, rufous-brown (c340) (grading to duller rufous-brown [37] on side of neck) with broad black streak at tip of each feather, giving strongly streaked appearance; rarely, streaks shorter on hindneck, giving spotted rather than streaked appearance. Supercilium, light grey (85) tinged buff anteriorly, extending almost from base of upper mandible to side of nape, broadening posteriorly; like that of grey morph but neater, bolder and usually broader. Thin, buff-grey partial eye-ring round underside of eye, like grey morph. Broad facial stripe, like grey morph but always narrower in front than

behind eye and remaining more distinct through to side of neck, mostly rufous-brown (340) with short black streaks at tips of feathers giving dark tinge, but not streaked appearance. Chin, dirty white grading to light-grey (85) throat and lower cheeks. **Upperparts** Feathers have grey (84) plumulaceous bases. Mantle and scapulars, rufous-brown (37–340) to rich-brown (121C) (when worn can fade to brown [c123]) with broad black central streaks at tips of feathers (typically centre 10 mm and edges 5 mm wide); usually slightly less rufous in general appearance than crown and hindneck, often contrasting markedly. Back and rump, dark reddish-brown (reddish 223A) to brown (c121B) at tip (distal half) of feathers with exposed dark-grey (83) bases giving dark mottled look; sometimes have dark-brown (121) tinge at extreme tips. Upper tail-coverts, black in centre of each feather with edges (one-third width of feathers) same colour as tips of feathers on rump; concealed bases, grey-black (82). **Underparts** Mostly quite uniform brownish-grey (c79) with concealed dark-grey (83) bases to feathers; usually lack pale spots on breast-band and barring on lower flanks. Varying olive-brown to reddish-brown band across upper breast, which can be rather broad to absent; feathers in band, olive-brown (olive 123) to brown (34) with slight reddish tinge, mottled rich brown (121C) along edges; wider bands tend to be richer (more reddish) and reasonably well defined; narrower bands tend to be duller, poorly defined, and often mottled, partly because dark-grey (83) bases exposed. Lower flanks and thighs, brown (33) tinged olive at edges of feathers. Vent, dark brownish-grey (dark 79) to dark olive-brown (129). Under tail-coverts, brown (c33) indistinctly barred olive-brown (c123) to rufous-brown (340). **Tail** Rectrices, black with irregular, rather narrow brown (123) edges tinged olive to rufous-brown (340). **Upperwing** Primaries vary: generally black with bold, broad red-brown (32) bars along edges but discontinuous down centre of feathers, separated by black centre; in darkest birds, primaries, black mottled red-brown (32) along edges (though one female from Kawau I. had all-black primaries; A.J. Beauchamp). Secondaries, similar but less boldly barred, more often tending to be black mottled red-brown (32) to rufous-brown (340) along edges; inner secondaries and tertials, like outer secondaries at bases but like scapulars at tips. Alula, like primaries. Greater and median coverts, generally barred like remiges but at bases of feathers, fading to duller tips like scapulars. Lesser coverts, like scapulars though often with less well defined and slightly paler (dark brown [22]) centres to feathers. **Underwing** Remiges, rufous-brown (340) with subdued black-brown (119) barring or centres. Coverts and subhumeral, rufous-brown (340) to brown (123), finely barred grey-black (82).

Downy young Down, long, soft, silky. Black to black-brown (119) at hatching, sometimes with greyer throat. In skins, often fades greyer, to dark grey-brown. Variation, little known; subspecies apparently vary little, if at all. One skin of *greyi* had black lower back to tail and crown (latter giving slight capped effect) and dark-brown (223) mantle and underparts. Those of *australis* and *scotti* generally lacked contrast in upperparts with no capped affect. Throat, usually paler (e.g. brown [219A]) but the specimen of *greyi* lacked pale throat. One skin of *scotti* had slight red tinge underneath, which may be indicative of chestnut morph.

Juvenile Highly varying; full range of variation not known. Generally rather similar to adults of respective morphs but with distinctive appearance because pattern, size and shape of feathers differ slightly. Body-feathers, significantly narrower than those of subsequent plumages (e.g. feathers of mantle average 11 mm wide in juvenile and 16 mm in adult) (Beauchamp 1987a). Tips of feathers, also generally more pointed, with loosely knit fringes and clinging wisps of natal down. Generally feather-tracts that

develop later more resemble those of adults. On upperparts, central streaks on feathers tend to be narrower and browner on average than those of adults; some *greyi* (at least) almost lack dark centres above, therefore appearing very rufous. Juvenile *greyi* can be lighter or darker grey below than adults and lack or have only indistinct breast-bands. Often have blotched rather than barred flanks. Subspecies *hectori* show less contrast in upperparts between browner centre and olive-buff edges and thus appear more uniform, less streaked above; more uniform olive below without distinct breast-band. Darker forms often have brown (e.g. 121C) spots or speckles in plumage, especially on sides of underparts and upper tail-coverts. Generally smaller than attendant parents during most of juvenile period.

First and second immature First alternate and basic. Plumage of head and body renewed; indistinguishable from adult. Juvenile wing-feathers and rectrices retained; thus juvenile remiges with pointed and frayed tips, in combination with adult-like body-plumage best guide to ageing, but also see Bare Parts. On Kapiti I., immature body-plumage, though not separable from plumage of adults, not always definitive plumage and slight changes sometimes occurred with first immature post-breeding moult to first adult plumage (Beauchamp 1987a); information for other populations not available.

Aberrant plumages Partial leucism common (c. 5% of specimens examined); varies from a few or many scattered white feathers to piebald pattern (usually asymmetrical) of white and normally patterned feathers, to almost totally white plumage. Discussed in more detail by Oliver. The holotype of '*G. townsoni*' (Mathews & Iredale 1914) is partially leucistic subspecies *australis*.

BARE PARTS Based on literature (Falla 1937; Coleman *et al.* 1983; Brothers & Skira 1984; Beauchamp 1987a; Oliver), photos (Moon 1992; NZRD; DOC Slide Library; unpubl.: D.J. James) and museum labels. Little known of variation between subspecies and morphs in young birds; development of colour with age based on birds from Kapiti I. (Beauchamp 1987a). **Adult** Bill: dark grey or grey culmen; rest is paler grey grading to cream at tip with red, dull-red or dark-pink base; some, especially dark morphs, have more brown or purplish-brown culmen; females may have slightly narrower pink bases and creamier tips than males (Beauchamp 1987a). Iris, bright red, deep red, reddish brown; colour can vary but reasons not known. Eyelids, black or black-brown; inner eyelids, cream. Legs, dull red or brownish red in light birds; brown, purplish brown, red-brown or pinkish brown in darker birds; soles, and sometimes back of tarsus, dark-brown to greyish brown. Legs of *hectori*, pink-red to orange-pink or pinkish yellow. Claws, brown-grey to dark brown-grey. **Downy young** Bill, black with white or pinkish-white egg-tooth; some have pinkish patches round nares. Iris, dark brown or dark yellow-brown. Legs, purplish, pink-grey, blackish or dark brown with dark-purplish or reddish tinge, turning brown or orange-brown over first 6 weeks. **Juvenile** Bill, dark grey by about Week 6, with dull-red base developing about Week 7. Iris, begins lightening to brown at 10 days; yellow-brown or greyish yellow at 60–100 days (Beauchamp 1987a); in Westland, reported as invariably olive-green (Coleman *et al.* 1983). Legs, gradually become redder, and generally like adults. **First immature** On NI and Kapiti I.: bill, becomes paler, more grey-pink along sides; some attain adult colour by 9 months. Iris, brown to red-brown at 5–8 months, greyish red to adult colour at 9–12 months (A.J. Beauchamp). Legs, as adults.

MOULTS Based on birds from Kapiti I., 1979–84, by Beauchamp (1987a) and other population studies in SI, NI, Kawau and

Chatham Is (A.J. Beauchamp); cursory examination of c. 160 skins (AWMM, CM, MV, NMNZ) provided little extra data. All forms hatch in natal down and soon begin pre-juvenile moult to juvenile plumage; juvenile plumage fully attained while still dependent on parents and held only briefly; post-juvenile moult to first immature non-breeding plumage, partial, generally retaining feathers of wing, but up to 10% of Kawau I. birds moulting some inner feathers (A.J. Beauchamp); probably partial immature pre-breeding moult of head produces immature breeding plumage; subsequently undergo complete post-breeding and some, a partial pre-breeding moult of head, each cycle producing alternating non-breeding and breeding plumages that are identical in appearance. Can breed at end of first year when in immature breeding plumage though this is rare on some offshore islands but more likely on the NI, SI and Chatham Is (Beauchamp 1987b; A.J. Beauchamp). **Adult post-breeding** Pre-basic. Complete; simultaneous or partly simultaneous. Begins with head, neck and lower breast; most other body-tracts begin within 10 days. Rectrices and tail-coverts, moult at same time, beginning a few days after head. Remiges begin c. 20 days after head, taking 50–90 days to finish; secondaries, sometimes moult at same time as primaries but usually slightly earlier; sometimes dropped rapidly over 5 days (simultaneous), more often in groups over slightly longer period (partially simultaneous), but finish growing at once; occasionally one or more remiges retained. Greater primary and secondary upper wing-coverts moult with respective remiges; alula, moulting 5 days after initiation of remiges; other tracts within 10 days of remiges. Greater under wing-coverts, last tract. Period of heaviest body-plumage replacement, c. 3 weeks after remiges finished. Begins from mid-Dec. to late Jan., depending on year, age and individual; total duration varies, usually 65–90 days for individuals, 110–180 days for population; rate of moult, generally slower in individuals beginning latest. Non-territorial adults began significantly earlier than territorial adults in some years, even in Nov. Moult normally when breeding finished, though may overlap. Breeding pairs normally moulted in synchrony (within 20 days of each other) if breeding failed, or when parental duties shared equally after early Jan., but out of synchrony if parental duties not equal in Jan. or one bird remained in breeding condition. Timing and rate differed between years at Kapiti I. Skins were in primary-moult from following localities and dates: NI, Dec. (1); Maud I., Apr. (2); Fiordland, Nov. (1); Macquarie I., Jan. (2), Mar. (2); Chatham Is, Jan (1). Timing on NI varies more than on Kapiti I.: at Opuia, in moult after breeding continuously June–Sept.; on Kawau I., from late Dec., 1991. On Chatham Is, began late Nov., 1987. **Adult pre-breeding** Pre-alternate. Partial, confined mostly to head and neck; probably not undertaken by all individuals; begins just before breeding season, possibly continuing through breeding (Beauchamp 1987a). One skin with moult on flanks, NI, Aug. **Pre-juvenile** Complete. Begins c. 9 days after hatching. Most other tracts active before remiges. Secondaries active by c. Day 16, with rectrices, alula and then primaries following in a few days. Under wing-coverts, last, finishing c. 100 days after hatching. Latter stages overlap with post-juvenile. **Post-juvenile** First pre-basic. Partial; wing feathers and rectrices, retained. Begins c. 70 days after hatching, frequently coinciding with end of parental care. Often begins with thighs and head; tail-coverts, fastest to grow and first to finish. **Immature pre-breeding** First pre-alternate. No data; probably limited partial moult like adult pre-breeding but might be suppressed. **Immature post-breeding** Second pre-basic. Similar to adult post-breeding, but begun earlier (like non-territorial adults, often Nov.) and completed sooner; immatures holding territories may moult later, nearer time of breeding adults.

MEASUREMENTS Nominate *australis*: (1–2) Ages combined, sexing based on labels, skins (AWMM, CM, MV, NMNZ): (1) mainland SI; (2) coastal islands of Fiordland and w. Southland. (3) Double Cove, Marlborough Sounds, adults, 1986 (A.J. Beauchamp). Wing and tail can abraid up to 20 mm in a year (A.J. Beauchamp).

	MALES	FEMALES	
WING	(1) 184.3 (10.0; 168–205; 14) (2) 192.3 (9.85; 180–203; 6)	171.6 (7.60; 160–183; 9)	ns
TAIL	(1) 128.2 (13.0; 108–146; 13) (2) 128.4 (10.9; 116–115; 5)	122.6 (10.4; 108–136; 8)	ns
BILL F	(1) 49.5 (3.04; 44.4–55.3; 15) (2) 43.3 (5.45; 37.1–54.0; 7) (3) 50.7 (2.43; 47.2–54.2; 22)	46.5 (2.00; 43.8–49.0; 9)	ns
TARSUS	(1) 60.9 (6.03; 52.8–69.5; 15) (2) 61.3 (5.07; 55.8–70.9; 7) (3) 61.0 (2.52; 53.7–67.9; 23)	55.7 (3.22; 52.0–61.1; 9)	ns
TOE	(1) 53.9 (1.77; 51.5–57.5; 12) (2) 56.0 (4.61; 48.1–62.1; 7) (3) 58.7 (2.21; 52.0–62.8; 23)	53.7 (1.42; 51.0–53.9; 9) 50.8 (2.58; 46.7–54.7; 8) 53.4 (1.80; 50.2–55.0; 9)	ns

Subspecies *scotti*: (4) Stewart I. and small neighbouring islands, ages combined, sexing based on labels, skins (AWMM, CM, MV, NMNZ); (5) Macquarie I., collected 1930–67, ages combined, sexing based on labels, skins (AWMM, CM, MV, NMNZ); (6) Macquarie I. freshly dead birds (Brothers & Skira 1984).

	MALES	FEMALES	
WING	(4) 176.2 (10.9; 160–198; 13) (5) 179.1 (6.42; 169–190; 12) (6) 184.4 (10.0; 165–226; 70)	166.9 (11.9; 155–199; 16) 163.3 (6.95; 155–172; 4) 162.5 (17.3; 110–180; 26)	ns * **
TAIL	(4) 129.8 (3.45; 116–125; 8) (5) 124.3 (5.09; 116–130; 13) (6) 125 (13.4; 74–175; 70)	114.6 (7.17; 105–128; 8) 101, 114, 114 120 (5.1; 110–130; 26)	ns * ns
BILL F	(4) 46.5 (2.71; 41.0–49.7; 13) (5) 47.8 (1.65; 45.5–50.8; 13) (6) 50.2 (1.8; 46.2–54.2; 70)	43.7 (2.51; 38.1–47.9; 16) 43.4 (1.64; 41.7–45.4; 6) 45.3 (2.1; 41.2–48.0; 26)	ns * **
TARSUS	(4) 54.6 (4.97; 48.5–64.2; 12) (5) 58.7 (2.19; 54.5–62.1; 14) (6) 58.4 (2.2; 52.3–62.1; 70)	40.4 (5.97; 43.3–60.5; 14) 52.5 (2.65; 48.5–57.2; 7) 51.7 (2.1; 45.5–54.5; 26)	ns * **
TOE	(4) 50.2 (3.13; 46.0–54.6; 5) (5) 52.2 (2.10; 48.9–55.0; 11)	45.5 (2.07; 43.3–49.2; 6) 47.6 (2.37; 45.1–51.7; 6)	ns *

Subspecies *hectori*: (7–8) Ages combined, sexing based on labels, skins (AWMM, CM, MV, NMNZ): (7) grasslands of e. and se. SI, nineteenth century; (8) Chatham Is, twentieth century. (9) Chatham Is, adults, 1987 (A.J. Beauchamp).

	MALES	FEMALES	
WING	(7) 188.0 (13.3; 155–202; 11) (8) 161, 185, 197	172.5 (7.77; 161–178; 4) 156, 163, 175	ns
TAIL	(7) 123, 130, 140 (8) 120, 145	107, 122, 125	
BILL F	(7) 48.0 (3.02; 42.6–51.7; 11) (8) 49.8 (1.85; 44.2–48.3; 4) (9) 51.4 (2.35; 47.2–53.0; 19)	44.6 (3.66; 40.9–49.0; 4) 42.0, 44.3, 44.4 47.5 (2.44; 43–50.4; 13)	ns
TARSUS	(7) 62.1 (4.75; 55.2–70.6; 11) (8) 60.9 (5.07; 53.4–64.5; 4) (9) 61.7 (3.51; 56.4–68.2; 19)	53.4 (3.36; 49.4–57.6; 4) 55.0, 55.4, 56.3 54.6 (3.09; 49.2–60.0; 13)	*
TOE	(7) 52.90, 59.5, 60.5 (8) 51.9 (0.68; 50.9–52.5; 4) (9) 58.8 (2.39; 54.2–64.9; 19)	46.0, 47.0, 47.0 54.2 (2.16; 50.2–58.2; 13)	

Subspecies *greyi*: (10) NI, ages combined, sexing based on labels, skins (AWMM, CM, MV, NMNZ); (11) Gisborne, dead birds (n=94 but numbers of each sex not known) (Carroll 1963b); (12) Kawau I., adults, 1993 (A.J. Beauchamp).

	MALES	FEMALES	
WING	(10) 175.8 (11.2; 160–198; 14)	169.8 (11.0; 155–188; 12)	ns
TAIL	(10) 113.1 (6.69; 99–122; 15)	107.2 (5.9; 98–118; 10)	ns
BILL F	(10) 44.8 (21.4; 41.8–48.2; 15) (11) 47.8 (47–50) (12) 48 (1.83; 46.0–51.0; 23)	42.4 (1.25; 40.0–43.6; 12) 43.1 (42–44) 45.8 (1.33; 44.1–48.0; 16)	*
TARSUS	(10) 58.7 (2.89; 53.4–63.5; 15) (11) 62.8 (59–68) (12) 60.7 (2.08; 57.0–64.2; 34)	56.2 (52.6–62.3; 12) 57.4 (54–58) 55.9 (2.02; 53–61; 16)	ns
TOE	(10) 49.9 (3.21; 43.4–54.8; 14) (12) 57.9 (1.87; 54–63; 33)	47.2 (2.89; 42.9–52.1; 10) 54.1 (1.96; 51.1–58.7; 16)	ns

(13) Kapiti I., NI, live birds, sexing based on behaviour of studied population and discriminant functions (Beauchamp 1987a).

	MALES	FEMALES	
WING	(13) 196.2 (7.3; 178–212; 114)	176 (8.1; 150–195; 138)	**
TAIL	(13) 126.6 (6.7; 115–145; 95)	118.4 (6.6; 99–140; 117)	**
BILL F	(13) 47.1 (1.8; 43–51; 122)	43.9 (1.5; 42–47; 152)	**
TARSUS	(13) 58.2 (2.2; 50–63; 126)	52.3 (2.1; 47–58; 164)	**
TOE	(13) 55.5 (2.3; 49–63; 126)	50.8 (2.1; 45–56; 164)	**

Size varies with geography, sex and age, though confident analysis of variation cannot be made because samples often small and probably include incorrectly sexed and young birds in samples from skins. However, clear sexual dimorphism in large samples from Kapiti I. and Macquarie I. Further, s. and n. populations of nominate *australis* not obviously different in size and subspecies *scotti* smaller than nominate *australis* (significant differences for wing, tarsus and toe of males; bill, tarsus and toe of females when samples for each subspecies combined), though considerable overlap. No convincing evidence of shift in size for birds transplanted long distances, namely subspecies *scotti* to Macquarie I. and subspecies *hectori* to Chatham Is. Beauchamp (1987a) describes growth and development of young.

WEIGHTS (1) Nominate *australis* (NMNZ index cards); (2) subspecies *scotti*, Macquarie I. (Brothers & Skira 1984); (3) subspecies *hectori* (NMNZ index cards); (4) subspecies *greyi*, freshly dead birds from Gisborne (n=94 though numbers of each sex not known) (Carroll 1963b).

	MALES	FEMALES	
(1)	978 (233; 612–1250; 9)	725 (270; 350–1035; 6)	ns
(2)	1034 (134; 600–1425; 70)	753 (87; 500–884; 26)	**
(3)	1255 (203; 925–1605; 8)	651 (139; 525–850; 4)	*
(4)	912 (532–1053)	699 (382–1010)	

Weights of both sexes shown to peak in late autumn and winter and reach lows in summer, corresponding with breeding season at Gisborne, Westland, Kapiti I. and Marlborough (Carroll 1963b; Coleman *et al.* 1983; Beauchamp 1987a,b). At Kapiti I., fluctuations up to 40% and 90% above minimum weight were recorded annually and over 5 years; declines of 150–200 g below mean weight would jeopardize survival invariably in winter and

in drought conditions in summer (Beauchamp 1987a). Downy young, 1–3 days old, on Kapiti I.: 35.8 g (7.6; 34) (Beauchamp 1987a); on Kawau I., 38, 42 g (A.J. Beauchamp).

STRUCTURE Large, flightless. Contour feathers, rather loosely knit and coarse. Wing, short, rounded. Ten primaries; p6 or p5 longest; c. 13 secondaries including about three tertials. Remiges, soft and floppy with narrow but stiff and wiry shafts; outer web of primaries rather broad (Stresemann 1932; Fullagar *et al.* 1982) (see Juvenile for use of primaries in ageing). Short, sharp curved wing-claw, typical of rails, present on alula. Tertials cover primaries and secondaries, or almost do, when wing folded. Tail, quite short, rounded, though never widely fanned; 12, occasionally 14, rectrices have rather thin, stiff, wiry shafts. Bill, rather heavy, tapering, wedge-shaped; laterally compressed; heavier than other *Gallirallus* species (see Fullagar *et al.* 1982); nostrils, horizontally oblong, perforate in large deep nasal groove that extends over half length of culmen. Tarsus and toes, very strong and heavy; scales, scutellate on front of tarsus and top of toes, reticulate elsewhere. Toes, slightly laterally compressed; pads, fleshy; outer toe 76–84% of middle, inner 71–79%, hind 21–29%. Claws, strong, curved, laterally compressed.

SEXING Sexually dimorphic in size; males larger (see Measurements). Discriminant functions based on standard measurements have been derived for adults in populations at Westland (Coleman *et al.* 1983), Macquarie I. (Brothers & Skira 1984) and Kapiti I. (Beauchamp 1987a); those based on populations at Gisborne (Carroll 1963b) do not work (A.J. Beauchamp). Generally length of tarsus and bill as well as width of bill are best measures for adults skins, but not effective for wild birds (A.J. Beauchamp); weight should be avoided as it fluctuates too much. Much geographical variation in size, and functions derived for one population should not be applied to others.

GEOGRAPHICAL VARIATION Considerable; historically up to eight species recognized. Plumages of each subspecies described above. Nominate *australis* and subspecies *scotti* distinguished only by slight differences in size; subspecies *scotti* smaller, though historical translocations may have confused boundary of *australis* and *scotti* between coasts of Fiordland, w. Southland and Stewart I. Some paler *scotti* large and essentially inseparable from grey-morph *australis*. Darkest chestnut-morph *australis*, from coastal islands of Fiordland, possibly as small as typical *scotti*. Subspecies *greyi* and *hectori* differ from *australis* mostly in plumage (see Plumages).

Generally, the ratio of morphs of nominate *australis* and subspecies *scotti* shows a geographic cline: grey morph predominant in Marlborough, less common in Fiordland and rather rare on the islands surrounding Stewart I.; black morph most common in Fiordland (though not predominant there, occurring in similar proportions to both grey and chestnut morphs), fairly common on islands surrounding Stewart I. and absent from n. Westland to Marlborough; chestnut morph predominates on Stewart I. and nearby islands and becomes less common northwards. Grey morph of *australis* and *scotti* palest and greyest in Marlborough, becoming darker towards S; some individuals possibly intergrade with chestnut morph in Fiordland and on Stewart I. but both morphs can be recognized at these localities.

Taxonomic status on Kapiti I., uncertain; *australis*, *scotti* and *greyi* have been introduced but which has contributed to gene-pool of extant population not known; appear intermediate between *australis* and *greyi*.

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Weka *Gallirallus australis* (page 506)

1 Adult, subspecies *greyi*; 2 Adult, subspecies *hectori*; 3 Adult, subspecies *australis*, grey morph; 4 Adult, subspecies *australis*, chestnut morph; 5 Adult, subspecies *scottii*, black morph; 6 Downy young; 7 Juvenile, subspecies *greyi*; 8 Juvenile, subspecies *australis*

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