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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: *Amauromis*, *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*. *Amauromis* (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 *Amauromis*. *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 *Amauromis*. *Gallinula* (2, 1) worldwide distribution, with three species in our area; also an *Amauromis* 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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Porphyrio porphyrio Purple Swamphen

COLOUR PLATE FACING PAGE 616

Fulica porphyrio Linnaeus, 1758, *Syst. Nat.*, ed. 10, 1: 152 — Asia, America = lands bordering the western Mediterranean Sea (Peters).

Aristophanes in his play *The Birds* used *πορφυρίων* as the name of a red-coloured waterbird, and it has been adopted here.

OTHER ENGLISH NAMES Azure-breasted, Black-backed, Purple Gallinule or Waterhen, Sultana Hen, Bald Coot, Blue Bald Coot, Blue-breasted Eastern and Western Swamphen, Macquarie Waterhen, Redbill, Tarlerbird.

NZ Pukeko.

Out of the many names used, **Purple Swamphen** is a reasonable compromise for shortness and description, **Purple Gallinule** being already used for *P. martinica*.

POLYTYPIC Extralimital: nominate *porphyrio* and about 14 other subspecies have been described; *melanotus* Temminck, 1820, Aust. except in sw. parts, and NZ; *bellus* Gould, 1840, sw. Aust.

FIELD IDENTIFICATION Length 44–48 cm; wingspan: male 700–880 mm, females 740–860 mm; weight: male 1050 g, female 850 g. Large ponderous rail with massive triangular red bill and frontal shield, long legs with thick knees and long slender toes; in HANZAB area, only Takaha *Porphyrio mantelli* larger. Mostly deep indigo-blue below, with prominent white under tail-coverts. Sexes similar; male larger with bigger frontal shield. Slight seasonal variation; frontal shield swollen during breeding season. Juvenile separable.

Description Adult Crown, nape and face, glossy black, grading into deep indigo-blue of chin, throat, neck, breast, upper belly and flanks; in sw. Aust., lower face, chin, throat, foreneck to lower breast and blue-coloured areas of wing, iridescent azure-blue contrasting with deep indigo-blue of belly, flanks and sides of breast. Rest of upperparts, glossy black except for narrow, deep indigo-blue leading-edge of innerwing and leading-edge of outer few primaries; in sw. Aust., upperparts, dark olive-brown when fresh, becoming browner with wear. Lower belly and vent, black; under tail-coverts, white. Underwing, glossy black. Bill and frontal shield, bright red, often slightly paler at tip and dusky on sides of bill. Iris, bright red. Legs and feet, pink-red with dusky joints; in sw. Aust., sometimes greenish. **Juvenile** Similar to adult but smaller at first, with smaller bill and shorter, narrower shield; duller generally, with darker, less bluish lower face, little or no blue on hindneck when fresh, and with much whitish mottling on underparts; bill and shield, duller, dirty pink, becoming blackish at tip; legs and feet duller greyish-pink, with less contrasting dusky joints; gradually attain adult size and coloration of bare parts during first year though recognizable by duller plumage and dusky markings on bill.

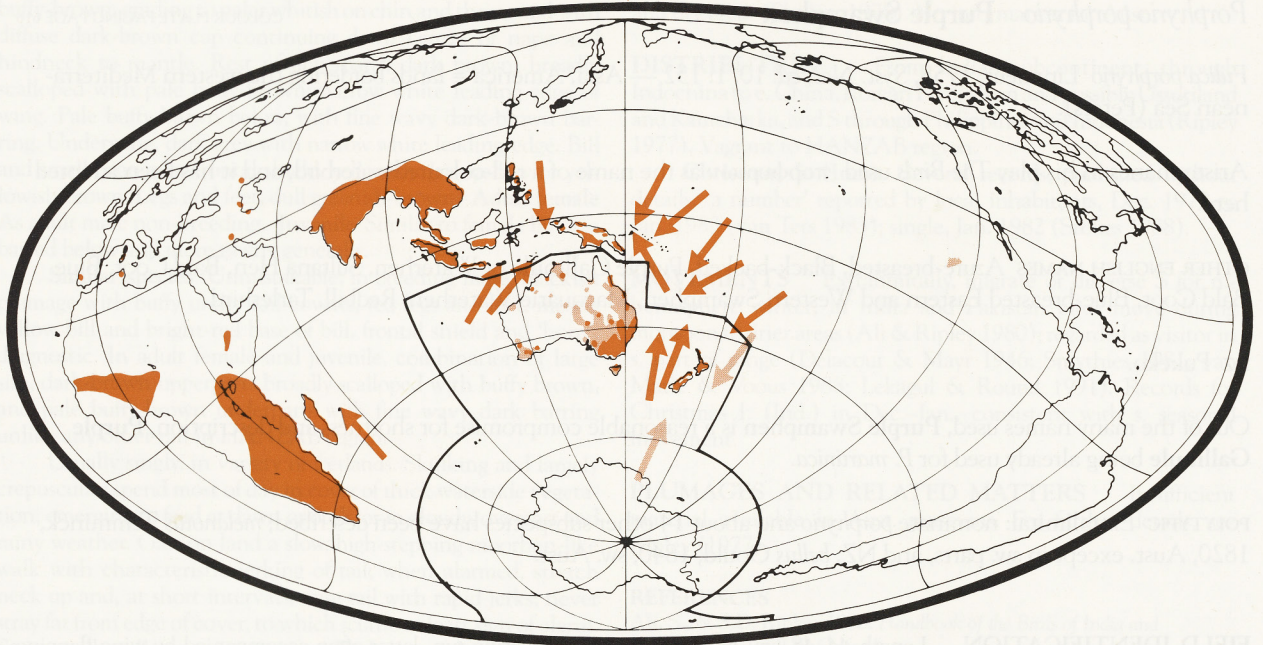
Similar species In Aust., large size, massive triangular red bill and frontal shield, deep-blue underparts and conspicuous white under tail-coverts make adult unmistakable. In NZ, unlikely to be confused with Takaha (q.v.).

Singly or in loose groups round margins of wetlands with much vegetation; often on town lakes. Shy in remote wetlands but tame in urban parks. During much of day, keep to denser reed beds where climb, wade through or roost in vegetation over water, but also move out into adjacent wet pasture and sward to graze. Gait less free than smaller relatives, with slow heron-like walk

and lumbering run, latter often accompanied by wing-flapping; climb well. Swim infrequently though well and buoyantly, with flat-backed profile rising to high stern, neck upstretched and head jerked back and forth, resembling large moorhen. Flick tail continually when walking or swimming, exposing white under tail-coverts. When disturbed, run quickly to cover, or dive and progress underwater partly or fully submerged. Run over water before laboured take-off, with legs dangling at first; flight stronger once fully airborne, with rapid shallow wing-beats on broad rounded wings, head and neck fully extended, shoulders hunched, and feet trailed behind tail. When feeding, have parrot-like habit of holding food firmly in one foot. Voice varies: most commonly heard call a loud, penetrating hacksaw-like screech; also soft clucking contact notes given while feeding.

HABITAT Terrestrial wetlands and adjacent grasslands; also estuarine and littoral wetlands. Usually 0–370 m asl but up to 2350 m asl; breeding group at c. 610 m asl (Bell 1961; Carroll 1966, 1969; Fordham 1983; Owen & Sell 1985; Tunnicliffe 1985). Open habitat next to wetlands such as grasslands, meadows and margins of forests but particularly agricultural land, lawns, parks, gardens, verges of roads, hedgerows, golf courses, sports fields and chicken-runs (Bull 1939–40; Bell 1961; Hobbs 1961; Carroll 1966, 1969; McKenzie 1967; Bravery 1970; Morris 1975; Brown & Brown 1977; Fielding 1979; Martin *et al.* 1979; Storr 1984; Leach & Hines 1987; Hutton 1990; Tas. Bird Rep. 1980; North). Occasionally occur some distance from water (Penniket 1955; Craig 1979).

Found in all sorts of wetlands from ponds and swamps to artificial dams, sewage ponds, drains, ornamental lakes, artesian and seismic bores (Badman 1979; Finlayson 1980; North). Usually on fresh or brackish water; sometimes at saline, eutrophic and turbid wetlands; permanent, semi-permanent, seasonal, ephemeral (Brown & Brown 1977; Martin *et al.* 1979; Craig 1980a; Corrick & Norman 1980; Corrick 1982; Norman & Mumford 1985; Goodsell 1990; Morris *et al.* 1990; Vic. Atlas). Aquatic vegetation round fringes of wetland, and terrestrial vegetation consists of many sorts of sedges, rushes, reeds, shrubs and trees; usually dense (Bravery 1970; Anon. 1973; Morris 1975; Badman 1979; Martin *et al.* 1979; Corrick & Norman 1980; Finlayson



1980; Corrick 1982; Broome & Jarman 1983; Czechura 1983; Norman & Mumford 1985). Known to perch and roost in trees and even move and feed in canopy (Brown & Brown 1977; Norman & Mumford 1985; CSN 19); occasionally feed on open mudflats (Pierce 1980; Fordham 1983; Norman & Mumford 1985). Numbers reduced by removal of marginal wetland vegetation (Czechura 1983), recreational developments (Morris *et al.* 1990), and sometimes by drainage of wetlands (Carroll 1969; BOAT 1982). Habitat adversely affected by silting and grazing in some regions (Carroll 1966; Storr 1984). Some forest clearance, swamp drainage and construction of artificial impoundments have produced additional habitat; species benefits from European settlement provided sufficient water and cover remain (Carroll 1969; Fordham 1983). On Lord Howe and Norfolk Is birds only established since clearing has produced dense areas of vegetation adjacent to open areas (Schodde *et al.* 1983; Hutton 1990).

DISTRIBUTION AND POPULATION Range from s. Africa (N to Angola and Uganda; also in Ethiopia, central w. Africa and from Morocco to Tunisia), N to Iberian Pen. and Corsica, E to Persian Gulf; from Indian subcontinent to se. Asia, Indonesia, NG, Aust., NZ, Melanesia and w. Polynesia, E to Samoa, Kermadec and Chatham Is.

Aust. Widespread in e. states. **Qld** Sporadic records from Gulf Country and C. York Pen., S from near Cooktown through e. and central Qld, with scattered records in w. districts. **NSW** Throughout, mainly in E (W to Western Slopes) and S, but also in W, specially round Darling R. Drainage Basin. **Vic.** Throughout. **SA** Mainly S of 34°S and E of 138°, but scattered records W to w. Eyre Pen., and N to mid-north, L. Eyre drainage basin and s. Simpson Desert (Aust. Atlas). **Tas.** Widespread in all regions except W; sporadic records round Peak Hill Dam, Strahan and Queenstown follow recent expansion of range (Thomas 1979; Tas. Bird Reps 9,10). Plentiful on King I. (Green & McGarvie 1971); scarce on Flinders I. (Newman *et al.* 1984; cf. Green 1969). **WA** In SW, from Mt Le Grand to Moora (Serventy & Whittell 1981; Storr 1987; Aust. Atlas). In Pilbara between lower Fortescue R. and Port Hedland (Aust. Atlas). In Kimberley Div., recorded from Fitzroy R., and in E from Broilga Springs to L. Argyle

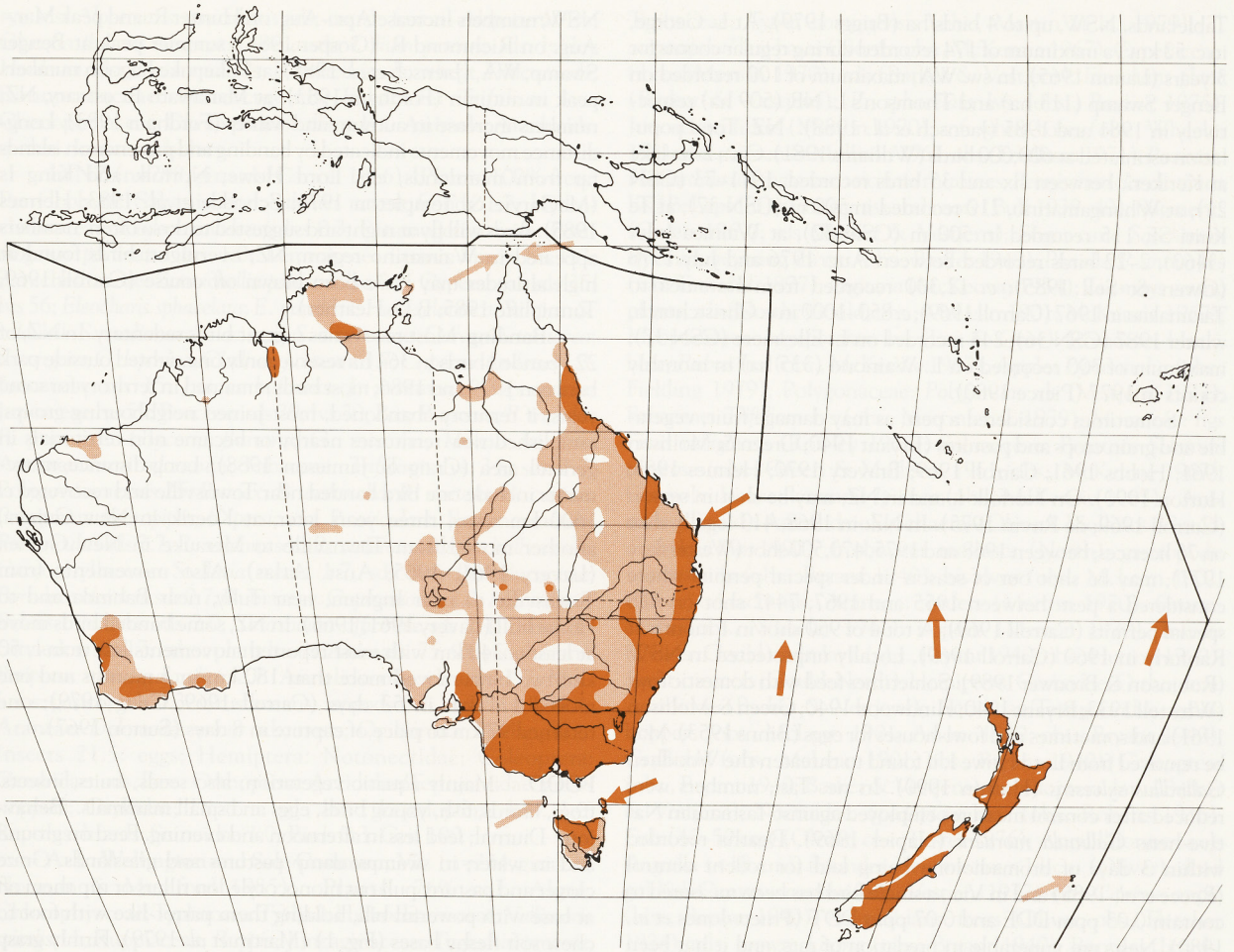
(Aumann 1991; Aust. Atlas). Recorded through greater part of the Division, S almost to Lagrange (Storr 1980). Isolated record in e. Great Sandy Desert from Sturt Ck Homestead (Aust. Atlas). **NT** Most records from Top End, where moderately common, S to Joseph Bonaparte Gulf and Mataranka, and E to Yirrkalla (Deignan 1964; Thompson & Goodfellow in prep.; Aust. Atlas). Sporadic records farther S, including round Alice Springs, and isolated records in SW at Uluru and Kata-tjuta (Storr 1977; Klapste 1978; Roberts 1981; Aust. Atlas).

NZ NI Widespread in W, from Northland S to Wairarapa; also e. Coromandel Pen., w. Bay of Plenty, East Coast and Hawke's Bay; scattered records or absent in central and ne. districts, including Volcanic Plateau, n. Wanganui, n. Manawatu, nw. Hawke's Bay and e. Bay of Plenty. Inshore islands (Carroll 1969; Westerskov 1977; NZ Atlas). **SI** Common in Golden and Tasman Bays; scattered records in Marlborough Sounds; coastal and subcoastal Canterbury, from round Conway R. to near Hampden; scattered records in inland Canterbury and Otago; throughout most of Southland, but few Fiordland records; sporadic records N from Kaipo (CSN 21) to Haast R., and thence abundant W of S. Alps ne. to Westport and Tasman Bay. Inshore islands (Carroll 1969; Westerskov 1977; NZ Atlas).

Norfolk I. Uncommon, self-introduced resident. First recorded late nineteenth century, before 1888 (Schodde *et al.* 1983; Hermes 1985). Not uncommon and breeding in early twentieth century (Basset Hull 1909); regularly recorded in 1960s and 1970s (Schodde *et al.* 1983). Total population of 40–50 birds in late 1960s (Wakelin 1968).

Lord Howe I. Recently established; self-introduced. First recorded 1882; subsequently recorded: 1884; 1891 (all specimens); 1934, 1936 (Hindwood 1940); two records between 1950 and 1965 (details unrecorded, McKean & Hindwood 1965); single, May 1985 (after strong winds from S–SE, NSW Bird Rep. 1985); two, Feb. 1986; three adults and two chicks, Aug. 1987; total population, 30, mid-1988 (Hutton 1990).

Kermadec Is Breed Raoul I. First recorded 1887; not recorded regularly till 1954 (Merton 1970). Eleven birds (eight adults, three juveniles), Blue L., Jan. 1967 (Merton 1970). Dead bird recorded on L'Esperance Rock (Tennyson & Taylor 1989).



Chatham Is Recorded Chatham and Pitt Is (Dawson 1955; Carroll 1969).

Campbell I. Occasional visitor (Westerskov 1960).

Breeding Aust. Mainly E of Great Dividing Ra. in Qld and e. NSW; throughout s. NSW, Vic., n. and e. Tas. and s. SA; sw. WA; scattered records from W. Plains of NSW; sw. Qld and L. Eyre drainage basin; Kimberley Div.; Top End (Thompson & Goodfellow in prep.; Aust. NRS; Aust. Atlas). Also Norfolk & Lord Howe Is. **NZ** Throughout most of range. Also Kermadec Is.

Range in HANZAB region generally extended. **Aust.** Construction of artificial lakes (Horton 1975; Roberts 1981) has enabled expansion into parts of interior (e.g. Mt Isa, Alice Springs). First record round Canberra, Apr. 1954; now regular inhabitant (McKelvie 1957). Recently extended into w. Tas.: first record at Strahan, Mar. 1980; at Queenstown, June 1979 (Tas. Bird Reps 9,10). Recently colonized n. Aust.: first recorded Fogg Dam, Sept. 1968 (Crawford 1972). Round Northam district, WA, formerly uncommon; disappeared after 1954 (Masters & Milhinch 1974), but recorded during Field Atlas (Aust. Atlas). **Lord Howe I.** Occasional sightings till mid-1980s, when became established (Hutton 1990). **NZ** Only locally common before 1850s (Falla *et al.* 1981). Extended range into several areas in 1860s, with first records from Whangarei, Amuri and L. Hawea in 1861–65 (Carroll 1969). Expansion of range also recorded at Tutira after 1890 and at Hunua Ras and Waimarino in early 1940s (Carroll 1969; McKenzie 1979). Local populations often fluctuate, with rapid increases recorded in many widespread regions in 1960s, and

possible further range expansion (Carroll 1969).

Introductions In Aust., introduced to Maria I., Tas., in 1970, presumably from Tas. mainland (Green 1989). Some liberated in Rotorua-Taupo district, NZ, where new colonies now flourishing (Carroll 1969). Extraliminally, unsuccessfully introduced to Hawaii (from India) in 1928, and Mauritius (from Madagascar) before 1812 (Long 1981). Possibly also to Argentina, but no supporting evidence (Aust. CL).

Irruptions In Aust., generally not subject to irruptive movements, but numbers in Atherton region fluctuate (Bravery 1970), and suddenly appeared round Cairns in good numbers after rains (White 1946). In NZ, appear more prone to irruptive movements (Carroll 1969; CSN 21). Fluctuations in number may be, at least partly, associated with modification to habitat: sudden influx in n. Canterbury coincided with declines in adjacent areas where wetlands drained (Carroll 1969).

Populations Aust. Annual indices of relative abundance from aerial survey (transect counts) covering wetlands in c. 12% of land area in e. Aust., between 1983 and 1989, were 77; 638; 7149; >10; 296; 1474 respectively; important areas from these surveys were wetlands of floodplains at confluence of Lachlan and Murrumbidgee Rs (41–60% of total numbers counted) (Braithwaite *et al.* 1985a,b, 1986, 1987; Kingsford *et al.* 1988, 1989, 1990). Over 300 recorded at Karumba Plain, Apr. 1985 (Qld Bird Rep. 1985); ≥2000 recorded at Minnamooka, near Charters Towers, June 1986 (Qld Bird Rep. 1986); >200 recorded on 20-ha wetland near Innisfail (White 1946). On four wetlands on n.

Tablelands, NSW, up to 4 birds/ha (Briggs 1979). At L. George, in c. 52 km², a maximum of 174 recorded during regular counts for 3 years (Lamm 1965). In sw. WA, maximum of 100 recorded on Benger Swamp (113 ha) and Thomson's L. NR (509 ha) respectively in 1981 and 1985 (Jaensch *et al.* 1988). **NZ** Total population estimated at 600,000 birds (Williams 1981). On a 2-ha lake at Kerikeri, between six and 35 birds recorded, 1971–73 (CSN 21); at Whangamarino, 210 recorded in 500 m (CSN 37); at Te Kuiti SF, 115 recorded in 500 m (CSN 32), at Waimea Inlet (3460), 2–22 birds recorded between Aug. 1976 and July 1978 (Owen & Sell 1985); c. 12,300 recorded from Karamea to Taramakau in 1967 (Carroll 1969); c. 850–1000 in e. Christchurch, winter 1987 (CSN 36); 243 recorded on L. Ellesmere (CSN 37); maximum of 300 recorded on L. Wainono (335 ha) in monthly counts in 1977 (Pierce 1980).

Sometimes considered a pest, as may damage fruit, vegetable and grain crops and pastures (Bryant 1940; Green & Mollison 1961; Hobbs 1961; Carroll 1969; Bravery 1970; Hermes 1985; Hutton 1990). On Norfolk I. and in NZ, may be shot in season (Carroll 1969; de Ravin 1975). In NZ: in 1968, 413 legally shot on 75 licences; between 1968 and 1975, 470,500 shot (Westerskov 1977); may be shot out of season under special permits where considered a pest: between 1955 and 1967, 7442 shot on 328 special permits (Carroll 1969). A total of 950 shot in 1 month at Ranfurly in 1960 (Carroll 1969). Locally unprotected in NSW (Robinson & Brouwer 1989). Sometimes feed with domestic fowl (Whittell 1933; Bryant 1940; Hindwood 1940; Green & Mollison 1961) and sometimes raid fowl-houses for eggs (Binns 1953). May be removed from Lord Howe I. if found to threaten the Woodhen *Gallirallus sylvestris* (Hutton 1990). In ne. Tas., numbers were reduced after control measures employed against Tasmanian Native-hens *Gallinula mortierii* (Napier 1969). Deaths recorded within 3 days of bromadiolone being laid for rodent control (Reece *et al.* 1985) and in Vic., a single bird has been measured to contain 0.03 ppm DDE and 0.07 ppm DDT (Pruett-Jones *et al.* 1980). Nests are vulnerable to predation of rats, and it has been speculated that some local declines in NZ were caused by rats eating eggs (Carroll 1969). Often struck by vehicles (CSN 31).

MOVEMENTS Some dispersive movements; possibly partly migratory; some territories maintained year round (Craig 1979, 1984); flock in some areas and transient birds apparent in at least some populations (Craig 1979; Fordham 1983). Mainly juveniles, but also adults, dispersed from Pukepuke Lagoon, NZ, most moved <25 km; farthest movement 90 km (Craig 1979; Craig & Jamieson 1988). Increases in local populations may occur according to availability of habitat (Carroll 1969; Gibson 1977; Vic. Atlas), e.g. high numbers where feeding opportunities occur such as areas of prolific growth of vegetation (Norman & Mumford 1985; Leach & Hines 1987); during floods, breeding occurs on inland swamps (Hobbs 1961), but flooding also suspected to reduce accessibility to some food plants, causing birds to move to drier or less inundated areas (Norman & Mumford 1985); sometimes move from areas where natural or artificial draining of wetlands (Bull 1939–40; Carroll 1969); lack of water suggested to be primary stimulus for movement (Carroll 1969).

No evidence of large-scale seasonal movement (Aust. Atlas; Vic. Atlas). Birds may migrate regularly across Torres Str. (Warham 1961; Storr 1984), where considered regular visitor, mainly in wet season (Draffan *et al.* 1983; Stokes 1983; Garnett & Bredl 1985; Ingram *et al.* 1986). Birds banded in n. Qld recovered from PNG and large fluctuations in numbers on rice fields in PNG attributed to migration (Hoogerwerf 1962). In some areas, numbers fluctuate seasonally e.g. on larger seasonal swamps in n.

NSW, numbers increase Apr.–Aug. on Hunter R. and peak Mar.–Aug. on Richmond R. (Gosper 1981); summer peak at Benger Swamp, WA, (Jaensch *et al.* 1988); at Pukepuke Lagoon numbers peak in autumn (Fordham 1983); at Manawatu R. estuary, NZ, numbers increase in autumn and winter (Fordham 1983). Long-distance movements indicated by banding and presence on islands far from mainlands, e.g. Lord Howe, Norfolk and King Is (McGarvie & Templeton 1974; Schodde *et al.* 1983; Hermes 1985). Birds will fly at night and suggested to do so often; numbers appeared in Waimarino region, NZ, overnight; birds found at high altitudes may have been blown off course (Carroll 1969; Tunnicliffe 1985; B.D. Heather).

Banding Most recoveries suggest birds sedentary. In NZ, of 223 banded birds in 364 ha reserve, only one sighted outside park between 1979 and 1986; most birds remained in territory for some years; if territory abandoned, most joined neighbouring groups, established new territories nearby or became non-territorials in general area (Craig & Jamieson 1988). Long-distance movements include one bird banded near Townsville and recovered c. 1600 km away, three years later, at Koerik in New Guinea, another moved from Townsville to Merauke in New Guinea (Lavery 1961, 1965; Aust. Atlas). Also movements from Townsville to near Ingham, near Tully, near Babinda and to Home Hill (Lavery 1961, 1965). In NZ, some banded birds move at least c. 240 km with most reported movements less than c. 50 km; two birds moved more than 180 km in 3 months and one moved 121 km in 52 days (Carroll 1969; Craig 1979); one returned 97 km to place of capture in 8 days (Sutton 1967).

FOOD Mainly aquatic vegetation; also seeds, fruits, insects, frogs, lizards, fish, young birds, eggs and small mammals. **Behaviour** Diurnal; feed less in afternoon and evening. Feed on ground and in water; in swamps, damp pastures and grasslands. Graze clover and pasture; pull out monocotyledon tillers or nip them off at base with powerful bill, holding them parrot-like with foot to chew soft fleshy bases (Fig. 1) (Martin *et al.* 1979). Firmly grasp figs by wedging them between toes to break them up; also squash figs in bill before swallowing (Rowley 1968). Glean insects and seeds. Dig for subterranean rhizomes and roots of clovers, grasses and irises; will immerse head and swim to reach new growth, but not seen diving. In NZ, mostly take clover in spring, seeds in summer and early autumn; increase intake of grit in winter. Opportunistic (Carroll 1966). Dieback in *Typha* in autumn results in less dietary reliance on swamps; *Typha* shoots taken in spring when available (Fordham 1983). In Vic., increased intake of grit in late autumn, insects in late spring, and decrease of fresh vegetation in autumn and winter with corresponding increase in subterranean foods in winter (Norman & Mumford 1985). Sometimes wash food before eating (Ridpath 1972).

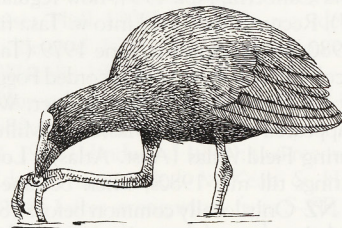


Fig. 1 Feeding

Adult In NZ (n=63, gizzards; Muggeridge & Cottier 1931). **Plants** Weed and other vegetation and sds; Lemnaceae: duckweed lvs; Juncaceae: *Juncus bufonius* sds; Cyperaceae: rush lvs, sds; sedge-weed lvs; *Carex* sds; *Eleocharis*; *E. orata* sds; Poaceae: lvs, sds;

rye sds; *Alopecurus geniculatus* sds; marsh foxtail *Alopecurus* lvs; *Glyceria fluitans* sds; oats *Avena* sds; *Lolium perenne* sds; barley *Hordeum* sds; *Poa annua* sds; *P. pratensis* sds; wheat *Triticum* sds; Ranunculaceae: buttercup sds; Fabaceae: *Trifolium* lvs; Chenopodiaceae: *Chenopodium album* lvs. **Animals** Arachnids: spiders. Insects: ads, larv.

In NZ (n=298, gizzards; Carroll 1966). **Plants** 100% freq.: Pteridophyta: Salvinaceae: *Salvinia natans* fronds 1.7; Hydrocharitaceae: *Elodea canadensis* lvs 0.3; Potamogetonaceae: *Potamogeton pectinatus* lvs 1.0; Lemnaceae: *Lemna minor* lvs 0.3; Zannichelliaceae: *Zannichellia palustris* lvs 0.6; Cyperaceae sds 35; lvs 56; *Eleocharis sphacelata*; *E. gracilis*; *E. neo-zelandica*; *Scirpus*; *S. caldwelli*; *S. medianus*; *S. lacustris*; *S. americanus*; *Carex*; *C. tes-tacea*; *C. virgata*; *C. leporina*; *Cladium junceum* 3.7; *Cyperus ustulatus* 1.3; Juncaceae sds 15; *Juncus bufonius*; *J. maritimus*; Cyperaceae/Juncaceae lvs 59; Poaceae: sds 29; lvs 70; *Poa*; *P. annua*; *P. trivialis*; *P. pratensis*; *Glyceria fluitans*; *G. maxima*; *Holcus lanatus*; *Anthoxanthum odoratum*; Fabaceae: *Trifolium* lvs 34; sds 1.7; Polygonaceae sds 25; *Rumex*; *R. acetosella*; *R. acetosa*; *R. crispus*; *Polygonum hydropiper*; *P. persicaria*; *P. aviculare*; Ranunculaceae: *Ranunculus* sds 2.7; *R. sardous* sds; *R. sceleratus* sds; *R. bulbosa* sds; Caryophyllaceae: *Stellaria media* 1.7, sds 3.4; Portulacaceae: *Portulaca oleracea* sds 0.7; Rubiaceae: *Coprosma* sds 1.0; Asteraceae: *Bidens tripartita* sds 2.0; *Taraxacum officinale* sds 1.4; other dicotyledon sds 17; other plant lvs 7. **Animals** 75: Onychophorans: *Peripatus novaezealandiae* 0.7. Annelids: oligochaetes 1.7. Molluscs: gastropods 0.3. Crustaceans: isopods 0.7. Arachnids 12.1: Araneae: *Dolomedes minor* ad., nests; Opilionida: Phalangida. Insects 21.5: eggs; Hemiptera: Notonectidae; Coleoptera: Carabidae: ads, larv.; Orthoptera: Acrididae/Tettigoniidae: grasshoppers; Gryllidae; Diptera: ad., larv.; Lepidoptera: larv. 1.0. Reptiles: lizards: Scincidae 1.0. Birds 0.3. Grit 100.

At L. Wellington and Sale Common, Vic. (n=234, gizzards; Norman & Mumford 1985). **Plants** 76% vol.: Algae: Chlorophyta: Typhaceae: *Typha* 2; Hydrocharitaceae: *Vallisneria spiralis* 11; Ruppiaceae: *Ruppia*; Juncaginaceae: *Triglochin procerum*; Poaceae 59: *Phragmites australis* lvs, rhizomes 34; others 25; *Poa*; *Glyceria australis*; *Avena*; *Cynodon dactylon* rhizomes; *Paspalum distichum* rhizomes; *Stenotaphrum secundatum* rhizomes; *Lolium perenne* rhizomes; *Microlaena stipoides*; *Pennisetum*; *Panicum*; *Vulpia*; Cyperaceae 17: *Scirpus* lvs, rhizomes 10; *S. validus* 2; *S. maritimus*; *S. fluviatilis*; *Eleocharis* sds; *E. sphacelata* lvs, sds 1; *Cladium procerum* lvs, sds 4; *Baumea articulatum* lvs, sds; *Carex*; Iridaceae: *Romulea rosea* lvs, rhizomes; Haloragaceae: *Myriophyllum propinquum* lvs; Polygonaceae: *Polygonum*; *P. hydropiper* sds; *P. lapathifolium* sds; Portulacaceae: *Montia fontana*; Fabaceae: *Trifolium* lvs, rhizomes 1; *Medicago*; Rubiaceae: *Rubus*; Asteraceae: *Cotula coronopifolia*; unident. rhizome 3; others 4. **Animals** 1: Crustaceans: amphipods: *Austrochiltonia*. Arachnids. Insects: Hemiptera: Corixidae: *Sigara*; Naucoridae: *Naucoris congregex*; Coleoptera: Hydrophilidae: *Helochaers australis* ad. and larvae; Scarabaeidae: *Sericesthis pruinosa*; Anoplognathus; *Repsimus*; Chrysomelidae; Elateridae; Dynestinae; Dytiscidae; Diptera: Chironomidae: larv.; Tipulidae: larv.; Hymenoptera: Formicidae: *Iridomyrmex*. Inorganic 23% vol., 100% freq.: quartzitic grit 96% freq.; shell-grit 0.9; shotgun pellets 6.0; ironstone 4.3.

Other records **Plants** Vegetable matter and roots of plants, especially swamp plants (obs., McLean 1901; McKeown 1934; Bull 1939–40; Merton 1970; Bayliss 1975; Vestjens 1977; Hutton 1990; Oliver; Cleland); aquatic plants (Lea & Gray); grain and vegetable crops (obs., Bryant 1940; obs., Bravery 1970; Gould; North); root crops (obs., McKenzie 1967); berries and seeds (Oliver); Gymnosperma: *Dacrydium cupressinum* fruits (obs., McLean 1901); Monocotyledon: lvs, stalks (Barker & Vestjens);

Typhaceae: *Typha domingensis* (obs., Martin *et al.* 1979); *T. augustifolia*? leaf bases (North; obs., McKenzie 1967); Cyperaceae: fibres (Merton 1970), sds (Barker & Vestjens); *Eleocharis plana* (Barker & Vestjens); *E. sphacelata* lvs (obs., Bayliss 1975); Juncaceae: fibres (Merton 1970); soft white bases (obs., Wheeler 1941; obs., Green & Mollison 1961; obs., Fordham 1971); Poaceae: *Hemarthria uncinata* var. *uncinata* rhizomes; *Pennisetum clandestinum* lvs (B. Lepschi); young grass and roots (Bull 1939–40); fragments (Green 1969); sds (Barker & Vestjens); Sugar-cane *Saccharum officinarum* young shoots (obs., Barker 1949); *Poa* sds; *P. annua* lvs (van Tets *et al.* 1977); *Digitaria* (McKeown 1934); *Zea mays* young plants, sds (North; Gould; obs., McLean 1901; McKenzie 1967); Myoporaceae: *Myoporaiaum* lvs (Lea & Gray); Rosaceae: blackberry *Rubus* fru. (obs., McKenzie 1967); Apples *Pyrus malus* (obs., Fielding 1979); Polygonaceae: *Polygonum* sds (Vestjens 1977); Fabaceae: *Trifolium* lvs (obs., Martin *et al.* 1979); Moraceae: figs *Ficus rubiginosa* (Rowley 1968); Solanaceae: Potatoes *Solanum tuberosa* (obs., Green & Mollison 1961; obs., McKenzie 1967); Convolvulaceae: kumaras *Ipomea* (obs., McKenzie 1967). **Animals** (Gould). Annelids: oligochaetes (Oliver). Molluscs (Gould; obs., Hutton 1990): freshwater molluscs (North); gastropods: water-snails (obs., Bryant 1940); bivalves (obs., McLean 1901; Oliver). Arachnids: Araneae: spiders (Merton 1970). Crustaceans (obs., Wheeler 1941): isopods (Merton 1970). Insects (Oliver; Gould): ads, larv. (obs., Bryant 1940; obs., Hutton 1990); aquatic insects (Gould; North); Hemiptera: Corixidae; Orthoptera: Acrididae (Barker & Vestjens); Acrididae/Tettigoniidae: grasshoppers (obs., McLean 1901; Anon. 1920; obs., Bryant 1940); Gryllidae (obs., McLean 1901; obs., Bryant 1940); Coleoptera (obs., Bryant 1940; Barker & Vestjens); Lepidoptera: larv (Barker & Vestjens); Noctuidae: *Spodoptera* larv. (obs., Roberts 1936). Fish (40–50 cm) (Oliver; obs., Lester 1976); Anguilliformes: eels *Anguilla* (<18 cm); flounder *Pleuronectes* <13 cm (Oliver); dead goldfish *Carassius auratus* (obs., Vestjens 1977); carp *Ciprinus carpio* (obs., Bryant 1940). Amphibians: frogs (Oliver; obs., Fletcher 1924); ads, spawn; *Litoria* (obs., Bryant 1940). Reptiles: lizards: Scincidae (Oliver). Birds: Anatidae: duck eggs (Oliver; Fitzgerald 1966; obs., McKenzie 1967); young birds (Oliver); ducklings (obs., McKenzie 1967; CSN 22); Muscovy Duck *Carina moschata* ducklings (obs., Lowe 1966); Chestnut Teal *Anas castanea* duckling (obs., van Tets 1965); Brown Teal *A. chlorotis* (obs., McKenzie 1967); Phasianidae: Domestic Chicken eggs (obs., Binns 1953; obs., Fitzgerald 1966); Blackbirds *Turdus merula* (obs., McKenzie 1967); Common Starling *Sturnus vulgaris* ad. (obs., Egan 1992). Mammals; carrion (NZRD). Raw or cooked meat (in captivity, Mathews); Bromadiolone rodenticide (Reece *et al.* 1985); wool (Merton 1970); grit (Merton 1970; Vestjens 1977; Lea & Gray); sand (McKeown 1934; Merton 1970); shell (Lea & Gray); gravel (McKeown 1934; North; Cleland).

Young Frogs (obs., Brown & Brown 1977).

Intake In Vic., inorganic matter: 6.1 g mean dry wt (3.1; 0–16; 235); significant difference between males, 6.5 g (3.1; 140), and females, 5.5 g (3.0; 95) (*t*-test, $P < 0.01$) (Norman & Mumford 1985). Important in transfer of minerals from swamp to pasture (Fordham 1985).

SOCIAL ORGANIZATION Well known in NZ; account based on major studies, mainly Craig (1976, 1977, 1979, 1980a,b, 1984), Craig & Jamieson (1988), Jamieson & Craig (1987a,c), Jamieson *et al.* (1987), and Fordham (1983); one minor study in Aust. (Wettin 1984). Throughout year in territorial pairs or groups, or as non-territorial birds in flocks; a few solitary non-breeding birds occur during breeding season; within all social groups hierarchies exist. Stable groups usually 'kin'; 'non-kin'

groups unstable (Craig 1980a); account refers nearly always to stable groups. Communally breeding groups that maintain territories typically consist of 2–7 breeding males, 1–2 breeding females, and up to seven non-breeding helpers, offspring from previous matings (e.g. Jamieson & Craig 1987c; Craig & Jamieson 1988). Size of flocks of non-territorial birds can change, but generally related to seasons; large flocks of up to 300 form summer–autumn, remain large in non-breeding season, then disperse before breeding, but small flocks of non-territorial birds remain (Craig 1979; Pierce 1980; Fordham 1983). Habitat also affects size of flocks; those in pasture larger than in swamp (Fordham 1983). Flock includes high proportion of young and males, but composition not constant; at Pukepuke Lagoon, large autumn flock included resident birds, young of year, and immigrants; any apparent family groups in flock become indistinguishable as size of flock increases (Craig 1979; Fordham 1983). Individuals in feeding flocks do not feed in co-ordinated fashion; sometimes territorial cohorts retain separate spatial identity within flock (Fordham 1983).

Bonds Mainly long-term monogamy and polygamy, but unstable groups could be considered promiscuous. Polygamous stable group, together all year, consists of 2–7 breeding males, 1–2 breeding females, plus helpers (see below); all breeding adults court and copulate with each other, so homosexuality frequent, but male–female interactions most common. Only most dominant females breed; if two breeding females present, lay in single nest (Craig 1980b); no evidence of dominant birds guarding their mates (Jamieson & Craig 1987a); incestuous matings common (Craig & Jamieson 1988), and multiple paternity in groups suggested (Craig & Jamieson 1985); report of dominant female of group dying and group dispersing (Craig 1979); also see Hierarchies in Social Behaviour. Unstable breeding groups usually unsuccessful, formed by birds from flock, and characterized by much aggression and many males (Craig 1980a,b; Wettin 1984). In Aust., breeding trios reported (Ridpath 1972). Mating system adopted and size of breeding group depends on structure of breeding habitat, length of territorial boundary, density, stability of breeding group, and size of surrounding breeding groups (Craig 1979; Jamieson & Craig 1987a,b). Pairs common in pasture and groups in swamp. Monogamy has highest breeding success, but only occurs where length of defended boundary short, and neighbours paired; only seen in most aggressive birds; 10–22% of populations breed as pairs (Craig 1979, 1980b). Males and females capable of breeding when 1 year old, but only noted in small populations; status also determines breeding age. Within groups, younger birds, typically 3 years old or less, do not usually participate in sexual activity; younger female from within group replaces dominant breeding female when she dies, but sometimes not until following year (Craig 1980a; Jamieson *et al.* 1987; Jamieson & Craig 1987a; Craig & Jamieson 1988). Sex-ratio generally equal (Dow 1980); of birds occupying territories, about equal; in flocks, high proportion of males (Craig 1979). **Co-operative breeding, Parental care** Four social systems for rearing young: (1) monogamous pair alone; (2) polygamous group of breeding adults; (3) as (2) but includes non-breeding birds; (4) any of above, but assisted by juveniles from earlier clutches of same season (Craig 1980b). Non-breeding birds in group usually young of previous year (Craig & Jamieson 1988); groups can recruit outsiders for defence (Craig 1984). Contributions by members of group to breeding attempt depends on status. Territorial defence shared by all members of breeding unit, including young of previous brood of season; degree of participation related to status and sex, dominant males being most effective. In monogamous pair, adult male performed 28% of defence; two males of previous brood, 50%; and female

and remaining brood did little; in groups adult males performed 74% of defence; adult females, 19%; and juveniles 7% (Craig 1979). Apparently groups rather than pairs required to maintain breeding territory in most areas (Craig 1980a). Pair or group may recruit extra males for defence if required; owners of surrounding territories often follow suit; recruited males may be expelled before breeding (Craig 1980a, 1984). Only males seen building nests (Craig 1980a), but in Aust. both sexes seen to do so (Aust. NRS). Incubation by all breeding adults. In groups, 9% of territorial defence also involves some non-breeding adults, but length of bouts shorter than for breeders, and some of these are first-year birds (*contra* Craig 1980a); incubation mainly by dominant female; females incubate more during day than males, whereas males incubate during night (Jamieson *et al.* 1987). In pairs, tendency for female to incubate more during day not apparent (Craig 1980a); also see Breeding. All birds in pairs and groups, including young of earlier broods of season, care for young by helping with feeding, leading, and brooding chicks; degree of participation varies with status (e.g. Craig 1980a; Craig & Jamieson 1988). When a few weeks old, hand-reared young feed younger chicks. In groups, less experienced non-breeders initially feed chicks more than experienced non-breeders (Jamieson & Craig 1987b). When pairs re-nest, non-incubating bird cares for young (Craig 1980a). Young fed until at least 2 months old; brooded until 4 months. Young of monogamous pairs forced to become independent earlier than in groups; evicted before following breeding season. In groups, most young remain in natal territory, often breeding incestuously if adult dies; not known how groups regulate size (Craig 1979, 1980a; Craig & Jamieson 1988). At Linton, NZ, first-year and non-territorial birds dispersed into neighbouring areas, slowly moving farther until vacant territory found (similar pattern to non-territorial birds at Pukepuke, NZ); sometimes first-year birds returned to natal territory between movements (Craig 1979; Craig & Jamieson 1988). In one population in NZ, c. 10% of birds (all males) actively dispersed from natal territory, most joining adjacent territories; males and one female of unknown origin joined territories (Craig & Jamieson 1988). High variation in degree of breakdown of territories outside breeding season; flocks apparently have fluid membership (few birds in flock for more than a year) and flocks may move away from area (Craig 1979).

Breeding dispersion Single egg-nest within territory, which, when two females in group, used by both. Trial, roosting, and brooding nests also built in territory; see Breeding. Breeding between neighbouring groups more synchronized than between neighbouring pairs; laying within group highly synchronized (Jamieson & Craig 1987a). **Territories** At some locations group defends all year, at others, territories break down to various degrees after breeding (Craig 1979, 1984). All-purpose; successful breeding territory requires minimum area of cover, and water at least c. 0.3 m deep (Craig 1980b). A few territories defended diurnally, then used as flock-roost at night. Defence of territory related to size of group; up to 0.5 ha may change ownership, and up to half territory may be lost before new male admitted. Size of territories, 0.7–3.0 ha (Craig 1979); in groups usually stable, but may vary if habitat alters, e.g. water dries out; less stable in pairs, e.g. territory larger when brood present to assist in defence (Craig 1979). Large territories usually have some undefined boundaries, while small territories usually bounded by other territories (Craig 1979). Territory often adjoins others at a boundary zone, up to 15 m wide, which typically centres on natural landmarks; individuals in group defend most of home-range but, in boundary zone, hierarchy exists involving members of adjacent territories; dominant males able to use area in zone, but access for other birds

depends on status both of bird in question and others nearby, e.g. subordinate may be able to use area only if dominant of its group present (Craig 1976). If territory lost, birds remain near natal area and most either join neighbouring groups or establish new territories with kin from original territory; a few become non-territorial (Craig & Jamieson 1988). Unstable breeding groups form in suboptimal territories (Craig 1980b).

Roosting Mainly nocturnal; crowd when roosting (Craig 1979). On platforms constructed in reeds; one bird on each platform, entering by climbing foot over foot (Bryant 1940). Also use logs and trees (McKenzie 1967; Morris 1978; Norman & Mumford 1985). Breeding birds mostly in territory; flocks roost together, sometimes invading several territories at night. During incubation, male sits on nest at dusk and relieved before dawn by female (Craig 1980a). Sun-bathe when sunny, often after bathing, with wings extended and partly folded on each side of tail or twisted downwards (Holyoak 1970). Brood-nests constructed for young at night; many egg-nests in *Typha* used as brood-nests (Craig 1980a).

SOCIAL BEHAVIOUR Account based on detailed behavioural studies in wild in NZ, mainly Craig (1977) but also Craig (1979, 1980a), Craig & Craig (1974) and Jamieson & Craig (1987c); some details from captive birds (Holyoak 1970), and voice studies (Clapperton 1987; Clapperton & Jenkins 1984, 1987); see also Voice. Large conspicuous bird, often in open habitat, that engages in noisy copulations, easily and often observed (Craig 1980a; Craig & Jamieson 1988). Different displays involving elevation of wings and tail, and position of shield and bill, important. Displays similar to those of other gallinules except Coot *Fulica atra*; larger vocal repertoire compared with other rallidae. Most groups stable kin groups and show more co-ordinated activities and less aggression between members than unstable, non-kin groups. N'yip Call, contact call between group members, and given by adults when calling chicks. Hiccup Call given by incubating bird to attract other birds, occasionally while feeding, and by bird when separated from group.

Agonistic behaviour Intraspecific aggression, complex. Within stable group, hierarchy maintained (see below); occasionally one displaces another from food; less often, dominant steals food from subordinate; aggression more apparent within newly formed groups. Aggression occurs mainly between neighbouring groups, and related to territorial defence; most common in spring; most effective defence by adult males. Crowing Call and Yelling associated with territorial behaviour; see Voice. Following displays from Craig (1977); not presented in order of increasing threat; sequences in which main displays often given shown in Figure 6 in Craig (1977). Bill very important in agonistic behaviour, but frontal shield also important; white under tail-coverts, which can be exposed when raising wings, important in submissive or escape displays; upright stance used in more aggressive threat postures; main element of attack appears to be positioning bill for peck. Postures of tail and wing related to agonistic display. **TAIL POSTURES:** AT REST: closed and held down at angle from body, and no white apparent. **TAIL-UP:** closed or expanded to some degree; five recognizable grades according to angle of tail to axis of body, ranging from Tail-down to Tail Fully Up; show increasing amounts of white from behind. **TAIL-FLICK:** rapidly flicks, at various rates and amplitudes, from lower to higher position and then back again, see Alarm. **WING POSITIONS:** AT REST: folded close to body along back. **WINGS PARTLY UP:** partly raised but closed, so tip of tail still projects above wings. **WINGS FULLY UP:** raised but closed, completely covering raised tail in side view. **EXAGGERATED WINGS-UP:** held extremely high with tips touching, but still closed.

WINGS OUT: held out either side of body, and accompanies any of preceding wing positions; usually bird Yells. Generally as wings become higher, tail becomes higher and expands; Wings-down and Tail-down most common in more aggressive displays (Craig 1977). **Displays** 'Aggressive' Upright and 'Anxiety' Upright, two extremes of graded UPRIGHT DISPLAY; degree adopted depends on status of opponent, and distance of opponent from territorial boundary; positions of wings and tail vary. 'AGGRESSIVE' UPRIGHT: (Fig. 2) head and bill point down c. 45°; neck varies from being extended to partly retracted (usually extended if two birds facing), and held either vertically or forward. Normally face opponent, so bill and shield show, and often advance; rarely given side-on or turned away from opponent; common aggressive display of low intensity. 'ANXIETY' UPRIGHT (Fig. 3): head and bill horizontal or pointing slightly upwards, minimizing view of bill and shield; usually neck unextended and vertical, plumage sleek; orientation of bird varies, but never moves towards opponent; appeasement posture. Upright may develop into FORWARD POSTURES, another graded display of which Horizontal Forward and Depressed Forward are extremes; both can lead to fighting; bird holding posture probably signals maximum threat, but will not react unless attacked. **HORIZONTAL FORWARD** (Fig. 4): face opponent with bill horizontal or slightly depressed; head and neck low, forward, and roughly horizontal, with neck frequently extended; body horizontal or tilted slightly forward, and usually body-feathers fluffed; shield and bill prominent; postures of wings and tail vary, but usually at least Partly Up and occasionally Out. Bird motionless, then slowly moves toward or Charges opponent; usually no call. **DEPRESSED FORWARD** (Fig. 5): similar to Horizontal Forward with bill pointing at opponent, but head and bill nearer ground, and body tilted forward forming angle of 20–60° with ground; postures of wing and tail mainly Fully Up or Exaggerated Up; occasionally move forward or backward slowly, or forward in rapid short jerks. **BOW DISPLAYS:** vary; characterized by bill pointing vertically downward or resting on ground; wing and tail postures Fully or Exaggerated Up, especially in Full Bow and Body Bow; body-feathers rarely fluffed. **HEAD-BOW** (Fig. 6): similar to Horizontal Forward but bill and head point downwards; orientation initially frontal, but usually Turns Away to side-on or Faces Away (see below). **FULL BOW** (Fig. 7): bill between legs or pointed at ground, and neck and body tilted forward at angle of 60°–90° to ground; usually remain rigid, but sometimes stamp one foot or rapidly peck ground; occasionally make low grating sound. **DIP BOW:** move toward opponent altering between Upright and Full Bow. **BODY BOW** (Fig. 8): extreme bow where body tilts well forward and downward so that bill, head, neck and breast rest on ground; usually bird rigid, but often backs away from opponent. **HUNCHES:** similar to female pre-copulatory posture; adopted by either sex, but mostly in disputes between males from adjacent territories; birds rarely attacked in these positions, presumably because they are appeasing. **ERECT HUNCH** (Fig. 9): depress head, bill and tail, hunch neck, and spread legs; body vertically upright, and wings close to body; orientation always away from opponent, and usually shuffle away. **WINGS-EXPANDED HUNCH** (Fig. 10): similar to Erect Hunch but primaries extended and expanded, and bird sometimes looks over shoulder; posture ceases when opponent moves; can precede threat or escape display. **CROUCH** (Fig. 11): crouch with head and bill horizontal, turned or tucked partly under body; feathers of body, sleeked; neck withdrawn and hunched; wings close to body and tail often down. Orientation of bird varies; nearly always by birds of low status or juveniles, which give juvenile Miaoow Calls. **FACING AWAY** (Fig. 12): face head and bill away from opponent; raise wings and tail; commonly seen in Bow, Depressed Forward, Crouch, Head-flick, and Upright; almost

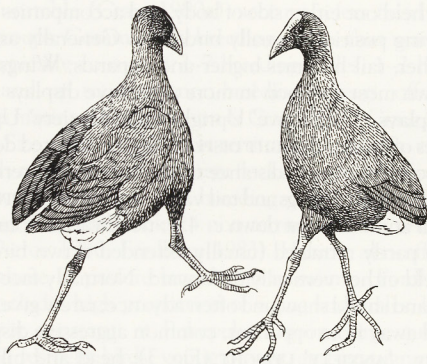


Fig. 2 'Aggressive' Upright

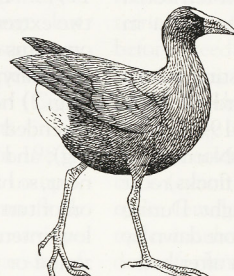


Fig. 3 'Anxiety' Upright

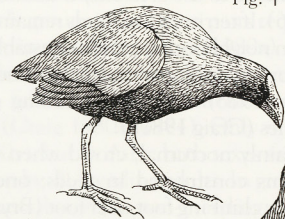


Fig. 4 Horizontal Forward

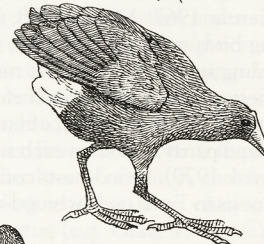


Fig. 5 Depressed Forward

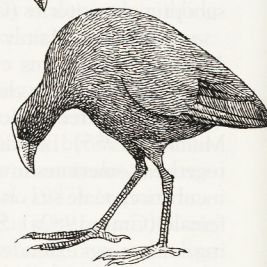


Fig. 6 Head-bow



Fig. 7 Full Bow



Fig. 8 Body Bow

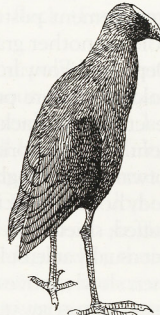


Fig. 9 Erect Hunch

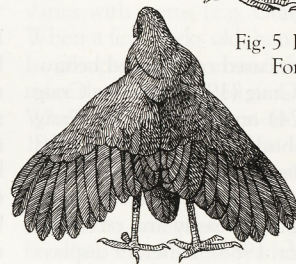


Fig. 10 Wings-expanded Hunch

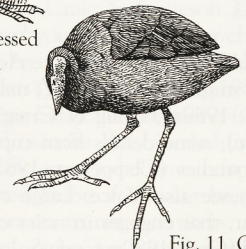


Fig. 11 Crouch



Fig. 12 Facing Away

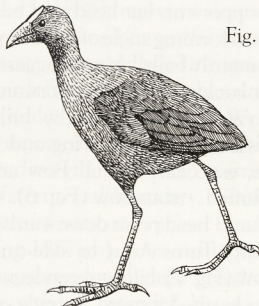


Fig. 13 Wings Drooped

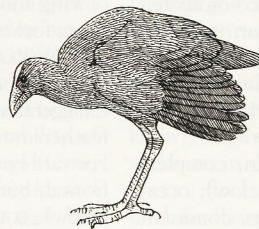


Fig. 14 Head-flick

always precedes TURNING AWAY in which turn away from frontal orientation before Moving Away (see below). Head-flagging occurs with alternate Facing-away to either side of body; seen only in Bows and Crouch. WINGS DROOPED (Fig. 13): similar to normal feeding posture, but primaries hang beside body as when sunbathing; orientation always side-on; normally only adopted by dominant males; few birds react aggressively towards another using it. WING-CLAP: partly spread wings and rapidly lift them to meet above back; usually in Upright posture; rarely given by isolated bird; loud call accompanies each clap. HEAD-FLICK (Fig. 14): flick head and bill vertically up and back; feathers of body normally sleeked, and almost always Tail Fully Up, and Wings Fully or Exaggerated Up; when extreme, extend and bend neck backwards so that head lies on back; removes frontal shield and bill from opponent's view. PECKING: direct open bill at head, neck or back of opponent; rare, occurring between juveniles and adults within group. CHARGE: run at bird with head and neck extended, and bill pointed downwards; lower neck as speed increases. Rarely reach opponent but, if so, peck it. Wing and tail positions usually higher with increasing status of opponent or closer to territorial boundary. SPLATTER CHARGE (Fig. 15) (Gullion 1952): flap wings to increase speed when charging. FIGHTING (Fig. 16) Two birds jump

at each other, feet first, ripping with claws; occasionally push apart and onto their backs; sometimes one manages to get astride belly or back of opponent and peck it; sometimes lock together, sitting on rumps, ripping at each other's breast with legs. Usually rapid, involving up to four birds. Occasionally two birds, in Aggressive Upright, slowly spar with one foot (Fig. 17). Fighting occurs at territorial boundaries; never between members of same group; less often in flocks (Craig 1977); occurs with Tasmanian Native-hen (Ridpath 1972). Unstable groups observed fighting on nest-ramp; may lead to damage or ejection of eggs. **Escape** In

Plate 45

Spotless Crake *Porzana tabuensis* (page 559)

Nominate *tabuensis*

1 Adult; 2 Small downy young; 3 Large downy young; 4 Juvenile; 5 Adult

Ruddy Crake *Porzana fusca* (page 557)

6, 7 Adult

White-browed Crake *Porzana cinereus* (page 567)

8 Adult; 9 Large downy young; 10 Juvenile; 11 Adult

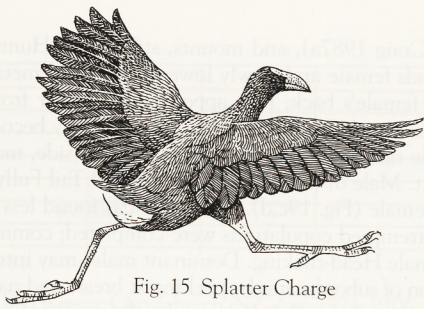


Fig. 15 Splatter Charge

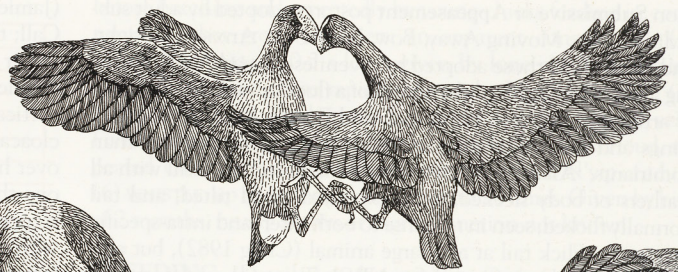


Fig. 16 Fighting

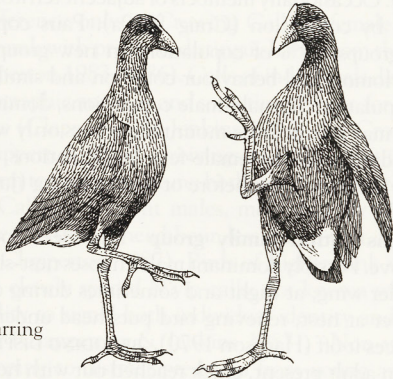


Fig. 17 Sparring

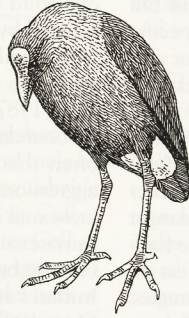


Fig. 18 Pre-copulatory Hunch

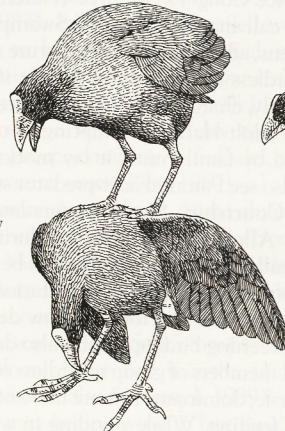


Fig. 19a

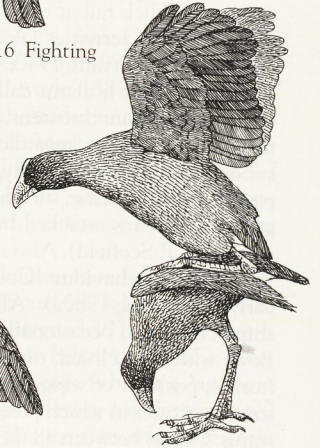


Fig. 19b

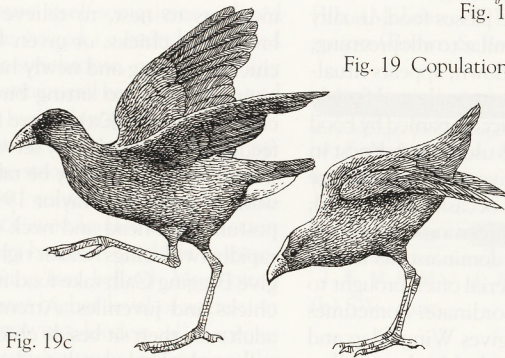


Fig. 19 Copulation

Fig. 19c

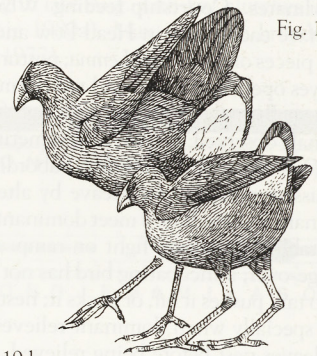


Fig. 19d

postures with high tendency to escape, bill placed on ground or removed from opponent's view (e.g. Facing-away and Turning-away), and with increasing desire to escape, wings increasingly raised; only in pure escape postures are white under tail-coverts prominent (Craig 1977). MOVE AWAY: move away from opponent, position of body depending on posture previously held, e.g. Bowing bird Moves Away with bill near ground, always with high elevation of wings and tail. Moving Away often leads to Erect Hunch, Wings-expanded Hunch, or Splatter Away. SPLATTER AWAY: same as Splatter Charge but away from opponent. GRASS-PULLING: after

territorial dispute, birds still facing each other, one pecks vegetation, throwing material sideways and backwards, then retreats; rare. **Hierarchies** Linear and consistent hierarchies occur in all social units, including pairs with young, and within and between territorial groups (Jamieson & Craig 1987a). Males dominant over females, and adults dominant over yearlings and juveniles; within each sex- and age-class, status higher with increasing weight and size of frontal shield (Craig 1979). Only most aggressive birds able to move between territories or maintain pair. Within group, only most dominant females breed; aggression between two breeding females rare; no evidence of tossing or destruction of eggs; dominant usually lays at least one more egg, and contributes to more clutches; also involved in more copulations, but apparently not because she is dominant; beta female does not always lay; subordinate non-breeding females may be of breeding age, but not harassed by breeding females (Craig 1980b; Jamieson & Craig 1987a,c). No relation found between rank of male and frequency of sexual activity; dominants may interrupt subordinates, but no mate-guarding (Craig 1980a; Jamieson & Craig 1987a). When birds in flocks or from same territory meet, subordinate normally assumes submissive or appeasement posture, but dominant remains in Upright. The com-

Plate 46

Watercock *Gallinula cyanoptera* (page 575)
 1 Adult male, breeding; 2 Adult female; 3 Juvenile;
 4 Adult female

Purple Gallinule *Porphyrio martinica* (page 576)
 5 Adult; 6 Juvenile; 7 Adult

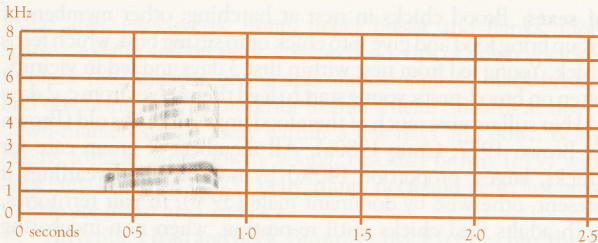
mon **Submissive** or **Appeasement** postures adopted by adult subordinates are: Moving Away, Bow, Body Bow, Anxiety Upright, and Head-flick; those adopted by juveniles or yearlings: Crouching and Head-flagging; when birds of a flock crowded round piles of artificial food, give Head-flick and Facing Away. In displays, wings and tails of submissive birds always more elevated than dominants. **Alarm** ALERT POSTURE: stand erect and still with all feathers of body sleeked, neck extended, head tilted, and tail normally flicked; seen in response to both inter- and intra-specific aggression. Flick tail at any large animal (Craig 1982), but also during routine activities (Aust. NRS). To avoid predators or if disturbed, fly (Bryant 1940; Craig 1977), dive (Fletcher 1924; Tunncliffe 1965); alarm call may be given. If Swamp Harrier *Circus approximans* threatens, adults adopt Alert Posture and form tight concentration, regardless of territory or status; if Harrier swoops, one or more birds fly, charge, and leap at it; after danger passed, much fighting; subadult Harrier attempting to take half-grown chick was attacked by family until it lay motionless on ground (R.P. Scofield). Also see Parental anti-predator strategies.

Sexual behaviour Courtship Mostly occurs late July to early Dec. (Craig 1980a). **Allopreening** Common during courtship period, and occasionally Mar. and July. Bird to be preened Bows with eyes closed, often Facing Away; orientation usually frontal; position of wings and tail and form of Bow depend on status; postures in which preening birds approach also depend on status. Occurs between all members of group regardless of sex, but usually female preening male; dominants initiate more often than subordinates. **Courtship feeding** While standing in water, two birds face each other in Head Bow and one passes food, usually small pieces of duckweed *Lemna*; postures similar to allopreening, but eyes open, and wings and tail normally down; appears ritualized; usually male to female, although female to male and female to female observed; rare in pairs; sometimes accompanied by Food Call (see Voice, 8b). **Greeting** Subordinates usually enter nest in submissive posture; often leave by alternative nest-ramp before dominant arrives; Bow if meet dominant, but occasionally pecked; less stable groups may fight on ramp. Allopreening common at change-over; if incubating bird has not left, dominant sits with it bill to tail, pushes it off, or pecks it; nest material often brought to nest, specially when dominant relieves subordinate. Sometimes bird leaves nest before being relieved, but gives Wing Clap and call, which usually attracts relief bird. After relief, bird, regardless of rank or sex, often brings nesting material (Craig 1980a). **Pre-copulatory displays** As many as six males may join in pursuit of female (Jamieson & Craig 1987c), and up to three may attempt to mount at same time; multiple participation tends to increase with number of birds in territory (Craig 1980a), and possibly important in synchronizing sexual cycles of birds in group (Craig 1980a). To avoid copulation, female may fly up tree or run away; beta female may run to alpha female, with effect of redirecting male pursuit to alpha female (Jamieson & Craig 1987a). **SEXUAL UPRIGHT**: posture similar to Aggressive Upright with bill depressed; neck usually extended, and wings and tail down; accompanied by Humming Call. In this posture male approaches female with high-stepping gait, then follows behind her. **SEXUAL FORWARD**: head and neck withdrawn, bill depressed, body slightly above horizontal and Humming Call given; usually follows Sexual Upright. **PRE-COPULATORY HUNCH**: (Fig. 18) posture of female, similar to Erect Hunch but back less upright. Becomes **PRE-COPULATORY POSITION**, with neck extended and curved downwards, head pointing at ground, and partly open wings held out from body. As male mounts female, head and neck point between legs, and body inclines until horizontal. **Copulation** (Fig. 19a-d) Male puts one foot on female's back, probably to induce Pre-copulatory Stance

(Jamieson & Craig 1987a), and mounts, still giving Humming Call; then treads female and slowly lowers body until metatarsi either side of female's back; toes appear to curl over front of female's partly extended wings; he flaps wings, slowly becoming vertical; female raises tail, and male moves tail to side, making cloacal contact. Male dismounts with Wings and Tail Fully Up, over head of female (Fig. 19c,d). Craig (1980a) found less than one-third of attempted copulations were completed; commonly stopped by female Head-flicking. Dominant males may interfere with copulation of subordinates by pecking at breast and nape of female so that she rises and dislodges subordinate (Jamieson & Craig 1987a). Occasionally members of adjacent territories drawn to boundary by copulation (Craig 1980a). Pairs copulate less often than groups; 19% of copulations in new groups involve aggression. Homosexual behaviour common and similar to heterosexual copulation. In male-male copulations, dominant male initiates and may mount or be mounted; occurs only where four or more breeding males. In female-female copulations, dominant initiates and mounts; occur before or during laying (Jamieson & Craig 1987c).

Relations within family group Also see Co-operative breeding above. Possibly dominant male chooses nest-site. Chicks brooded under wing; at night and sometimes during day; when changing over at nest, relieving bird puts head under brooding bird, and forces it off (Harrison 1970). **BROODING DISPLAY**: to enter nest when adult present, chick reached out with head toward adult, who reciprocated, their bills touched, and chick then entered nest (Brown & Brown 1977). Food Call attracts group members to nest, to relieve or feed incubating bird, to feed brooder or chicks, or given by adults to attract chicks. When chicks hatching and newly hatched, group members bring food, giving it either to sitting bird to feed to chicks, or directly to chicks (Craig 1980a); before feeding, food often passed between feeding birds, which may serve to break it down (Harrison 1970); if food too large, it may be taken back and re-offered; adult may wash or wet food (Taylor 1990). **BEGGING**: crouch in hunched posture with head and neck extended, horizontal, and forward, rapidly twirl wings held at right angles, and sometimes Head-flag; give Begging Call; take food from edge or tip of adult bill; seen in chicks and juveniles. Attention Call of chick attracts adults; adult may then sit beside chick. N'yip Call given by adults when calling chicks. Juvenile males may try unsuccessfully to copulate with their mothers and sisters (Craig 1980a); some subadult males show reduced sexual behaviour in presence of their mothers (Craig & Jamieson 1988). Young of monogamous pairs forced to become independent earlier than in groups, and evicted before following breeding season; in groups, most young remain in natal territory. **Anti-predator behaviour of young** Dive, squat in cover, flee from nest (Tunncliffe 1965; Craig 1977); by 2 months old, spend much time alone but close to cover (Craig 1980a). Tail-flicking occurs in young (Aust. NRS). **Parental anti-predator behaviour** Rush to young if Harrier nearby. **DISTRACTION DISPLAY**: Wing-clap (see above) used to lead predator from nest or young birds; when performing, bird appears to be losing balance, but does not feign any specific injury (Craig 1977). Dominant male tends to return first to nest after disturbance (Craig 1980a); also see Alarm.

VOICE Well known; detailed study by Clapperton & Jenkins (1984), used here for description of calls of adult and young; includes sonagrams. Extralimitally, summarized in BWP. Large repertoire of calls; no intricate song because there is no complex muscular control over action of syrinx. Sternotrachealis thicker in female (2.5–5.0mm; 8) than male (1.0–1.5mm; 5), but marked



A L. McPherson; Christchurch, NZ, Apr. 1974; P106

sexual difference only in Crowing Call: in female harsher and more guttural; with practice, distinguishable from that of male by ear (Clapperton 1983, 1986). Calls of individuals distinguishable by spectrographic analysis, and sometimes by ear, for N'yip Call of both sexes (Clapperton & Jenkins 1987) and Crowing Call of male (Clapperton 1987). Crowings of birds living in a group do not conform to group signature; both sexes respond to playback of Crowing Calls of different males, most strongly to Crowing of stranger, less to that of neighbour, less still to that of fellow group member (Clapperton 1987). Birds of higher rank within group give more closely spaced N'yip calls; not known whether make use of ability to signal both individual identity and status using N'yip call (Clapperton & Jenkins 1987). **Non-vocal sounds** Wing-clapping to distract predators from young and to attract relief when incubating (see Social Behaviour).

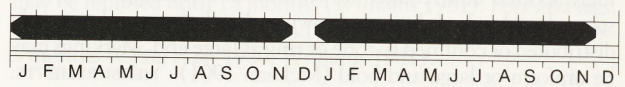
Adult Contact calls (1a) N'YIP CALL: soft and varying; two syllables often separated by brief pause, itself sometimes replaced by up to eight staccato notes. Double-voiced, i.e. sounds produced by the two sides of the syrinx, not synchronic, one continuing after the other has ended. Used as contact call between adults and from adults to chicks. (1b) HICCUP: harsh, low-pitched; short initial note followed by series of staccato notes, usually ending in yip. A harsher extended n'yip, with more staccato notes. Given more often by female. Appears to be loud contact call used by birds separated from rest of group. (1c) SQUAWK: loud and harsh; often accompanies Wing-clap display. May be given singly or as introductory call when Yelling or Crowing (see below). More often given by high-ranking birds; indicates higher level of aggression than N'yip. **Territorial calls** (2a) CROWING: loudest call of species (sonagram A); up to three introductory Squawks or Crowing-like calls (see below), followed by up to four Crowing Calls, increasing in length and loudness. Crowings of sexes differ, female harsher and more guttural. Given when moving about territory, after territorial interactions, and, for no apparent reason, while feeding. Dominant birds appear to crow more often than subordinate group members. (2b) YELLING: harsh sounds used in aggressive displays between neighbours. **Other calls** (3) DISTRESS CALLS: short (0.1–0.5 s), loud, and often repeated. (4) FLIGHT CALLS: similar to Squawk. Short, often repeated, given only in flight. (5) CROWING-LIKE CALLS: given by birds flying, running, landing, or wing-clapping. (6) N'YICK CALL: disyllabic, appears to reinforce submissive display when chased by more dominant bird. (7) DEFENCE CALLS: up to 0.5 s, sometimes incorporating preceding Yip note. Given by whole group at approach of Swamp Harrier, in nest defence against predators, and territorial defence against conspecifics. (8) SOLICITING CALLS: (8a) PRE-COPULATORY HUMMING: soft, nasal and monotonous. (8b) FOOD CALL: short note (0.05–0.1 s), rapidly repeated. Given to attract another member of group, by incubating bird seeking food or relief, or by adults that have food to attract other adults and chicks.

Young (1) BEGGING CALL: continuous note or rapidly repeated series of short notes. (2) TWERP and TWEEP: given in hours

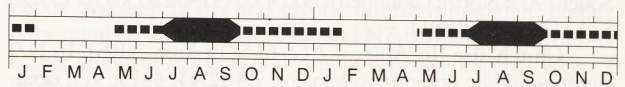
before hatching and repeatedly by young chicks feeding in company of other group members; an apparent contact call. (3) ATTENTION CALL: c. 0.5 s long, given by lone chick; becoming more intense and more rapidly repeated when adult close. (4) TRISYLLABIC CALL: loud, given by juveniles at any time of year. Function not known. (5) CAT-LIKE CALL: lasts c. 0.5 s, loud, repeated. Given by juveniles. Probably develops into N'yip of adult. (6) WHISTLE: up to 3 s long, repeated up to 20 times. Given by bird of 2 months, nearly always at night. Function not known.

BREEDING Detailed studies in NZ by Craig (1976, 1980a,b), Craig & Jamieson (1988), Jamieson & Craig (1987a) and Jamieson *et al.* (1987). In Aust., no detailed work; 138 records in Aust. NRS up to June 1992. Communal; monogamous, polygamous and promiscuous (see Social Organization); one record of simultaneous polyandry (Wettin 1984). In NZ, breed in groups of 3–7 males and 1–2 females and lay eggs in single nest. In Aust.: breeding groups comprise 2–5 adults; pairs more common along narrow watercourses (Dow 1980).

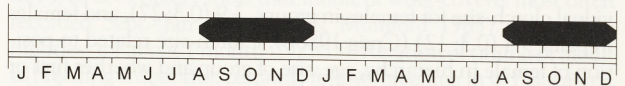
Season Aust. In n. Aust.: clutches found, Jan.–Nov.; depends on wet season (Hall 1903; Le Souëf 1903; Lavery 1986). In s. Aust.: Vic.: mid-Aug. to Dec. (Bedgood 1970); WA: laying, usually Aug.–Dec., some clutches laid in Feb. (Aust. NRS); in sw. WA, clutches started in all months except Feb.–Apr. but main breeding season July–Sept.; timing of laying highly correlated with peak rainfall + 2–3 months, temperature and increase in photoperiod (Halse & Jaensch 1989). **NZ** Usually breed Sept.–Dec. but may begin laying in late Aug. with last clutches in late Feb. (McLean 1901; Craig 1980a). May raise two broods in a season (Brown & Brown 1977).



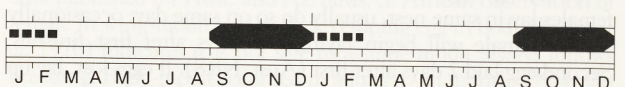
(a) N. Aust.



(b) SW. Aust.



(c) Vic.



(d) NZ

Site In reeds in swamps, dams, usually in water but occasionally in isolated tussock up to about 180 m from water; one nest found in barley crop c. 800 m from water (McLean 1901; Czechura 1983). Build nests on platform of beaten-down reeds or rushes; one nest on fallen bough among rushes and tea-tree (Sandland & Orton 1922). **MEASUREMENTS:** height of nest, 29 cm (17; 0–80; 55); height of plants round nest, 131 cm (59; 10–225; 49) (Aust. NRS); depth of water, 30–120 cm (Fletcher 1909; Stidolph 1939). Nests have path leading from one end (McLean 1901).

Nest, Materials Grass or reeds beaten down to form platform c. 20 cm thick; shallow saucer-shaped nest, or oval-shaped

bowl constructed in centre out of blades of grass, reeds and *Typha*, which may be flattened to hold eggs better; lined with dry grass (McLean 1901; Hall 1903; Brown & Brown 1977). Some nests with multiple bowls, each containing eggs and incubated simultaneously (Craig 1980a). Material added to nest during incubation (Brown & Brown 1977). **MEASUREMENTS:** outside diameter, 30 cm; depth, 10–20 cm; diameter cavity, 19–30 cm (n=4); depth, 3–10 cm, may increase during incubation as material added (McLean 1901; Fletcher 1909). Build number of trial nests about 1 month before laying; often roughly constructed, lacking definite bowl, but some well shaped. As laying approaches, usually make two or more ready for laying (Craig 1980a). Construct numerous roosting nests round egg-nest; male builds nursery nests after eggs hatch; often abandoned and new ones built usually closer to regular feeding areas; one nursery nest built on top of nest of Eurasian Coot that was still being used to brood chicks at night (Fletcher 1909; Stidolph 1939; Brown & Brown 1977; Craig 1980a).

Eggs In Aust.: oval, some somewhat compressed towards smaller end; close-grained, smooth, slightly lustrous; ground-colour varies from pale buff-brown to faint creamy brown with evenly scattered dots, spots and small irregular-shaped blotches of dull red, purplish red or purplish brown, intermingled with fainter underlying markings of pale slate-grey or purplish grey and light inky-grey, latter being almost invisible. Some eggs have dull blood-red dots, spots and light violet-grey blotches, some more heavily blotched than others, occasionally with straight short lines of spots oriented longitudinally down shell (North). In NZ: ground-colour varies; pale cream to rich brownish-cream (McLean 1901) or light greenish-stone, tinged buff (Stidolph 1939), sparingly spotted dull reddish brown and slate (Stidolph 1939), or spotted or blotched chestnut-brown and underlying violet, evenly distributed or confined to zone or ring at large end. Markings may be uniform or large and bold (McLean 1901). **MEASUREMENTS:** Aust.: 50.8 (2.92; 46–58.4; 33) x 36.6 (2.01; 33.5–41.9; 34) (Le Souëf 1903; North; Campbell); NZ: 49.8 (47–53.3) x 35.1 (33.3–37.8) (McLean 1901).

Clutch-size In Aust., 4.2 (2–6; 51) (Aust. NRS). In NZ: clutches laid by one or two females, 7.4 (2.43; 4–13; 37), occasionally larger (Craig & Jamieson 1988); clutches laid by one or two females (for all pairs and groups), 6.0 (0.3; 46), with individual clutch-size for females in groups, 3.9 (0.3; 27), and females in pairs, 5.4 (0.3; 12) (Craig 1980b). Clutch-size related to position of female in hierarchy, age, size of group and whether first or subsequent clutch (Craig 1980b; q.v. for more information).

Laying Eggs laid daily, usually just after dawn; where two females lay in same nest, usually do so on same day; occasionally second female will begin laying 2–3 days after first finishes. Second egg laid 2 days after first (Aust. NRS). If eggs lost, lay up to three replacement clutches. Maximum of 56 days between laying of first and second clutches (Brown & Brown 1977).

Incubation Begins when clutch complete (Fletcher 1909); in NZ: usually begins mid-clutch, irregular at first, with eggs left for up to 10 h. By all adults in group and occasionally by non-breeding members, females more than males with dominant female doing most; males, usually dominant male, sit at dusk and are relieved by a female immediately before dawn; for pairs, each incubates for shift of c. 3 h during day. Incubating bird fed on nest (McLean 1901). Hatching asynchronous. **INCUBATION PERIOD:** from first egg laid to first hatched, 25–27 days (n=2) (Aust. NRS); in NZ: average 25 days (23–27; 12) after incubation begun, earlier eggs in clutch could take up to 29 days.

Young Semi-precocial, nidifugous. Down, dark bluish-black with silvery tips; bill, ivory (McLean 1901). **Parental care, Role**

of sexes Brood chicks in nest at hatching; other members of group bring food and give it to chick or to sitting bird, which feeds chick. Young led from nest within first 3 days and fed in vicinity, often on brood-nests; young start to feed themselves from c. 2 days old but still receive much of their food until 2 months old (Brown & Brown 1977; Craig 1980a). All members of group care for chicks, largest proportion (40%) by non-breeding yearlings if present, otherwise by dominant male (39%). In pair territories, both adults feed chicks until re-nesting, when non-incubating bird alone cares for chicks; chicks of second clutches cared for by older chicks. Young squat or hide beneath nest at approach of danger (Fletcher 1909; Hood 1935).

Fledging to maturity Both sexes capable of breeding in first year; age of first breeding in males varies, most first- and second-year males rarely sexually active; if a dominant female dies, young female will replace her but may not breed until following year.

Success From 69 eggs laid, 42 hatched (Aust. NRS). In NZ: hatching success high (90%, n=13 nests), most chicks (75%) die within 3 months of hatching; survival of young high, up to at least 70% of clutch in wet summers, none or only one survive in dry summers; each group produced a mean of 1.2 (0.2; 57) young per year. Hatching success and survival rate varies between groups and from year to year. Early clutches more successful than later ones. For all groups and pairs: from 276 eggs laid, 206 (75%) hatched, 59 (21%) survived to 4 months; equalling 2.1 chicks per territory and 0.5 chicks per bird. Of 91 eggs known to be lost before hatching: 38% taken by predators, 22% deserted, 16% ejected; last eggs deserted when hatched chicks led from nest. Rising water floods nests (Aust. NRS); Swamp Harriers take eggs from exposed nests. Chicks that hatch well in advance of majority of clutch often die in nest. Loss of chicks high in first 2 months, even more so in first few days; dead chicks often found in territories within first 2 weeks after hatching. For details of geographical variation and effects on success of nest-site, territory size and group size, see Craig (1980b).

PLUMAGES Prepared by D.I. Rogers. Subspecies *melanotus* from Aust.

Adult Second and subsequent plumages; attained when c. 1 year old but some first-basic individuals not readily distinguished from adults. **Head and neck** Head, blackish (c82); when fresh, purplish blue (74) sheen extends from sides of throat to malar area. Neck, purplish-blue (74) and glossy; blackish (82) bases of feathers slightly exposed and become more so with wear. **Upperparts** Mantle, glossy purplish-blue (74). Rest, blackish (89). **Underparts** Breast and flanks, glossy purplish-blue (74), grading to blackish (c119) belly and thighs. Concealed brownish-grey (c83) bases to feathers of breast more extensive and slightly exposed towards belly. Under tail-coverts, white. **Tail** Blackish (c119). **Upperwing** Marginal coverts and upper rows of lesser coverts, purplish-blue (74). Other feathers, black (c89); remiges take on black-brown (119) tinge with wear; alula, primary coverts and p6–p9 have purplish-blue (74) outer edges. **Underwing** Remiges and greater coverts, grey-black (82), reflecting dark grey (83) in some lights. Other coverts, similar but less glossy; they have purplish-blue (74) fringes, narrowest on median coverts and very broad towards leading-edge of wing.

Downy young When newly hatched, black (89) head, upperparts and wing-pads grade to brownish-black (c119) underparts. On upperparts and neck, tips of most filaments of down enclosed in fine white sheaths, these looking like fine white spines scattered over neck, mantle, back and wing-pads; on at least some newly hatched chicks, white spines also scattered over

malar area, ear-coverts, rump, upper breast and flanks; more sparse caudally and on sides. On forehead, tips of down enclosed in black (89) sheaths, giving appearance of glossy black bristles and obscuring much of anterior frontal shield. Sheaths at tips of down-filaments wear away within a few days and down below begins to fade; large downy young, blackish brown (c19) with dark greyish-brown (c121) belly, rump, neck and vent; last areas to fade are malar area and face.

Juvenile Head and neck Brownish-black (c82); chin, throat and lower hindneck have slight bluish (73) tinge caused by varying dark-blue (73) tips. **Upperparts** Mantle as lower hindneck. Rest of upperparts, blackish brown (119), becoming browner (121) with wear. Traces of down adhere to upper tail-coverts. **Underparts** When fresh, breast and flanks, dark blue (73), with strong greyish tinge and heavy whitish mottling. Feathers, dark blue (73, duller than adult) with white or cream-white tips, c. 3 mm long. With wear, lose white tips and much of blue on feathers; exposed parts of bases develop brownish (121) tinge, giving worn juveniles dark greyish-brown breast with slight blue wash. Belly, white at first with indistinct grey mottling; feathers, dark grey (c83) with broad white tips up to 10 mm long; belly becomes greyer as white tips fray. Under tail-coverts, white. **Tail** Blackish (c119), all feathers having thin buff fringes, broadest near tip. Down adheres to tips, giving pointed shape. **Upperwing** Similar to adult but primaries tend to be more pointed at tip. Strands of faded pale-brown (c123B) down can adhere to tips of tertials and wing-coverts until post-juvenile moult under way. **Underwing** As adult.

Immature First basic. Similar to adults. Some can be aged on basis of scattered juvenile feathers retained in underparts (especially centre of belly and breast), mantle, rump and tail.

Aberrant plumages Subspecies *melanotus* in NZ seems prone to albinism (Ripley 1977; Oliver; CSN 6). Records include: (1) pure white individuals; (2) normal individuals with white wings; (3) normal individuals with varying paler-brown or white mottling. Cunningham (1955) recorded three or four isabelline individuals in colony in Wairarapa, NI. Adult was pale isabelline-brown, darkest in areas that are jet-black in adult, with white under tail-coverts and lavender-violet throat and upper breast; bare parts seemed similar to normal *melanotus*. A small downy young was pale buff, browner in upperparts, with white spines like those of typical chicks; bare parts were also normal except for pink-majenta (*sic*) iris.

BARE PARTS From photographs (NPIAW 1985; Moon 1988; NZRD; Aust. RD; NZ DOC Slide Library; unpubl.: J.N. Davies) and labels (HLW, MV, NMNZ, SAM).

Adult Frontal shield and bill, mainly red (13–c210), generally with pinker (c17) tinge to tips and mandibular rami. In 31 of 54 photographs examined of birds in definitive plumage, bill had roughly triangular dark-brown (20, c119A) patch on sides, largest near base of lower mandible; this patch has been photographed in five incubating birds and is unlikely to be restricted to first immatures; birds without patch appear to have larger bills, perhaps suggesting they are male. Brown patch on bill has not been recorded systematically on labels, so suggestion untested. Iris, usually red (c11), occasionally red-brown (c340) to brownish red (c132B, c15) or brown (c119); possible that brown eyes only occur in birds in first-basic plumage, and that red-brown eyes occur more often in NZ; neither suggestion tested because rapid post-mortem acquisition of brown tinge in eye makes label data unreliable. Feet and legs, pink (c7) to pinkish red (c13), with dark-grey (83) joints. Claws, dark brownish-grey (c83). **Downy**

young Basal third of bill varies, red (13–14) to crimson (108), perhaps darkening with age; on upper mandible, red base narrows at cutting edge and at culmen. Tomia, narrow, black (89); broadens slightly near tip of bill; tomia have also been described as red (Bryant 1940); rest of bill, white, sometimes with faint grey-blue or pink tinge; sharply demarcated from base of bill, often by narrow grey (84) line. Frontal shield, small and fan-shaped at this age, apex of fan separated from culmen by black bristles; initially mauve (75) to light violet (172D), later becoming light pink (pale 7). Down, sparse and bristly on nape, hindcrown and distal wing-pads, exposing well-defined areas of orange-red (15) skin. Orbital ring, thick; pinkish red (c10) to pink (c7, c10), latter perhaps developing shortly after hatching. Iris, black-brown (119). Feet and legs, orange-pink (c5); with age, light-brown (c223C) or brown (c119B) centres develop on scales on top of toes and front of tarsus, these being most extensive at joints. Claws, grey (84). Large downy young have: grey-black (c82) bill and shield, with grey-brown (c119C) culmen and base; may have white patch at tip of culmen; dark-brown (–) iris. Entire bill and shield may become grey-black (82) and legs attain juvenile colour before down lost. **Juvenile** Bill, grey-black (82) with light-brown (119C) bases to cutting edges. Frontal shield, grey-black (82) grading to light brown (c119D) at rear. Iris, dark brown (–). Tarsus and toes, light pinkish-brown (grey 219D); tibio-tarsal joint, grey (c84). **Immature** Bill, similar to adults with brown bill-patches, but in some (presumably younger birds), brown patch large, occupying c. 50% of bill; younger individuals have separate blackish-brown (c119) strip on culmen. Iris, dark brown (c119); brick-red (–) also reported on one Aust. label (HLW); in NZ, iris appears 'olive' at 5 months; at 9 months, red with narrow inner ring of 'olive' that may be retained until 18 months (Williams 1981). Feet and legs, as adult. In NZ, adult shield and leg-colour may be attained at 4–5 months (Craig *et al.* 1980; Williams 1981).

MOULTS **Adult post-breeding** Complete; primaries simultaneous. Apparently shy and cryptic during wing-moult; despite large numbers collected in Aust. and NZ, virtually no records of active moult of remiges, and timing is poorly known. Wear of primaries suggests that moult in se. Aust. usually occurs late summer or autumn (Norman & Mumford 1985; skins: HLW, MV), as does observation that moult of wing-coverts most often recorded Sept.–Jan. (Norman & Mumford 1985). Said to be flightless for about 1 month (NZRD). Relation of timing of moult to breeding is doubtful; certainly follows breeding in w. Palaearctic (BWP) and has been said to do so in NZ (NZRD). However, little data published for Aust. and NZ birds; S. African observation of female in wing-moult and with developing egg in body (Fagan *et al.* 1976) indicates it is not safe to assume moult always follows breeding. Body-moult recorded in adults in all months (Norman & Mumford 1985); generally, feathers of head moult first, then breast, belly and nape; mantle and rump moult in association, as do tail-coverts, flanks and tail (Norman & Mumford 1985). Not yet possible to say whether apparent difference from sequence described for nominate *porphyrio* (BWP) is real; nor is there sufficient information to say if there is separate pre-alternate moult of some body-feathers. Tail-moult, centrifugal or (rarely) asymmetrical in se. Aust. (Norman & Mumford 1985); almost simultaneous in *madagascariensis* and nominate *porphyrio* (Fagan *et al.* 1976; BWP). **Post-juvenile** Partial, never involving remiges. Moult begins on head and upperparts; rate of replacement of feathers probably decreases in late stages of moult. Some individuals not distinguishable from adults at c. 5 months (Craig *et al.* 1980; Williams 1981), which suggests that post-juvenile moult of body-feathers may be completed at this age. Some retain a few

feathers in centre of underparts and in tail until (complete) second pre-basic moult.

MEASUREMENTS Subspecies *melanotus*: (1) se. Aust. mainland, adult and first-basic skins; BILL S = bill-length from back of frontal shield to tip of culmen; BILL LP = bill-length from loreal point; BILL N = bill-length from front margin of nares (HLW, MV). (2) Gippsland, Vic., freshly dead, definitive birds with no Bursa of Fabricius (Norman & Mumford 1985). (3) N. NT and e. Kimberley; adult and first-basic skins (ANWC). (4) Tas., adult and first-basic skins; methods, unknown (ANWC). (5) NI, NZ, freshly dead adults (NMNZ). (6) Adults, possibly including some first-basic birds over 6 months old (Williams & Miers 1958).

	MALES	FEMALES	
WING	(1) 275.5 (7.16; 267–291; 8)	271.4 (6.84; 262–285; 7)	ns
	(2) 283.5 (7.47; 114)	268.2 (8.12; 66)	**
	(3) 265.2 (9.44; 251–276; 4)	260.2 (4.52; 254–267; 8)	ns
	(4) 292.0 (3.70; 284–295; 6)	272.7 (10.33; 252–289; 7)	**
	(5) 284.0 (9.82; 271–294; 4)	273.1 (5.84; 263–280; 8)	ns
8TH P	(1) 191.5 (3.94; 185–198; 8)	190.8 (4.91; 186–201; 7)	ns
TAIL	(1) 101.7 (4.63; 95–109; 8)	100.2 (3.37; 95–105; 7)	ns
	(5) 116.7 (4.09; 110–121; 4)	101.1 (7.12; 87–113; 7)	**
BILL S	(1) 70.7 (3.10; 63.9–74.2; 8)	65.6 (4.72; 58.3–72.4; 7)	*
	(2) 73.0 (3.20; 114)	67.0 (2.43; 16)	**
	(3) 65.0 (6.00; 55.8–71.6; 4)	64.3 (4.51; 55.9–69.6; 8)	ns
	(4) 67.3 (2.74; 62.5–70.5; 6)	64.7 (2.55; 59.0–67.7; 7)	ns
	(5) 70.4 (6.56; 59.7–77.2; 4)	66.0 (3.38; 61.1–71.8; 8)	ns
	(6) 75 (3.29; 67–82; 37)	67 (3.80; 56–75; 42)	**
BILL LP	(1) 43.4 (1.53; 41.2–45.6; 8)	41.3 (2.78; 46.6–37.3; 7)	ns
	(3) 40.1 (2.70; 35.5–42.1; 4)	39.2 (1.66; 36.7–41.5; 8)	**
	(4) 42.6 (1.42; 41.1–44.6; 6)	39.7 (1.20; 37.3–41.2; 7)	**
	(5) 42.6 (1.42; 41.1–44.6; 6)	39.7 (1.20; 37.3–41.2; 7)	**
BILL N	(1) 31.7 (1.32; 29.3–33.5; 8)	30.3 (1.97; 27.3–33.6; 7)	ns
	(3) 32.0 (2.89; 27.1–34.6; 4)	31.3 (1.33; 29.1–33.3; 8)	ns
	(4) 34.6 (1.06; 33.1–36.2; 6)	31.5 (0.84; 29.8–32.5; 7)	**
	(5) 34.6 (1.06; 33.1–36.2; 6)	31.5 (0.84; 29.8–32.5; 7)	**
TARSUS	(1) 95.2 (4.13; 87.7–102.6; 8)	93.0 (5.99; 81.7–101.1; 7)	ns
	(2) 96.4 (4.27; 114)	89.6 (4.06; 66)	**
	(3) 96.1, 101.8	86.6 (3.45; 81.5–94.1; 8)	
	(4) 97.1 (4.10; 89.6–101.3; 6)	86.7 (3.06; 82.1–90.6; 6)	**
	(5) 100.6 (3.04; 98.0–106; 4)	93.5 (2.78; 88.1–96.8; 8)	**
TOEC	(1) 108.3 (4.40; 103–114; 4)	107.9 (5.42; 101–114; 5)	ns
	(2) 94.3 (3.20; 114)	88.8 (4.06; 66)	**
	(5) 106.5 (2.55; 104–111; 4)	101.8 (1.65; 98.0–104; 8)	**

Subspecies *bellus*: (5) sw. Aust., adult, skins; methods as above (HLW, SAM).

	MALES	FEMALES
WING	(5) 281.0 (8.89; 268–290; 5)	266, 270, 278
8TH P	(5) 195.6 (4.28; 188–198; 5)	192, 197, 196
TAIL	(5) 108.8 (7.46; 101–120; 5)	115, 105, 110
BILL S	(5) 68.4 (3.99; 62.1–73.2; 5)	63.2, 60.2, 65.3
BILL LP	(5) 45.8 (2.46; 42.4–49.2; 5)	41.6, 43.2, 45.7
BILL N	(5) 34.4 (2.59; 31.5–35.4; 5)	30.8, 32.7, 37.8
TARSUS	(5) 93.1 (1.60; 91.0–95.1; 5)	92.3, 79.7, 99.2
TOEC	(5) 107, 106, 113	–

WEIGHTS (1–3) Gippsland Ls area, Vic., specimens taken throughout year (Norman & Mumford 1985): (1) ages combined; (2) adults without Bursa of Fabricius; (3) adults with Bursae. (4) NI, NZ, samples taken in May and Aug., ages unknown but, given collection dates, all likely to be over 6 months old (Williams & Miers 1958).

	MALES	FEMALES
(1)	1091.2 (94.9; 785–1310; 148)	885.4 (98.5; 679–1252; 97) **
(2)	1096.3 (87.5; 114)	902.5 (100.7; 66) **
(3)	1080.5 (114.3; 33)	849.2 (84.6; 31) **
(4)	1060 (77.1; 920–1200; 36)	860 (77.2; 700–1100; 42) **

In Vic., males heavier Mar.–Sept.; females lighter in July, heavier Mar.–May; in males, no significant correlations between weight and size of gonads, and possession of Bursa did not affect weight; in females, birds with Bursae were significantly lighter (Norman & Mumford 1985). Seasonal variation common in NZ, especially in breeding females (Craig *et al.* 1980). See above references for more information and Suttie & Fennessy (1992) for information on weights of body-components.

STRUCTURE Wing, short and broad. Ten primaries; p8 longest; p10 17–18 shorter, p9 0–3, p7 0–2, p6 5–10, p5 12–21, p4 27–40, p3 44–53, p2 55–65, p1 71–90. Fourteen secondaries, including five tertials. Tail, rounded, 12 soft feathers; t1–t6 28–38. Bill, heavy, laterally compressed, deep at base; culmen decurves gradually towards sharply pointed tip; tomia slightly decurved, gonys nearly straight. Nostrils, large, ovate. Frontal shield swollen while breeding (Craig *et al.* 1980; BWP); smaller in juveniles than in adults; in se. Aust., width of shield in males 24.1 (2.33; 8), in females 22.5 (2.32; 7). Tarsus, laterally compressed and scutellate; tarsus and toes, long and slender. Outer toe, c. 84% length of middle, inner c. 76%, hind c. 50%; claws, long, thin, sharply pointed.

AGEING, SEXING Information on growth of chicks in Cordonnier (1983). Best character for separating immature (first basic) from adult is remnant juvenile plumage on underparts and tail; this is not retained in all individuals, and in some first-basic immatures, colour of iris may be only guide to age. Colour of bill and legs little use as guide to breeding status (Norman & Mumford 1985). Bursae of Fabricius also of little use because Bursae can be found in some males with active testes, in some females with enlarged follicles. Adult males larger than females; Craig *et al.* (1980) used several combinations of bill measurements and weights in discriminant analyses. They concluded that weight and measurements involving bill-shield vary too much seasonally (and geographically for weights) to be reliable guides to sexing, and recommended use of bill-length from nares, and bill-depth. Bill-shield smaller in juveniles and in individuals that are socially prevented from breeding, may remain juvenile-sized until 18 months, male shields thus falling within size-range of females (Craig *et al.* 1980).

GEOGRAPHICAL VARIATION Considerable; six subspecies groups occur in Old World and Oceania. Two subspecies in our region, *bellus* in sw. Aust. and *melanotus* in e. and n. Aust., Tas., Kermadec Is and NZ and as migrant to New Guinea (Mees 1982). Birds from Chatham Is previously considered a separate subspecies (Sharpe 1894; Ripley 1977) but the two skins examined (type specimen in BMNH, another in NMNZ collected in 1906) fall within range of size and plumage of *melanotus* (P. Colston; P.R. Milliner; D.J. James). In addition, shortage of subfossil records from middens on Chatham Is implies there may not have been an established population on Chatham Is before European times (P.R. Milliner). Not known if size varies within *melanotus*; birds from NZ and Tas. perhaps larger than in se. Aust. mainland; birds occurring in Aust. Tropics may be smaller (see Measurements and

Craig *et al.* 1980). Birds from Kermadec Is may be smaller than those from NZ mainland (Merton 1970) but more data needed.

Subspecies *bellus* has shorter bill-shield than *melanotus*, not extending behind eye; base of shield squarer than in *melanotus* and bill perhaps deeper on average. In adult *bellus*, chin, throat, malar area, marginal coverts, upper row of lesser coverts and upper breast are cobalt blue (c64) and iridescent. In juveniles, breast and flanks light blue (c65), pale tips to feathers slightly broader than in juvenile *melanotus*. In both adult and juvenile *bellus*, back, scapulars, rump, upper tail-coverts and most of upperwing, black-brown (c119), usually paler and browner than in *melanotus*. Fringes of dorsal feathers, especially scapulars and upper wing-coverts, varying tinged yellowish olive (50). Purplish-blue (74) outer edges to primaries and greater primary coverts, generally broader than in adult *melanotus*. Hindneck, blackish brown (119), with varying purplish-blue (74) tips that perhaps make some look similar to *melanotus*. Once, *bellus* said to have grass-green legs with darker joints (e.g. Gould). It now appears that colour of legs of *bellus* varies and often similar to *melanotus* (e.g. Whittell 1934; Serventy & Whittell 1951; photo in NPIAW 1985), but more information needed to find if greenish and hazel-brown legs reported on several labels are typical.

Other members of *melanotus* subspecies group occur on islands from Pelew Is, n. Sulawesi and Moluccas, E to Samoa; all characterized by rather small shields and short toes, blackish upperparts and cobalt-blue to indigo throat and foreneck. Subspecies limits of *melanotus* group not well known; generally two subspecies recognized on basis of colour of breast and upperparts (Ripley 1977; White & Bruce 1986). In W of range, *melanotus* group merges with *indicus* group (two subspecies) of se. Asia and Greater Sundas which is characterized by large frontal shield with lateral ridges, black upperparts and upper wing-coverts both with green tinge; underparts turquoise-green to blue. Subspecies *pulverulentus* group of Philippines has only one subspecies; whole body intensively tinged grey, and mantle and scapulars olive-brown or reddish brown. The *poliocephalus* group occurs from Nicobar Is and w. Thailand, through India to Caspian region and Iraq; characterized by blue scapulars, wing-coverts, throat, upper breast and sides of head; crown, mantle, back and flanks, dark blue; head and sometimes edges of other feathers, tinged silver-grey. Size increases from SE to NW of range of *poliocephalus* group.

African *madagascariensis* group (one subspecies) has dark-blue crown, upper mantle, wing-coverts and upperparts; blue sides of head, throat and chest; lower mantle and scapulars bronze-green or blue-green, varying geographically. Nominative *porphyrio* group (one subspecies) occurs on borders of w. Mediterranean; crown, nape, upperparts and upper wing-coverts, dark blue to dark violet-blue; sides of head and chin to upper breast, blue, sometimes violet-blue. For more detailed accounts of extralimital variation, see BWP and Ripley (1977).

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Volume 2, Plate 47 [caption error corrected from original]

Takahe *Porphyrio mantelli* (page 593)

1 Adult; 2 Downy young, newly hatched; 3 Juvenile, not fully grown; 4 Worn juvenile in post-juvenile moult

Purple Swamphen *Porphyrio porphyrio* (page 577)

5 Adult, subspecies *melanotus*; 6 Adult, subspecies *bellus*; 7 Newly hatched downy young, subspecies *melanotus*; 8 Large downy young, subspecies *melanotus*; 9 Juvenile, subspecies *melanotus*, not fully grown; 10 Immature, subspecies *melanotus*; 11 Adult, subspecies *melanotus*