Order **PSITTACIFORMES**

Distinctive, familiar, and often strikingly coloured birds, with characteristic shape and structure. Often highly conspicuous. Small to large, ranging in size from tiny pygmy-parrots *Micropsitta* of New Guinea, the Moluccas and the Solomon Is (*c.* 9 cm in length and weighing 10–18 g) to large macaws of South America (up to *c.* 1 m in total length including tail, and weighing up to 1.7 kg), large cockatoos (e.g. Red-tailed Black-Cockatoo *Calyptorhynchus banksii*; up to 60 cm in total length including tail, and weighing up to 870 g), and flightless Kakapo *Strigops habroptilus* of NZ (up to 64 cm in total length, including tail, and weighing up to 2 kg). Third largest non-passerine order. Roughly 329–356 species in 76–93 genera, distributed on all continents except Antarctica; most are tropical; distributed widely in s. hemisphere, including some subantarctic islands of HANZAB region; in n. hemisphere occur as far N as Safed Koh Mts in e. Afghanistan (Slaty-headed Parakeet *Psittacula himalayana*). Greatest morphological and ecological diversity in A'asia and probably originated in A'asian sector of Gondwana, radiating from subtropical rainforests (Homberger 1991; see also Forshaw & Cooper 1989). In HANZAB region, 60 species in 27 genera. Appear to lack close living relatives, and nearest allies difficult to determine. Suggested that nearest allies are Columbiformes (pigeons) (Burton 1974; Forshaw & Cooper 1989), but this rejected by others (Sibley & Ahlquist 1990). Recent DNA–DNA hybridization studies suggest they should be placed between cuckoos and swifts (see Collar 1997; Rowley 1997). Other groups suggested as close allies include hawks, owls and piciforms (see Sibley & Ahlquist 1990). Recent works (e.g. Forshaw & Cooper 1989; Collar 1997; Rowley 1997) recognize three main groups: (1) cockatoos; (2) lories and lorikeets; and (3) parrots. However, taxonomic level of each varies: some (e.g. Forshaw & Cooper 1989) classify each at same level, but others (e.g. Collar 1997) group parrots with lories and lorikeets. On basis of biochemical (Christidis *et al.* 1991a) and chromosomal (Christidis *et al.* 1991b) studies, cockatoos were found to form a monophyletic lineage separate from all other Australo-Papuan parrots and lories. As such, Christides & Boles (1994) recognized two distinct families within Aust.: Cacatuidae (cockatoos) and Psittacidae, including the Loriinae (thus, parrots and lorikeets); an arrangement also supported by morphological and behavioural studies (Brereton & Immelmann 1962; Smith 1975; Homberger 1991). This arrangement followed here; both families represented in HANZAB region. Relationships between extralimital groups have not been examined closely and are in need of review. In recent works, extralimital subfamilies or tribes have been grouped with Aust. Psittacidae (Forshaw 1989; Collar 1997); that treatment has been followed here. The most widespread alternative taxonomy places all cockatoos and parrots in a single family, Psittacidae (e.g. Sibley *et al.* 1988; Forshaw & Cooper 1989; Sibley & Ahlquist 1990; Sibley & Monroe 1990; Peters). Many alternative taxonomies have been proposed; for reviews see Smith (1975), Sibley & Ahlquist (1990), and Schodde & Mason (1997); for discussion of Aust. taxa, also see alternative treatment of Wells & Wellington (1992).

Structure rather homogeneous. Bill distinctive: upper mandible downcurved, usually extending well beyond tip of lower mandible; lower mandible upcurved, and usually broad with rather square tip that fits neatly into inside of upper mandible. Usually have prominent cere. Rostrum movable, with hinge-like articulation at skull. Palate, desmognathous. Nares, holorhinal, impervious, always in cere. Basipterygoid process absent. Head usually large in proportion to body, and neck rather short; 13–15, usually 14, cervical vertebrae. Pelvic muscle formula, AXY. Sternum fenestrated or indented. Tongue, thick and muscular, tactile, grooved; moved by hyoid apparatus with large median foramen in entoglossum; tongue brush-tipped in some species (notably lorikeets in HANZAB region; see below). Feet, zygodactylous, with Type 1 flexor tendons (cf. Piciformes and Cuculiformes, which zygodactylous but with Type 6 flexor tendons). Crop present; no caeca. Oil-gland tufted or absent. Furcula weak or absent in some. Syrinx with three pairs of intrinsic muscles. Wings vary in shape from broad with rounded tip to narrow with pointed tip. Ten primaries; 10–14 secondaries; diastataxic. Tail short to very long; *Prioniturus* have ornate, projecting raquet-shaped central rectrices. Usually 12 rectrices. Aftershafts, short and downy. Legs, short and strong; tarsus short, with small granulate scales or papillae; middle toe longer than tarsus. Orbital ring usually complete. Whole body covered in down. Powder downs present; especially in uropygial region. Young ptilopaedic.

Adult plumage often brightly coloured (especially in Psittacidae), though also white, grey and black (especially in Cacatuidae); coarse in texture; and arranged in diffuse tracts. Bare parts mostly dull colours, but some species have brightly coloured bills, irides, lores and facial skin. Sexes alike (e.g. Rainbow Lorikeet *Trichoglossus haematodus*) or highly dimorphic (e.g. Eclectus Parrot *Eclectus roratus*).

Adults undergo a post-breeding (pre-basic) moult each cycle; usually complete, but some species can arrest moult before it is finished. Adult pre-breeding moults not reported (Forshaw & Cooper 1989). Usually moult once a year, but some possibly take longer than a year to finish; in HANZAB region, timing varies (see Family introductions). Moult of primaries of adults usually centrifugal, from mid-primaries, but starting position varies. Moult of secondaries of adults often starts from s10 at about time moult of primaries starts, and replaced outward to finish with s1, but sequence also often irregular (see Forshaw & Cooper 1989). Moult of tail usually starts after moult of primaries well advanced, but usually finishes before last primary shed; sequence irregular (see Forshaw & Cooper 1989). Young altricial; blind at hatching, covered by sparse pale down. Juvenile plumage often similar to, or slightly duller than, adult plumage, but remiges and rectrices usually more pointed than adults. Rate of maturation and attainment of adult plumage and bare parts varies greatly; slow in some species. Sequence of plumages to adult and timing of moults varies greatly. Post-juvenile (first pre-basic) moult typically partial, but some possibly compete (e.g. Nestorinae). Some species have one or more immature plumages.

Worldwide, occur in wide variety of habitats, from dense rainforest to open, treeless grassed plains, though predominantly, and with greatest diversity, in tropical rainforests (Forshaw & Cooper 1981). In HANZAB region, widespread throughout alpine, tropical, temperate, semi-arid and arid zones; occur in most habitats, from coasts to high altitudes, including above treeline in alpine zones.

No species of Cacatuidae can be regarded as completely migratory (Rowley 1997), though some populations of some species undertake regular movements and considered partly migratory. Other Cacatuidae are resident, sedentary, or dispersive. Worldwide, Psittacidae considered resident, dispersive, nomadic or irruptive (Collar 1997); only two species considered migratory; at least one other species is partly migratory (Collar 1997; see Psittacidae below). Few species of Psittacidae are considered sedentary, usually island forms, and some of these occur in HANZAB region.

Herbivorous. Most feed on seeds and fruits, supplemented by a wide range of other food, such as flowers, nectar, pollen and leaves. Many species include small quantities of invertebrates, mostly insects and insect larvae, in their diet; almost all eat some seed, which always husked before swallowing (Forshaw & Cooper 1981; Campbell & Lack 1985). Specialization evident in some groups (see Family accounts below). Feed arboreally and terrestrially; in HANZAB region, *c.* 35% of species feed mainly arboreally, *c.* 35% feed mainly on ground, and the rest feed both arboreally and terrestrially. Of those considered primarily arboreal or terrestrial, about a third of species within those categories occasionally feed on other substrates. When feeding in trees or shrubs, agile and acrobatic, and clamber actively through outer branches and foliage, stretching to reach food, and often hanging upside down; use both bill and feet; while climbing among foliage of trees, often use bill to grasp branches and then clamber up or across from previous position. On ground, equally active, picking up fallen seeds or fruits from ground, or taking them directly from flowering or seeding heads; when food beyond reach, will stetch up to reach, or stand on stalks of plants, felling them to ground; many also use bill to dig up underground roots, corms or bulbs, or scratch soil with feet (Forshaw & Cooper 1981; also see species accounts). Many use bill to tear away or crush hard seed capsules, such as those of *Eucalyptus* and casuarina, and extract seeds from them; bill also used by some to tear open trunks of trees and branches for wood-boring insect larvae. Many use feet to manipulate food and to bring food to bill (Smith 1971; Forshaw & Cooper 1981); some show preference for use of particular foot, usually left (Forshaw & Cooper 1981; Joseph 1989; Magrath 1994). In HANZAB region, Glossy Black-Cockatoos *Calyptorhynchus lathami* exclusively or predominantly left footed (Joseph 1989; Magrath 1994; Pepper 1996), Yellow-tailed *Calyptorhynchus funereus* and Red-tailed Black-Cockatoos, Gang-gang *Callocephalon fimbriatum* and Palm *Probosciger aterrimus* Cockatoos predominantly left footed; while Eastern *Platycercus eximius* and Pale-headed *P. adscitus* Rosellas predominantly right footed (Cannon 1977; Prendergast 1985; Joseph 1989). Drink water at least once during day; most come to drink early in morning, some in morning and late afternoon, and some throughout day depending on heat of day; most drink by scooping water in lower mandible, then tilting head back (Campbell & Lack 1985); also drink water by lapping, ladling or suck-pumping (Schodde & Mason 1997).

Usually very vocal. Calls described as squawks, screeches, squeals, shrieks, whistles, cackles, chatters, buzzes or twitters. Many calls harsh, guttural and described as strident, but other calls can be musical rolling screeches and melodic whistles or warbles, often piping in quality. Many calls loud and distinctive; sometimes raucous. In HANZAB region, exceptional calls are those produced by mechanical means by Palm Cockatoos, and remarkable Booming made by male Kakapo during displays (see those texts for details). In HANZAB region, voice not well studied, though several notable exceptions (see below and family introductions). Repertoire of calls of Budgerigar *Melopsittacus undulatus* well known from studies in captivity and in wild; otherwise, repertoires poorly known. Size of repertoire appears to vary greatly between species, though this may be more a reflection of lack of knowledge of many species. Some species have as many as 20 or more described calls. Brereton (1963a,b, 1971a,b) and Pidgeon (1981) compared repertoires of a number of Aust. species. Brereton (1971b) suggested that the information content of vocalizations low in species occurring mainly in habitats with abundant resources, and most complex when resources at intermediate levels, but again simpler with increasing scarcity of resources. Suggested that some calls of Budgerigar functionally equivalent to song of passerine birds (see account for Budgerigar); this may also be true of calls of some other parrots. Within species, variation in calls sometimes complex, with some described as grading from one to another across a wide range of intermediates; these variations generally not well understood. Individual variation often used for individual recognition within pairs, and used to recognize members within family or other groupings (e.g. *Calyptorhynchus*, Galah *Eolophus roseicapillus* and Budgerigar). Some calls sexually distinctive in many species of both families. In HANZAB region, little or no information on seasonal variation for most species. Regional variations in repertoire and variations in call characteristics little studied in HANZAB region but rarely apparent. However, known from at least three species in HANZAB region (Australian Ringneck *Barnardius zonarius*, Red-crowned Parakeet *Cyanoramphus novaezelandiae* and Kaka *Nestor meridionalis*). Calls of young often show similarity in structure between related species. Courtney (1974, 1986, 1993, 1996, 1997a,b,c) studied development of calls in young of many species of Aust. parrots. Food-begging Calls of many young parrots change with age. Brereton & Pidgeon (1966) speculate on ontogeny of calls in Eastern Rosella and provide illustrative sonagrams. They suggest adult calls develop from simple squawk given by nestlings. In exceptional instance of Galah being reared in wild with brood of Major Mitchell's Cockatoo *Cacatua leadbeateri*, Galah adopted calls of foster parents (Rowley & Chapman 1986). Mimicry almost absent in wild (but see Palm Cockatoo), but common in many species in captivity, especially cockatoos and Budgerigar, but also Rainbow Lorikeet, *Polytelis*, Swift Parrot *Lathamus discolor*, Red-crowned Parakeet and Turquoise Parrot *Neophema pulchella*.

For discussion of Social Organization and Social Behaviour, see family accounts below.

Breeding well known for most species in HANZAB region, poorly known extralimitally. Breeding generally seasonal, though some species can breed at any time if conditions suitable. Nest mainly in hollows in trees; some species nest on ground, under rocks or vegetation, or in tunnels excavated in arboreal or terrestrial termitaria. Eggs white. Clutch-size varies; in HANZAB region, largest clutches laid by Psittacinae and most species of Platycercinae in temperate areas and tropical semi-arid areas. Incubation by female only in Psittacidae and some Cacatuidae, by both sexes in *Cacatua*, *Callocephalon*, *Eolophus* and *Nymphicus*. Young altricial, nidicolous. Naked at hatching; generally develop down within first week. Young usually fed by female at first, then by both sexes. Fledgelings usually remain with parents for some time (Forshaw & Cooper 1981).

Worldwide, at least 90 species of parrots (*c*. 25% of all species) considered threatened (King 1981; Collar & Andrew 1988; Collar *et al*. 1994). In the HANZAB region, the only extinct taxa are: the Paradise Parrot *Psephotus pulcherrimus* (the only species extinct on mainland Aust.), probably through combined effects of overgrazing and drought; the Norfolk Island Kaka *Nestor productus*, which was killed for food and whose habitat was largely cleared; Lord Howe I. subspecies of Red-crowned Parakeet *Cyanoramphus novaezelandiae subflavescens*, possibly killed off by hunting and trapping; and the Macquarie I. subspecies of the Red-crowned Parakeet *C.n. erythrotis*, which was extirpated by cats (Garnett 1993). However, many more species are threatened: Garnett (1993) lists another 22 taxa in Aust. that are nationally threatened; of these, seven species are endangered, five vulnerable, five rare, and five insufficiently known. In addition, of the eight species of parrots native to NZ, the Kakapo is endangered; Orange-fronted Parakeet *Cyanoramphus malherbi* is rare; Kaka, Forbes' Parakeet *C. forbesi* and Antipodes Island Parakeet vulnerable; and Yellow-crowned Parakeet *C. auriceps* and Kea *Nestor notabilis* near threatened (Taylor 1985; Collar *et al*. 1994). In temperate woodlands and grassy woodlands of s. Aust., one species of woodland-dependent parrot, the Paradise Parrot, is extinct, and six others threatened; another three species of woodland-associated parrots are also threatened (Robinson & Traill 1996).

Overall, major threatening process is extensive clearance and fragmentation of habitat, particularly in S. America (King 1981; Collar & Andrew 1988; Collar *et al*. 1994). In HANZAB region, degradation, clearance and subsequent fragmentation of natural habitats for agriculture and forestry, including collection of firewood, have adversely affected many species (e.g. Glossy Black-Cockatoo, e. population of Regent Parrot *Polytelis anthopeplus*); small and isolated remnants are often too small to support viable populations of birds. Overgrazing and altered fire-regimes also change structure of vegetation, and have reduced populations and range of several species (e.g. Golden-shouldered Parrot *Psephotus chrysopterygius*, Scarlet-chested Parrot *Neophema splendida*, Ground Parrot *Pezoporus wallicus*). In Tas., preferred feeding habitat of Swift Parrot threatened by clearfelling and woodchipping of forests of Tasmanian Blue Gum *Eucalyptus globulus*. Orange-bellied Parrots *Neophema chrysogaster* threatened by destruction of coastal saltmarsh, the main feeding habitat on mainland Aust. In some areas, removal of hollow-bearing trees causes local shortages of nesting hollows, which, in turn, then reduces opportunities to breed. In s. Aust., harvesting of forests for firewood usually removes old dead trees, which often contain hollows; as a result, the reduction in the number of hollows available for nesting has caused declines of populations of many parrots throughout range (Robinson & Traill 1996). There is little replacement of suitable hollow-bearing trees, e.g. in sw. WA, the lowest average age of nest-trees used by parrots was estimated at 275 years and 446 years for cockatoos (Mawson & Long 1994, 1997; *contra* Stoneman *et al*. 1997). Further, introduced hollow-nesting species, such as Common Starlings *Sturnus vulgaris* and Common Mynas *Acridotheres tristis*, and some introduced parrots (such as Sulphur-crested Cockatoos *Cacatua galerita* in WA and Crimson Rosellas *Platycercus elegans* in NZ and on Norfolk I.), as well as Common Brushtailed Possums *Trichosurus vulpecula* and feral honeybees *Apus mellifera*, appear to compete with some species for use of hollows; this problem exacerbated in areas where hollows in short supply as a result of changes to habitats (Smithers & Disney 1969; Dawe 1979; Saunders *et al*. 1985; Garnett 1993).

Conversely, populations of some species (e.g. Elegant Parrot *Neophema elegans*) have increased, and ranges expanded after native vegetation cleared and converted to farmland, which has created habitat of similar structure to preferred natural habitats. Other species (e.g. Rainbow Lorikeet) have experienced increases in populations and expansion of range since the 1970s, probably resulting from greater availability of food after the establishment and maturation of native trees in parks and gardens in urban areas (Veerman 1991). In some areas, changes to habitats through establishment of agricultural production, particularly grain production, and provision of water for stock, has allowed some species, notably Galahs, Sulphur-crested Cockatoos and Little *Cacatua sanguinea* and Long-billed *C. tenuirostris* Corellas, to undergo dramatic increases in population and expansion of range, to the extent that they are considered pests in some rural areas (Saunders *et al.* 1985; Rowley 1990; Serventy & Whittell). Worldwide, some species are threatened by persecution in agricultural areas, where seen as pests to crops (e.g. Blue-winged Macaw *Ara maracana*, Hispaniolan Parakeet *Aratinga chloroptera*); the Carolina Parakeet *Conuropsis carolina* of N. America was hunted to extinction in late 19th and early 20th centuries because it was considered a pest of agriculture (Halliday 1978; Collar *et al.* 1994). In agricultural areas of sw. Vic., one of the most common causes of death of Long-billed Corellas is shooting by farmers (Emison *et al.* 1994); in WA, an open season declared on feral Sulphur-crested Cockatoos (Saunders *et al.* 1985), and several other species of parrots are also legally shot (Robinson & Brouwer 1989). In NZ, large numbers of Red-crowned Parakeets were formerly shot as pests around crops (Turbott 1967; Taylor 1985; Oliver).

Popular cage-birds. Throughout world, illegal taking of eggs or young from nests, or adults from wild populations for avicultural trade a major threat to continued survival of some species, e.g. Red-and-Blue Lory *Eos histrio*, Spix's Macaw *Cyanopsitta spixii*, Hyacinth Macaw *Anodorhynchus hyacinthinus*, Thick-billed Parrot *Rhynchopsitta pachyrhyncha*, Green-cheeked Amazon *Amazona viridigenalis* (King 1981; Collar & Andrew 1988; Ridgely 1989; Snyder *et al.* 1989; Juniper 1991; Collar *et al.* 1994). However, the effect of illegal collecting is exacerbated by threats posed by loss of habitat as described above (Collar *et al.* 1994; Forshaw). In HANZAB region, several species of cockatoos and parrots with small populations are threatened by illegal collecting for aviculture, for both local and overseas markets, e.g. Eclectus Parrot and subspecies *narethae* of Blue Bonnet *Northiella haematogaster* (Garnett 1993). In Aust., many hollows destroyed by collectors hacking holes in trees to get access to nest-hollows and eggs or young. Hollows that are not destroyed often repeatedly robbed, either in subsequent seasons or after birds re-lay in same season after theft of clutch (Forshaw). In NT, trial programme introduced to legally exploit wild populations of Red-tailed Black-Cockatoos, involving collection of eggs, nestlings and adults (Anon. 1995). Similar schemes have been proposed in other areas of Aust., involving other abundant or pest species, but have not been accepted. Extralimitally, extinction or declines in populations have also been blamed on human persecution, especially if thought to be pest of agricultural production, and including hunting (e.g. Snyder *et al.* 1989).

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Family **PSITTACIDAE** parrots and lories

Usually brilliantly coloured, and vary greatly in size. About 310–335 species in 70–87 genera (Schodde & Mason 1997); 46 species in 21 genera in HANZAB region. Distributed on all continents except Antarctica; most diverse in A'asia, but other centres of diversity in Old World (Africa and Indian subcontinent) and New World (S. America and s. N. America) (Smith 1975; Forshaw & Cooper 1989; Schodde & Mason 1997).

Taxonomy at subfamily level not clear at present time. Different authors have recognized 5–11 different groups within Psittacidae (see Smith 1975; Forshaw & Cooper 1989; Sibley & Ahlquist 1990; Collar 1997). Eleven infrafamilial groups have been recognized here, following Schodde & Mason (1997) for those with representatives in HANZAB region, and Collar (1997) for those wholly extralimital. The following four groups occur extralimitally: Psittrichadini (Pesquet's Parrot *Psittrachas fulgidus*, monotypic); Micropsittini (pygmy parrots, six species); Psittacini (Afrotropical parrots, 12 species); and Arini (Neotropical parrots, 148 species); these not considered further below.

Schodde & Mason (1997) recognized six infrafamilial groups in Aust. and its territories. However, since relationship between species in some of these groups is still not clear, they treated only the three more clearly defined groups as subfamilies (Nestorinae, Loriinae and Platycercinae) and considered the other three groups as unplaced tribes (Psittaculini, Cyclopsittacini and Polytelini). Another subfamily, Strigopinae, is endemic to NZ (NZCL). Collar (1997) differs slightly in which groups he treats as subfamilies and which he treats as tribes; also does not recognize Polytelini, which he includes within Psittaculini. The seven groups occurring in the HANZAB region (based on Schodde & Mason [1997] unless stated and which see for further references):

SUBFAMILY STRIGOPINAE: Monotypic Kakapo *Strigops habroptilus*; endemic to NZ. Large, flightless. Furcula cartilaginous; keel vestigial (Holyoak 1973; Smith 1975). Barred remiges and rectrices (Smith 1975). Scratch head over wing (Smith 1975).

SUBFAMILY NESTORINAE: Kakas. One genus, *Nestor*, with two species endemic to NZ, and a third isolated and extinct species on Norfolk I. Large and short-tailed, with spines extending from tips of rectrices. Remiges barred (Smith 1975). Parahyoid process joined; styohyoideus muscle reduced; left carotid superficial; tongue thick and muscular with fringe of hair-like papillae on outer edge; pigments fluorescent (Holyoak 1973).

SUBFAMILY LORIINAE: Lorikeets and lories. Small, brightly coloured, and arboreal parrots. Eleven to 13 genera, distributed across e. Indonesia, New Guinea, islands of sw. Pacific and Aust. with greatest diversity in New Guinea, where 8–10 genera occur; three genera in HANZAB region: *Glossopsitta*, *Psitteuteles*, *Trichoglossus* (Schodde & Mason 1997). Most have permanent underwing-stripes (Smith 1975; Forshaw & Cooper 1989; Courtney 1997b); present only in some juveniles of extralimital *Charmosyna* (Courtney 1997b). Parahyoid process joined; styohyoideus muscle reduced or absent; tongue has brush of papillae at tip (Holyoak 1973; Smith 1975; Forshaw & Cooper 1989). Also characterized by pointed wings and tails, dashing flight, and short intestinal tract with inelaborate crop and gizzard.

SUBFAMILY PLATYCERCINAE: Broad-tailed parrots. Diverse group of small to medium-sized parrots. About 14 genera containing 35–38 species distributed across Aust., NZ and New Caledonia and on some associated islands; 11 genera and 28 species in HANZAB region: *Barnardius*, *Cyanoramphus*, *Lathamus*, *Melopsittacus*, *Neophema*, *Neopsephotus*, *Northiella*, *Pezoporus*, *Platycercus*, *Psephotus*, *Purpureicephalus*. Underwing-stripe present in juveniles and most adult females, but usually 'deciduous' in adult males (Holyoak 1973; Courtney 1997c); permanent in *Melopsittacus* and *Pezoporus* (Courtney 1997b,c); absent in extralimital *Prosopeia* (Courtney 1997c). Characterized by crescentic auditory maetus; foss at base of zygomatic process; orbit open below (except *Melopsittacus*); parahyoid process more or less converging; tongue has shallow grooves; furcula cartilaginous (except *Lathamus*); stylohyoideus muscle often wide; left carotid often superficial; fluorescent yellow pigment in plumage; scratch head over wing (Holyoak 1973). Except for *Geopsittacus* and *Pezoporus*, all have small patch of feathers on nape with white or pale yellow bases, instead of the usual grey, and which forms a nape-spot (Smith 1975), though spot hidden unless feathers of the region are erected or worn.

Unplaced tribes: PSITTACULINI: Palaeotropic parrots. Medium-sized arboreal parrots with heavy bills. Composition uncertain; about 11 genera, distributed from India to A'asia. Two genera in Aust.: *Eclectus* and *Geoffroyus*. Both tongue and dental pad ridged or grooved. No stripe on underwing.

CYCLOPSITTICINI: Fig-parrots. Small, green, arboreal fruit-eating parrots. Five species in 1–3 genera, with distribution centred in New Guinea; single species in genus *Cyclopsitta* in HANZAB region. Have stout ridged bills; wedge-shaped tails; marked sexual dimorphism; permanent double stripes on underwing; and completely ossified orbital ring free from well-developed zygomatic processes (Smith 1975; Courtney 1997b).

POLYTELINI: Long-tailed parrots. Slender medium-sized parrots. Eight species in three genera, with distribution centred in Aust. Five species from all three genera in HANZAB region: *Alisterus*, *Aprosmictus* and *Polytelis*.

Characterized by long, attenuated pink-tipped tails (Schodde & Mason 1997); inner webs of lateral rectrices have rose-pink edging, a character not possessed by any other parrot (Courtney 1997a). Other characters include: marked sexual dimorphism; no stripe on underwing; tongue ridged or grooved; soft palate; extrinsic syringeal muscles evidently attached to lung membrane.

Generally slim bodied, with short necks and short bills. Plumage coloured by carotenoid pigments and back-scattering of light through hollow cortical cylinders in feather barbs (Dyke-texture or Tyndall-texture). All feathers of body (except nape of some groups) have grey bases. None has erectile crests, though Horned Parakeet *Eunymphicus cornutus* of New Caledonia has elongated feathers on crown forming an immovable crest (Forshaw & Cooper 1989). Maxillae attached to skull by a flexible joint. Carotid arteries paired, fused, or left carotid superficial. Syrinx bronchial, the first rings upcurved, ossified and fused (except in Nestorinae). Zonary proventriculus present. No gall bladder. See introduction to order for characters shared with Cacatuidae.

Adult plumage often bright and colourful; ground-colour commonly green, with blue, red or yellow markings. In most, sexes similar or differ only slightly in plumage; in *Eclectus*, *Psephotus* and some *Neophema*, sexual dimorphism in plumage marked. In those groups that have stripe on underwing, presence often related to age or sex. Adult bare parts vary greatly: dull greys, browns and creams in many, but can be bright red or orange in many others. In most species, males slightly larger than females. Adult post-breeding (pre-basic) moult usually complete. Moult of primaries centrifugal; usually begins from p6, but in some can begin with any primary between p5 and p8. Nestlings usually hatch with sparse covering of down; a few hatch naked or nearly naked. A second, mesoptile, down develops in many species. In most, juvenile plumage duller than that of adults (and often resembles dull version of adult females in species where sexes differ). Post-juvenile (first pre-basic) moult partial in most species. Time to attain adult plumage varies greatly between species; in some, young birds not separable from adults after a few months, in others, adult appearance not attained until *c*. 4 years old. Similarly, time of first breeding can vary between species, from within first year to 4 years or older.

Occur in most habitats, from arid and semi-arid zones to tropical rainforest. Some species wholly arboreal, e.g. Loriinae, Cyclopsittacini, Eclectus Parrot *Eclectus roratus*; most others at least partly arboreal; a few strictly terrestrial, e.g. Night Parrot *Pezoporus occidentalis*, Ground Parrot *P. wallicus*. Though recorded in most habitats, some are specialists: e.g. fig-parrots *Cyclopsitta* mostly restricted to tropical and subtropical rainforests; Kaka *Nestor meridionalis* mostly inhabits temperate beech, broadleaf or podocarp rainforests; and Ground Parrot mainly confined to heathland in s. and e. Aust. In contrast, rosellas *Platycercus* may occur in a wide variety of treed habitats. Most require hollows, and therefore old trees, in which to nest, and are adversely affected by the removal of hollow-bearing trees (see Introduction to Order).

Patterns of movements vary greatly: from sedentary (e.g. Ground Parrot, Kakapo *Strigops habroptilus*), resident (e.g. Australian Ringneck *Barnardius zonarius*), to highly nomadic or dispersive (e.g. Budgerigar *Melopsittacus undulatus*). Several species migratory: Swift Parrot *Lathamus discolor* and Orange-bellied Parrot *Neophema chrysogaster* breed in Tas. and most or all of population moves to mainland Aust. for non-breeding season; further, Tas. breeding population of Blue-winged Parrot *Neophema chrysostoma* also apparently mostly migratory, moving to mainland Aust. Kakapo of NZ flightless. As with Cacatuidae, movements of many species poorly known, and many types of patterns have been attributed to them (e.g. Superb Parrot *Polytelis swainsonii*), probably in ignorance of actual movements, but possibly because movements vary between years or areas. Movements of lorikeets in Aust. (Loriinae) often considered to be related to flowering of food-trees. Many other species in HANZAB region appear to move in response to rainfall; in Budgerigar, both rainfall and temperature act indirectly on control of movements and breeding by affecting production of food (Wyndham 1980, 1983). Some species might make altitudinal movements (e.g. Eastern Rosella *Platycercus eximius*). Even suggested that movements of Golden-shouldered Parrots *Psephotus chrysopterygius* possibly linked to those of Black-faced Woodswallows *Artamus cinereus* (Garnett & Crowley 1995). Major studies of movements have been carried out on some species in HANZAB region (e.g. Crimson Rosella *Platycercus elegans*), using standard leg-banding, radio-tracking, and, in case of Ground Parrot, even cotton and spool method (Jordan 1987, 1988).

Almost all are herbivorous, feeding mainly on seeds, though many also take insects and their larvae. Most gregarious. Feed on ground, in trees, or both. Drink water by lapping, ladling or suck-pumping. All (except monotypic Psittrichichadini of New Guinea) husk seeds in same way: seed held between tip of lower mandible and notch on horny palate of upper mandible (which also corrugated to improve grip); the tip of the lower mandible driven into husk, between seed and husk, which is thus removed. The seed is then split and eaten; very hard nuts are held in part of bill nearest gape, where pressure between mandibles greatest (Collar 1997). Handling of other items similar. In HANZAB region, groups show variety of adaptations and behaviour; the following based on Forshaw & Cooper (1981), Schodde & Mason (1997), Forshaw, and species accounts, unless stated. LORIINAE: Almost exclusively arboreal, feeding mainly on nectar and some pollen and fruit. Specialized for harvesting pollen and nectar, with: narrow and protruding bills, brush-tipped tongues (see Churchill & Christensen 1970; Hooper & Burbidge 1979), non-muscular gizzard, and compound glands arranged linearly along wall of proventriculus (Steinbacher 1934). Gizzards of lorikeets much smaller than those of seed-eating parrots of similar body weight, and intestine substantially shorter (Richardson & Wooller 1990). Gregarious, feeding in noisy flocks that continually move from one stand of flowering trees to another. When feeding, very active, clinging to and climbing all over flowering branches. PSITTACULINI: Arboreal, mainly in canopy of rainforest trees. Feed on fruits, seeds, flowers and nectar; said to prefer rainforest fruits. Usually feed in pairs or small flocks. CYCLOPSITTICINI: Wholly arboreal, but may descend to *c.* 1 m from ground to feed on low branches and trunks of fig-trees. Frugivorous, eating mainly figs, though tend to extract seeds from fruit and discard pulp rather than eat fruit. Bills broad, stout and ridged. Feed in pairs or small parties. POLYTELINI: Arboreal and terrestrial, granivorous. *Alisterus* and *Aprosmictus* arboreal, feeding mainly on seeds of native trees, such as *Eucalyptus*; *Polytelis* spend more time on ground feeding on seeds of grasses and herbaceous plants. Feed in pairs or small flocks, though *Polytelis* usually feed in flocks. PLATYCERCINAE: Terrestrial and arboreal. Diet: (1) mainly seeds of grasses, herbs and trees, procured from ground or from shrubs and trees (*Barnardius*, *Neopsephotus*, *Northiella*, *Platycercus*, *Polytelis*); (2) mainly seeds of grasses and herbs obtained almost exclusively from ground (*Melopsittacus*, *Neophema*, *Pezoporus*, and *Psephotus* [except Mulga Parrot *P. varius*, which feeds both on ground and in trees]); (3) nectar (*Lathamus*); (4) leaves of grasses and sedges (*Cyanoramphus*). Some highly specialized, e.g. Red-capped Parrots *Purureicephalus spurius* have narrow projecting bill and feed on seeds extracted from capsules of Marri *Eucalyptus callophylla*. Many also supplement main diet with flowers, nectar, or fruits, and almost all take some invertebrates. One, Antipodes Island Parakeet *Cyanoramphus unicolor*, known to take dead and nesting seabirds. Most feed in small flocks; some feed in large flocks (e.g. Budgerigar); others often feed singly or in pairs (e.g. *Platycercus*). Feeding behaviour varies widely depending on nature of food and where obtained; for details see individual species accounts. NESTORINAE: Mainly herbivorous but omnivorous, taking wide range of plant foods and invertebrates. Arboreal and terrestrial, forage at all levels from ground to canopy of trees. Use wide range of foraging methods, including gleaning, probing, digging, stripping and chiselling bark, excavating wood, and licking nectar from flowers; unlike other parrots, feed on sap by stripping bark and exposing cambium, and then lick sap from damaged surface. Feed singly, in pairs or small flocks, though Kaka more often singly. STRIGOPINAE: Mainly herbivorous, partly granivorous. Forage at all levels, including canopy of tall forest, but most foraging on or near ground. Sense of smell thought to be well developed and of importance in foraging, and at least some birds can locate foods by smell alone. Short, powerful and compressed bill, and short, broad and thick tongue adapted for browsing, crushing, grinding and extracting juices from fibrous plant tissues. Solitary.

In HANZAB region, all species gregarious to some extent with notable exception of Kakapo. In most species, flocks typically of up to *c.* 30 birds. However, some species in flocks of 100s and, in Budgerigars, 1000s. Most species more gregarious in non-breeding season, though even in breeding season, many species often form flocks when feeding. All monogamous, with exception of Kakapo, in which the sexes come together only at leks. Pair bonds life-long and mates remain together year round. Co-operative breeding does not occur, with probable exception of Eclectus and Red-cheeked *Geoffroyus geoffroyi* Parrots (Psittaculini) and possibly, but rarely, Regent Parrot *Polytelis anthopeplus* (Polytelini). Only female incubates but both sexes involved with feeding of young, except in Kakapo, in which female raises young alone, and possibly Ground Parrot, in which male appears responsible for feeding of young. In most species, young generally leave natal area by 3–6 months old. Aust. lorikeets, *Polytelis*, *Eclectus*, and some *Neophema* often nest in loose colonies; others strictly solitary nesters. Generally defend only nest-hole. Most gregarious species roost communally, at least when not breeding.

Often conspicuous, vocal and active but may be hard to observe when feeding in tree-tops or on ground. All species courtship feed, except Kakapo; in some, occurs year round e.g. *Trichoglossus*. Many known to, or likely to, allopreen, except rosellas *Platycercus*, Australian Ringneck, *Cyanoramphus*, *Neosephotus*, *Neophema*, Red-winged Parrot *Aprosmictus erythropterus*, Australian King-Parrot *Alisterus scapularis*, possibly Red-cheeked Parrot, and assumed not to in Kakapo. Sexual and aggressive displays generally fairly simple, consisting of actions such as bobbing, eye-blazing, arching of wings, fanning and wagging of tail and calls. However, in *Trichoglossus* and Varied Lorikeet *Psitteuteles versicolor* (Loriinae), displays complex and performed in many social contexts; in *Trichoglossus*, displays often performed either reciprocally or in unison by both members of a pair. Other notable displays are aerial circling performed by Eclectus and Red-cheeked Parrots, and distinctive calling behaviour of Kakapo and Ground Parrot.

Calls usually described as whistles, chatterings or pipings, though some are shrieks. Calls often melodic and some are extraordinarily complex, such as Warble song of Budgerigar, and highly varying yodelling calls of Kaka *Nestor meridionalis*. Booming of Kakapo at lek unique form of vocalization in parrots. Sexually differentiated calls known in many species in most genera. Food-begging Call of all Aust. lorikeets a repeated sharp high-intensity hissing note that begins with a structureless hiss, which gives way abruptly to a brief high-energy blip preceding a structured hiss (see Courtney 1997b). For details of Food-begging and other calls of platycerine parrots see Courtney (1997c, which was not available for summary in species accounts).

Breeding well known in HANZAB region. Extralimitally, breeding of most species of Loriinae, Platycercinae and Cyclopsittacini virtually unknown; some species of Psittaculini moderately well known. Plum-headed Parrot *Psittacula cyanocephala* and some lovebirds *Agapornis* (Psittaculini) breed colonially (Forshaw & Cooper 1981), and Large Fig-Parrot *Psittaculirostris desmarestii* (Cyclopsittacini) thought to breed colonially within hollow trunks of large trees (Rand 1942; Beehler 1982). Breeding generally seasonal but some species will breed at any time of year if conditions suitable, and some species can raise two or more broods in a season. Most species nest in hollows in trees, though some nest on ground, under rocks, vegetation or in burrows; some species excavate tunnels in termite mounds. Extralimitally, Red-flanked Lorikeet *Charmosyna placentis* (Loriinae), Orange-breasted Fig-Parrot *Cyclopsitta gulielmitertii* (Cyclopsittacini) and some *Agapornis* (Psittaculini) nest in holes excavated in arboreal termitaria (Rand 1942; Bell & Coates 1979; Forshaw & Cooper 1981; Coates 1985). Hollows generally unlined, or lined with wood dust chewed from sides of hollow; extralimitally, *Agapornis* and hanging parrots *Loriculus* (Psittaculini) line hollow with pieces of leaves or bark or both; female carries material in bill or tucked among feathers of rump, flanks or lower back (Abdulali 1964; Ali & Ripley 1969; Forshaw & Cooper 1981). Eggs invariably white but can become stained in nest. Mean size of eggs varies from 19.5 × 16.4 for Little Lorikeet to 50.5 × 37.2 for Kakapo. Extralimitally, smallest egg (16.8 × 13.5) laid by Pygmy Lorikeet *Charmosyna wilhelminae* (Forshaw & Cooper 1981). Loriinae, Nestorinae, Strigopinae, Cyclopsittacini, Ground Parrot and most Psittaculini generally lay small clutches (2–4); a few species of Psittaculini and most Platycercinae generally lay 4–7 eggs, but can lay up to nine. Incubation lasts 18–23 days for most species; up to 25 days for Rainbow Lorikeet *Trichoglossus haematodus*, 26 days for Eclectus Parrot, between 3 and 4 weeks for Kea *Nestor notabilis* and 25–30 days for Kakapo. In all species, female incubates; male usually feeds female at nest or nearby. Young altricial, nidicolous. Most hatch naked and develop whitish to grey down in first few days. Generally, young fed by regurgitation, by female only, or by female for first few days then assisted by male; only male Ground Parrots feed young; male Kakapos play no part in nesting. Young of most species fledge at 5–7 weeks, 7–10 weeks for Rainbow Lorikeet, Kaka and Kakapo, 11–12 weeks for Eclectus Parrot, and 13 weeks for Kea; Ground Parrot has the shortest fledging period, *c.* 24 days. Fledgelings usually remain with parents for some time (Forshaw & Cooper 1981).

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Strigops habroptilus **Kakapo**

COLOUR PLATE FACING PAGE 641

Strigops habroptilus G.R. Gray, 1845, *Gen. Bds* 2: 427 — New Zealand = Dusky Sound.

The generic name is compounded from the Latin *strix, strigis*, owl, and Greek ὤψ, face, countenance, and alludes to the owl-like facial disc. The specific name describes the soft body-plumage (Greek ἁβρός, delicate, and πτίλον, feather).

OTHER ENGLISH NAMES Ground, Night or Owl Parrot.

MONOTYPIC

FIELD IDENTIFICATION Length 58–64 cm; wingspan 84, 91 cm (n=2); weight: male 2 kg, female 1.5 kg. Very large and bulky parrot with short broad wings; short, rather scruffy and decurved tail; characteristic owl-like facial disc of hair-like feathers; prominent swollen cere at base of short broad bill; and massive fleshy legs and feet. Unmistakable: mostly green, intricately streaked and barred black-and-yellow above and more boldly streaked yellow below, with contrasting forehead and facial disk and darker patch on ear-coverts. Sexes differ markedly in size but plumages alike. No seasonal variation. Juvenile separable. Flightless, nocturnal and secretive; male utters distinctive booming call during breeding season. Endangered. **Adult male** Head and neck, bright green, varyingly and finely mottled and barred black, with straw-yellow or brownish-grey facial disc and diffuse darker patch on ear-coverts (bordered above by yellow). Rest of upperbody, bright green, intricately streaked, mottled and barred with irregular fine black-and-yellow markings. Uppertail, olive-brown, densely vermiculated black, and barred black at sides. Upperwing: most of coverts as rest of upperparts; remiges and greater primary coverts duller, olive-brown, finely vermiculated and narrowly barred black; inner web of outer primaries barred irregularly to tip, sometimes faintly (cf. adult female). Underbody like upperparts but paler, yellow-green, and with broader and more conspicuous pale-yellow streaking and weaker dark barring or mottling. Undertail like uppertail but slightly paler. Underwing: leading coverts, pale yellow to yellow-green, heavily blotched and barred black; greater coverts and remiges, dark grey with irregular pale-yellow barring or vermiculation. Bill, light blue-grey with off-white tip, cutting edge and lower mandible. Cere, blue-grey with pale-grey bloom. Iris, dark brown. Orbital ring, blue-grey. Legs and feet massive and fleshy, blue-grey with paler soles and rear or tarsi. **Adult female** Much smaller than male, with narrower and less domed head; narrower and proportionately longer bill; smaller cere; smaller and oblong nostrils; much more slender legs and feet; and proportionately longer tail. Plumage like that of adult males: distal 3–4 cm of inner edges of outer primaries not barred or mottled (cf. adult male); also appear to have less yellow in plumage, and barring and mottling on underparts is paler. Cere, blue-grey with little or no grey bloom (cf. adult male) and legs and feet pale pinkish-grey. **Juvenile male** Very similar to adult but duller and darker, dull olive-green, with finer, more uniform and more pronounced black barring and less yellow in plumage; on underparts, barring tends to be pale and indistinct, yellows are largely replaced by greens, and have indistinct broad pale-yellow band across upper breast; face is paler grey than that of adult, with prominent darker-grey lores; distal 3–4 cm of inner web of outer primaries strongly barred in some birds (as in adult males), weakly barred (like a watermark) in others. Tail and wings shorter than in adults (markedly so in fledgelings), and bill shorter, smaller and with more pronounced curve near tip. Primaries narrower with pointed tips (rounded in adult), and vestiges of down adhere to tips of remiges and rectrices at first. Orbital ring paler grey than in adults. **Juvenile female** Like juvenile male but smaller, and distal 3–4 cm of inner webs of outer primaries without obvious markings (as difference between adult male and female) (D.V. Merton).

Similar species None.

Rarely seen in wild. Now confined to several offshore islands of NZ. Normally solitary, though males (but not always annually) gather in lek display during courtship (see Social Organization). Nocturnal and secretive, roosting by day in natural crevices or dense vegetation. Freeze when disturbed but otherwise remarkably tame and often allow close approach. On leks, make well-worn tracks through dense vegetation, especially along ridges and spurs; use characteristic depressions, or bowls, for booming and associated visual courtship displays (not for dust-bathing). Flightless but can leap or parachute, with aid of wings, 2–3 m at steep (<45°) downward angle (do not glide). Walk rather than hop, holding body horizontal and head close to ground. Clamber up leaning trunks and branches, grasping vegetation with bill and using spread wings constantly for support and to aid balance; also use wings to help break fall when occasionally jump or parachute. Aside from distinctive well-worn track-and-bowl system, presence also indicated by tightly compressed 'chews' close to or hanging from fibrous vegetation; by neatly clipped vegetation; by large compact, coiled, cylindrical droppings of finely ground plant material and white traces of uric acid (with herb-like smell when fresh); occasionally by bill impressions in grubbed earth. Calls distinctive but birds seldom call except during courtship (mainly Dec.–Mar. of some years) when male utters characteristic repeated low resonant booming notes at lek; normally boom at night and sound can be heard for up to 5 km; males also utter repeated high-pitched metallic nasal *ching* at leks. Throughout year, but mainly during breeding season, both sexes occasionally utter a repeated high-pitched *skraark*; also utter brief isolated grunts, squeals, hoarse croaks and screeches.

HABITAT Based on contribution by D.V. Merton. Generalist; inhabit range of vegetation types, and altitudinal and climactic zones; mainly in ecotones and in seral vegetation, rather than climax forest associations. Mostly on ground, though regularly climb up to 10 m in small trees and shrubs and sometimes up to 30 m to canopy of trees. Formerly occurred from near sea-level to upper limits of woody vegetation, >1200 m asl, in rolling to steep landforms, and in areas of high to low rainfall (Lyall 1852; Hector 1863; Reischek 1884, 1930; Henry 1903; Williams 1956; Johnson 1976; Gray 1977; Millener 1981; Holdaway 1989). In Fiordland occurred in subalpine zone at edges of beech forest, among scrub, and in tussock grassland and herbfields above treeline in head-basins and steep walls of glaciers; those observed in Fiordland remained in snow in these habitats during winter, rather than descending to snow-free valley floors (Henry 1903; Merton 1976b; Morris & Smith 1995; D.V. Merton). On Stewart I., population inhabited rolling hilly peatlands with low floristic diversity, supporting mosaic of rata *Metrosideros*–podocarp *Podocarpus* forest, subalpine scrub dominated by bogpine *Dacrydium*, leatherwood *Olearia* and *Dracophyllum* and peat-bog associations. Kakapo released on Little Barrier and Maud Is mostly inhabit cool, moist and shaded s.–sw. slopes (Moorhouse & Powlesland 1991; Merton 1994; NZRD), but have also adapted to unfamiliar habitats (Moorhouse & Powlesland 1991), including pastures (Gray 1977). Historically, often occurred near edge of temperate rainforests, especially beech *Nothofagus* forests but also including lowland podocarp forests (Williams 1956; Gray 1977) and, characteristically, tussock grasslands (Lyall 1852; Haast 1864; Henry 1903; O'Donoghue 1924; Pascoe 1957; Merton 1975; Johnson 1976; Gray 1977); most often in ecotone between forest, scrub, herbfields, tussock grassland or seral associations (Henry 1903; Johnson 1976; Gray 1977; Best 1984; Butler 1989). Also often in dense, diverse pioneer or seral vegetation on banks of streams, old slip-faces, subalpine terraces, avalanche screes and areas of wind-thrown trees (Johnson 1976; Gray 1977).

Breed in natural cavities, such as small caves, hollow tree-stumps or logs, up to 400 m asl; near rich feeding areas (D.V. Merton). Availability of food controls breeding. Successful breeding can occur only when abundant, high-quality food within walking distance of nest, and that food remains available throughout incubation, nestling and fledging periods (6–8 months). Periodic heavy crops of fruit and seed, known as masting in NZ, occur irregularly at intervals of up to 6 years and are believed to be determined by climatic conditions during the summer preceding a masting event (Norton & Kelly 1988). Climatic conditions during months immediately preceding masting determine whether a crop will develop and ripen. During 1990s, two mastings of Rimu *Dacrydium cupressinum* have occurred on Codfish I. Both crops aborted and failed to ripen, causing breeding failure in those Kakapo not receiving supplemental food.

Lekking sites, which are traditional, usually located away from nesting and feeding areas. Mostly above bush-line, on open shoulders or crests of ridge-tops overlooking valleys. Shallow track-and-bowl systems or courts excavated in sites with good acoustics, usually at base of overhanging rocks, rock-faces or tree-trunks, which act as sound reflectors (D.V. Merton).

Forage at all levels, from ground to canopy of forests (up to 30 m), mostly in crowns of small trees and shrubs 1–10 m above ground; round edges of temperate rainforest and montane beech forest; also in scrub, tussock grasslands and subalpine herbfields (D.V. Merton). Often in disturbed areas, such as recent or regenerating debris of landslips and avalanches, or among wind-thrown trees (Johnson 1976; Gray 1977; D.V. Merton). On Stewart I., tended to feed on crests of ridges and on well-drained sunny slopes, where variety of vegetation generally greater and more concentrated than elsewhere (Best 1984).

Usually roost on steep damp shaded heavily vegetated slopes, often with a southerly aspect (D.V. Merton). Mostly on or near ground beneath dense cover in forest, scrub or bracken; also in natural cavities, such as caves, beneath boulders, or in hollow tree-stumps. Also roost up to 3 m above ground, on horizontal limbs in understorey of forest or scrub, with dense cover overhead; rarely higher, but up to 30 m occasionally (D.V. Merton). Sometimes loaf in direct sunlight in crowns of trees, especially after wet weather (D.V. Merton).

Thought that widespread burning of forest, scrub and tussock-grass by Maori important factor in contraction of range (see below). Subsequent clearance by European settlers is unlikely to have seriously affected habitat, because Kakapo were already confined to a few remote sites, most of which have still not been cleared (D.V. Merton). Also adversely affected by degradation of habitat by introduced herbivores, though tracks developed by people and other animals, such as deer, are used for both foraging and movement (D.V. Merton). On Stewart I., population was centred on an area of scrub and forest, much of which had been burned repeatedly during the late 19th and early 20th centuries; the distribution of lek sites shows that neighbouring (often less modified) areas were occupied by Kakapo in the recent past (D.V. Merton).

DISTRIBUTION AND POPULATION Based on contribution by D.V. Merton. Endemic to NZ; thought to be extinct throughout natural range (NI, SI and Stewart I.). Currently only on four offshore islands, where introduced between 1974 and 1997.

NI Last confirmed record in Huiarau Ra. in 1927 (Williams 1956); now only on Little Barrier I. off ne. coast (see Introductions below). **SI** Last confirmed records: Tutoko and Transit Valleys, Milford Sound, Fiordland, 1987 (Rasch 1989); now only on Maud I. in Marlborough Sounds. **Stewart I.** Last known individual removed 1997 (D.V. Merton); now only on Codfish and Pearl Is off Stewart I. Last natural populations on mainland occurred in Fiordland, but not recorded there since 1987 (Rasch 1989); last natural population survived on Stewart I. till transferred to offshore islands (D.V. Merton).

Chatham Is Suggested former occurrence on Chatham Is (Williams 1956; Dawson 1959, 1960) incorrect (Millener 1981; Holdaway 1989).

Breeding Assumed to have been throughout former range. Currently only on Little Barrier, Maud and Codfish Is.

Change in range Subfossils and remains from Maori middens indicate that formerly occurred throughout much of NZ, from far N of NI, S to s. Stewart I. before and during early Maori occupation (Williams 1956; Dawson 1962; Scarlett 1979; Millener 1981; Holdaway 1989). No evidence of a significant decline in populations before arrival of Maori *c*. 1000 years ago (D.V. Merton; *contra* Williams 1956), but after Maori colonization, range contracted rapidly by modification of habitat, hunting, and predation by introduced dogs (Kuri) *Canis domesticus* and Pacific Rats (Kiore) *Rattus exulans*. At time of first European contact in late 18th century, range had already contracted considerably, but still inhabited parts of central and s. NI (e.g. Kaimanawa Ra., Urewera and Wairarapa districts) (Best 1942); reported from Hunua Ra. in 1912 (McKenzie 1979) and Huiarau Ra. in 1927 (Williams 1956). In late 18th century, extinct in e. SI but was abundant in parts of n., w. and s. SI. Populations declined and range contracted further after occupation by Europeans in 19th century and introduction of other mammalian carnivores, especially cats and dogs and Brown Rats *Rattus norvegicus*, and herbivores (Wodzicki 1950; Atkinson 1973; D.V. Merton). After 1880, remaining populations throughout NI and SI declined rapidly, coinciding with establishment of Stoats *Mustela putorius*, Black Rats *Rattus rattus* and various herbivores. Decline in population in Fiordland was first noted late in 19th century, after an irruption of mustelids and rats (Henry 1895–1908; Hill & Hill 1987; Clout & Craig 1995; Clout & Merton 1998); by early 1970s, species thought to be extinct. However, by 1977, 18 birds, all old adult males, had been located in some remote valleys in Fiordland (Merton 1976b, 1987; Butler 1989; NZRD). The population became extinct by 1989, declining from 15 males in 1977 to six in 1981 and 3–4 in 1987 (Merton 1989; Clout & Craig 1995). The only known survivor of the Fiordland (in fact, mainland) populations, affectionately known as Richard Henry, now lives on Maud I., where he was relocated in 1975. In 1977, a population of 100–200 was discovered on Stewart I. (Merton 1984; Powlesland 1989; Powlesland *et al*. 1992; Clout & Craig 1995), and the survival and recovery of the species became tangible in 1980 after four females were discovered there, the first seen for *c*. 70 years.

Introductions Kakapo first introduced to predator-free islands as conservation measure in 1890s by Richard Henry, who captured and transferred *c*. 300 to Resolution I. in Fiordland (Henry 1903; Hill & Hill 1987; Butler 1989), but introduction failed when Stoats invaded island soon after 1900. Other early, unsuccessful, attempts at translocation included release of three onto Little Barrier I. in 1903, and three onto Kapiti I. in 1912, where they were last seen in 1936 (Best & Powlesland 1985). In 1974, two from Fiordland were introduced to Maud I. where they survived for 3 years; another ('Richard Henry') was introduced in 1975; and two more in 1981, which disappeared soon after release (Merton 1976a; Butler 1989). After females were discovered on Stewart I., three females and one male were transferred to Maud I. in 1980–81; one of the females died a few days after being transferred but the others survived.

In 1982, Stoats temporarily invaded Maud I., and the four Kakapo (including 'Richard Henry') were relocated to Little Barrier I., from which cats had recently been eradicated (Veitch & Bell 1990). Between 1982 and 1997, all 61 Kakapo located on Stewart I. were relocated: in 1982, 18 were introduced to Little Barrier I. (followed soon after by the birds from Maud I.) (Butler 1989; Merton & Empson 1989); between 1987 and 1997, 31 more were released on Codfish I., from which predatory Weka *Gallirallus australis* and Common Brushtail Possums *Trichosurus vulpecula* had been eradicated (Veitch & Bell 1990); between 1989 and 1991, six from Stewart I. were released on Maud I. after it had been cleared of Stoats; and in 1992, the last two male Kakapo known from Stewart I. were released onto Mana I., from which House Mice *Mus domesticus* had been eradicated in 1989 (Todd & Miskelly in press), but both had died by 1994 (D.V. Merton). In 1996, 'Richard Henry' was returned to Maud I. (D.V. Merton). The survival rate of translocated Kakapo has been high: at least 47 (78%) of 61 birds removed from Stewart I. have survived until 1997 (D.V. Merton); on Little Barrier I., 16 of the 22 birds released in 1982 survived to 1997 (overall survival rate of 98.2% p.a.); similar rates of survival (26 of 30 released) recorded on Codfish I. (D.V. Merton). Overall, the translocation of Kakapo has effectively arrested the dramatic rate of population decline recorded in early 1980s (Lloyd & Powlesland 1994; Clout & Craig 1995; Powlesland *et al.* 1995; Clout & Merton 1998) but has not yet reversed it (D.V. Merton).

Status Endangered; extinct in wild (Baillie & Groombridge 1996). Surviving population ageing; there are also few females, which greatly reduces recruitment to breeding population. Breeding frequency of Kakapo among slowest for any bird; natural production and current productivity are low; combination of physiological and behavioural traits means that females and young are highly vulnerable to depletion of food during 10-month breeding cycle, and eggs and nestlings are uniquely vulnerable to predation by introduced mammalian carnivores; sex-ratio also heavily biased against females. Only eight of 19 adult females are known to have laid fertile eggs in past 10 years; possible that much of female population may already be too old to breed effectively. **Populations** Total population in 1998 is 54 birds: LITTLE BARRIER I.: 12 (three females, nine males), *c.* 1 bird/250 ha; MAUD I.: Seven (three females, four males), *c.* 1 bird/43 ha; CODFISH I.: 31 (14 females, including one juvenile, and 17 males, including three juveniles), *c.* 1 bird/45 ha; PEARL I.: four males, *c.* 1 bird/250 ha (D.V. Merton). In 1980, total population on Stewart I. was *c.* 140, but after severe predation by cats in early 1980s (see below), population was reduced to *c.* 70 in 1982 (Karl & Best 1982; Clout & Craig 1995; Powlesland *et al.* 1995; D.V. Merton). Sex-ratio heavily male-biased (see Social Organization). **Longevity** Believed to be long-lived. Oldest known bird, a male first captured in Fiordland in 1975, and aged as adult, was alive and in good health in 1998. Survival following independence is high: eight of nine juveniles that reached independence since 1981 survive in 1997. The survival rate of 60 translocated from Stewart I. between 1980 and 1992 has been high, despite the fact that all but three (one male, two females) were adults of unknown age when transferred; at least 47 of the original 60 still survive (78%); 44 are now at least 18 years old, and most are likely to be significantly older than this; all known birds are now radio-tagged, so deaths can be readily detected. On Little Barrier I., 16 of 22 birds released in 1982 known to have survived to 1997; the overall survival rate for the 16 years since 1982 averages 98.3% p.a. On Codfish I., the survival rate of translocated birds has been similarly high, >98% p.a.; 26 of the original 30 birds released there since 1987 are known to have survived to 1998, including all ten females. None of the 15 Kakapo known to be present in Fiordland in 1977 is known to have survived beyond 1987, and the species is now believed extinct in Fiordland (Merton 1989; Clout & Merton 1998).

Often killed by introduced mammalian carnivores, such as dogs, rats, mustelids, feral cats and Common Brushtail Possums; also adversely affected by competition from introduced herbivores (Merton 1976a,b, 1994; Atkinson 1978; Campbell 1978; Anderson 1981; Cassels 1984; King 1984; Best & Powlesland 1985; Merton 1989). Cats were introduced to Stewart I. in the 19th century. Soon after Kakapo were discovered on Stewart I., predation of adult birds by cats was clear: remains of Kakapo were found in six of 225 cat droppings collected 1977–79 (Karl & Best 1982); subsequently, corpses of 15 Kakapo killed by cats were found in 18 months during 1980–82 (Best & Powlesland 1985). The predation rate on adult radio-tagged Kakapo reached 56% p.a. in 1981–82 (Moorhouse & Powlesland 1991). Since the population of Kakapo on Stewart I. could not have withstood this level of predation for a century, when it had presumably coexisted with cats, the increased level of predation was likely because one or more individual cats had learnt to hunt Kakapo (Butler 1989). Predation apparently stopped soon after intensive cat control began on s. Stewart I. in 1982, and no cat-killed Kakapo were recorded after 1983, though cats continued to use the area inhabited by the surviving birds (Butler 1989). Formerly hunted for food by both Maori and Europeans. Kakapo skins were highly sought after by Maori for cloak-making. A Maori proverb states: '*You have a Kakapo cloak yet still complain of the cold!*' Populations now monitored daily by radio-telemetry (D.V. Merton).

MOVEMENTS Account prepared by D.V. Merton. Sedentary. Both sexes generally stay within individual, overlapping home-ranges of 15–50 ha for much of year (Merton *et al.* 1984; Moorhouse & Powlesland 1991; Powlesland *et al.* 1992).

In a single night, radio-tagged individuals known to have ascended more than 300 m in altitude or walked at least 5 km in a direct line (Best & Powlesland 1985). Individuals of either sex occasionally move up to several kilometres from home-ranges where they may remain for several days, weeks or even months (Best & Powlesland 1985). Such movement often, but not always, related to availability of abundant food, such as a heavy fruit-crop, or to breeding activity; possibly also related to climatic factors. In Fiordland, where home-ranges within subalpine zone were snow-covered for 3–4 months, each winter males usually remained within home-ranges, but at least occasionally descended to snow-free areas (D.V. Merton).

MALES: During Sept.–Dec. of some years, adult males visit traditional leks, which can entail movement of a few hundred metres (if court within or near male's home-range) or of several kilometres. In those years when intense courtship activity occurs, adult males move to lek some time between Oct. and early Jan. Each male occupies and defends a court for duration of courtship (Booming) period, which may begin any time between Nov. and early Jan., and end in late Mar. or early Apr.; timing and duration varies from season to season and was generally earliest in n. NZ (Merton *et al.* 1984; Powlesland *et al.* 1992). One radio-tagged male travelled more than 5 km from home-range to lek (D.V. Merton). FEMALES: Adults commonly move beyond their home-ranges between Dec. and Feb., particularly in those years when intense Booming occurs. Females also make brief (1–3 night) visits to leks in order to copulate.

While feeding young, one female on Stewart I. made two return trips per night to a grove of heavily fruiting trees 1 km from nest.

Little known of post-fledging dispersal and movements of juveniles. Juveniles remain in or close to natal home-range till *c.* 9 months old. One 14-month-old male was recaptured more than 5 km from natal home-range, and a 9-year-old female was recaptured *c.* 3 km from site where hatched. Being flightless and confined to offshore islands, surviving birds now physically restricted in movements.

Banding All surviving birds are banded; since 1993 most radio-tagged. First bird banded in 1975, an adult male from Fiordland, was alive in 1998, 23 years later (D.V. Merton).

FOOD Account prepared by D.V. Merton. Exclusively herbivorous; feed on leaves, twigs, bark, nectar, fruit, seeds, fern pinnae and rhizomes, and fungi (Haast 1861, 1864; Potts 1873; Henry 1895–1908; Best 1908; Pascoe 1957; Gray 1977; Best 1984; A. Grant; NZ DOC). Eat broad range of foods, many available only for short periods, with seasonal and annual variation in use of plant species and parts of plants eaten. Birds released on Maud I. underwent a period of adaptation and learning; the range and number of plant species exploited increased with time, and birds also adopted feeding regimes in harmony with seasonally abundant food that they had not previously encountered. Report of entire lizards in crop of one bird (von Hugel 1875) only exception to herbivory and now regarded as erroneous (D.V. Merton). **Behaviour** Solitary; forage alone, mainly within home-range. Occasionally move beyond home-range for a few days or up to a few weeks, to exploit locally abundant food; at such sources, may feed briefly in loose association with others. When feeding arboreally, silent, though periods of feeding usually interspersed with noisy movement of foliage and much wing-flapping when changing position. Foraging normally interspersed with long periods (up to 60 min) of inactivity. When supplementary foods provided on Little Barrier I. (see also below), birds learnt within 3 weeks to lift protective flaps to obtain food (Powlesland & Lloyd 1994). TIMES OF FEEDING: Normally nocturnal, though occasionally, especially individual females with dependent young, forage during daylight, at dawn or dusk. FORAGING SITES: Forage at all levels (see Habitat), including canopy of tall forest, but most foraging on or near ground. Skilled climbers and able to climb quickly into and through canopy. Use bill, powerful feet and long neck to climb and move from tree to tree through canopy. Use wings constantly for balance and support when climbing and foraging in trees. On Stewart I., readily scaled vertical tree-trunks and limbs, and foraged in crowns and outermost branches of trees at least 15 m high (Best 1984). Descend from higher to lower limb or from lower branches to ground by wing-assisted leaping or parachuting; wing-assisted leaps of 2–3 m at a steep downward angle <45° normal when foraging. On ground, often move between feeding sites in rapid jogging gait, along animal or human tracks when available. One bird travelled 5 km in one night; another made two return trips each night from its nest to a food source 1 km away, running at speed throughout each trip. METHODS OF FEEDING: Use bill as grubber to excavate subterranean foods, including roots, tubers, rhizomes and stolons. When roots of ferns grubbed out, leave fist-sized depression in ground; many square metres of *Lycopodium* or moss may be intensively grubbed in a single night. Usually browse foliage attached to plants. Blades of grass eaten from tip down; *Aciphylla* browsed at mid-blade so as to avoid thorny tips, which are left intact; the chewed, fibrous mid-sections soon bleach and remain attached to plant for many months. Snow-tussock *Chionochloa* and *Gahnia* tillers are stripped from plants and basal portion alone consumed. Seeds of grasses and tussock seed stripped by running bill up spikelet in scythe-like motion (Gray 1977). Berries and fruit, including most seeds, pulped in bill, though seeds of some fruits swallowed whole. Also use bill to remove bark to get to underlying tissues and sap of trees, such as rata *Metrosideros*, totara *Podocarpus* and shrubs such as Manuka *Leptospermum scoparium*. Use feet constantly to stabilize or hold food items, but rarely use feet to lift items to bill. Do not use feet to scratch or dig for food. SELECTION OF FOOD AND CHANGES IN DIET: Selective feeder. Species of plant and parts of plants eaten vary seasonally. Eat wide variety of seasonal foods, which may only be available for short periods or in intermittent years; well adapted for survival in an environment where pronounced fluctuations in food quality and availability occur (Merton 1994). On Stewart I., 1977–85, marked seasonal and annual variations in diet, as well as differences between male and female diets. When pollen and fruits available, usually eaten in preference to other items; increased proportions of fruit in diet reflect massive increase in fruit availability associated with masting events. During spring and summer, when new growth available, leaves form larger proportion of food eaten. Rhizomes important during autumn and winter, particularly in years when masting does not occur. On Stewart I., feeding patterns often inconsistent, even in areas of similar habitat at same time, indicating strong individual food preferences. This inconsistency of feeding pattern even more noticeable when short-lived foods of sporadic occurrence were heavily exploited at some sites but remained untouched at others (Best 1984). Similar individual food preferences recorded with provision of supplementary foods on Little Barrier I. (Powlesland & Lloyd 1994). In 1989, a program of providing food supplements was begun on Little Barrier I. to try to induce breeding; of 45 foods offered, two appeared not to be touched, 20 were tasted and rejected, and 23 were eaten regularly (mainly root vegetables, seed and nut kernels, and fleshy fruit). Six foods eaten in quantity by all birds in study and subsequently supplied nightly were Apples, kumara, kernels of Almonds, Brazil Nuts and Walnuts, and Sunflower seeds (Powlesland & Lloyd 1994). ADAPTATIONS FOR FEEDING: Sense of smell thought to be well developed and of importance in foraging (Best 1942); olfactory lobes of brain exceptionally well developed and at least some birds can locate foods by smell alone (J.C. Hagelin). When walking, birds adopt near-horizontal posture that brings lower rictal bristles of facial disc into contact with ground. Sensory perception may be important, not only when traversing unfamiliar terrain in the dark, but also when feeding at night on certain foods, such as *Aciphylla*, which have long rigid needle-like thorns. Sight considered poor, but have facial disc, like that of an owl, and eyes orient forward, providing some of binocular vision. Short powerful compressed bill and short broad thick tongue are adapted for browsing, crushing, grinding and extracting juices from fibrous plant tissues (Kirk *et al.* 1993). Use lower mandible and tongue to grind food against finely grooved upper mandible and palate. Foods compressed and ground, and usually only finely masticated material ingested. Alimentary tract typical of parrots, though vitelline diverticulum and caeca absent and, given bulky and fibrous diet, gizzard not as muscular as expected. The lack of muscular development of gizzard suggests that Kakapo rely on specialized tongue and palate and vigorous chewing to break coarse plant material into small fragments suitable for digestion (Kirk *et al.* 1993). Fibrous material is not ingested but ejected in form of characteristic kidney-shaped, tightly compressed pellets or balls called 'chews', which often remain attached to plant in which bird feeding or, more often, drop to ground beneath. Chews bleach and can remain intact for many months.

Detailed studies In FIORDLAND (plant cuticles and other tissues identified in >350 faeces from 42 locations, additional items identified from examination of feeding signs; Gray 1977); in total, ate 79 species of plants: FERNS: Unident. mean of 8% of cuticle content (range of 1–32%; 31 of the 42 locations); palea 204 (1–14; 4); annulus rings 4 (1–11; 5). MOSSES: 1 (1; 5). GYMNOSPERMS: Podocarpaceae: *Podocarpus nivalis* 14 (1–48; 15). MONOCOTYLEDONS: Agavaceae: *Phormium cookianum* 1 (1; 1); Cyperaceae: *Carex* 8 (1–24; 4); Liliaceae: *Astelia* 2 (1–9; 5); *Astelia* scales 2 (1–7; 6); Poaceae: Unident. grass 3 (1–9; 15). DICOTYLEDONS: Apiaceae: *Aciphylla crenulata* 1 (1–2; 2); *Anisotome haastii* 12 (1–20; 20); Araliaceae: *Pseudopanax colensoi* 8 (8; 1); Asteraceae: *Celmesia* 2 (1–3; 3); *Olearia colensoi* 1 (1–2; 2); Epacridaceae: *Dracophyllum* 6 (1–15; 8); Ericaceae: *Gaultheria* 5 (1–9; 3); Fagaceae: *Nothofagus menziesii* 14 (3–31; 6); Gunneraceae: *Gunnera monoica* 2 (2; 1); Hymenophyllaceae: *Hymenophyllum* 8 (1–41; 12); Rubiaceae: *Coprosma* 2 (1–3; 2); Scrophulariaceae: *Hebe* 2 (1–4; 3). Unknown cuticles 8 (1–37; 36); miscellaneous tissue 62 (29–97; 42); exocarp 2 (1–6; 3); petiole 2 (1–7; 9); tomentum 10 (1–22; 8); trichomes 2 (1–7; 10); seed fragments 3 (3; 1). On Maud I., an additional 28 plant species also identified from feeding signs and cuticle analysis (for details see Gray 1977).

On STEWART I. (plant cuticles identified from *c.* 400 faecal samples, 1977–85; A. Grant); food species eaten throughout year include: **Plants** FERNS: Unident. reproductive fronds; Blechnaceae: *Blechnum* rhizomes, lvs; Lycopodiaceae: *Lycopodium* rhizomes. GYMNOSPERMS: Podocarpaceae: *Dacrydium* pollen; *D. biforme* fru.; *D. intermedium* fru.; *D. cupressinum* fru. MONOCOTYLEDONS: Cyperaceae: *Gahnia procera* lvs. DICOTYLEDONS: Asteraceae: *Olearia colensoi* lvs; Epacridaceae: *Cyathodes juniperina* fru.; *Dracophyllum longifolium* lvs; Myrtaceae: *Leptospermum scoparium* lvs, fru.; *Meterosideros umbellata* nectar; Rubiaceae: *Coprosma* fru.

Other records Plants Leaves, twigs, bark, nectar, fruit, seeds, fern pinnae, rhizomes, fungi[1,2,3,4,5,7,9]. MOSSES: Unident. shoots, leaves[10]. GYMNOSPERMS: Podocarpaceae: *Dacrydium biforme* fru.[8]; *Podocarpus* sap[12]; *P. hallii* lvs[11]. MONOCOTYLEDONS: Agavaceae: *Cordyline* fru.[6]; *C. indivisa* fru.[10]; *Phormium* sds[6,11]; Poaceae: *Danthonia* sh.[6], lvs[11]. DICOTYLEDONS: Araliaceae: *Neopanax arboreum* fru.[6]; *Pseudopanax* lvs[11]; *Schefflera digitata* fru.[6]; Coriariaceae: *Coriaria* fru.[10]; *C. arborea* fru.[6]; Elaeocarpaceae: *Elaeocarpus dentatus* fru.[6,10]; Epacridaceae: *Pentachondra pumila* fru.[11]; Fabaceae: *Carmichaelia* lvs[6,10]; Lauraceae: *Beilschmiedia tawa* fru.[6,10]; Myrtaceae: *Leptospermum scoparium* lvs, fru.[8]; *Meterosideros umbellata* nectar[10]; Onagraceae: *Fuchsia exorticata* fru.[6]. (REFERENCES: Haast [1] 1861, [2] 1864; [3] Potts 1873; [4] Henry 1895–1908; [5] Best 1908; [6] Williams 1956; [7] Pascoe 1957; [8] Best 1984; [9] Forshaw & Cooper 1989; [10] Oliver; [11] A. Grant; [12] M. Merton.)

Young Diet of nestlings and fledgelings poorly known. Nestlings fed on vegetable matter by female by direct regurgitation. Young continue to receive some food from female for at least 3 months after fledging. One female that raised two nestlings on Stewart I. in 1981 fed heavily on ripe fruit of Rimu *Dacrydium cupressinum* throughout nestling phase (Powlesland *et al.* 1992). Ripe Rimu fruit has lipid value of *c.* 25–30% and protein level of *c.* 15%. Nestlings receive *c.* 10% of their bodyweight in food per feed. During 1997 breeding event on Codfish I., females raising young fed heavily on sheath-bases of *Dracophyllum longifolium*, in addition to up to 400 g nuts provided nightly as a supplement (D.V. Merton).

Intake Survive for long periods (but do not breed) on diets of low quality. Have exceptionally low field metabolic rate (D.M. Bryant). At times when foods rich in fats and energy abundant (e.g. during masting of certain plants or when protein- or lipid-rich supplements available), store considerable energy in form of body-fat; at such times weight increases of 40–100% are normal (Powlesland & Lloyd 1994; D.V. Merton). Both sexes undergo large periodic and seasonal shifts in weight, resulting from storage and mobilization of massive energy reserves: magnitude of such changes probably greater than that of any other terrestrial bird (Merton 1994). On Little Barrier I., supplementary foods taken nightly during winter, but less often by both sexes in summer, with frequency of female visits decreasing in Sept. and male visits declining in Nov. (Powlesland & Lloyd 1994).

SOCIAL ORGANIZATION Account prepared by D.V. Merton. Unless stated, all information from published (Merton 1975; Merton *et al.* 1984; Powlesland *et al.* 1992) and unpublished studies by D.V. Merton and colleagues. Both sexes solitary except during courtship, when males congregate and display at traditional leks and females visit for up to several nights. Reports of gregarious behaviour, including chasing, fighting and noisy vocal interaction (Buller 1877; Henry 1895–1908, 1903; Best 1942; Pascoe 1957) no doubt refer to lekking behaviour.

Bonds Lek mating system and so no permanent bonds between sexes. Females visit lek for either a few hours and copulate with only one male; once visited for up to five nights and copulated with two or more males. Sex-ratio male-biased, probably as result of differential predation of females, particularly by mustelids and cats; in translocated population on Little Barrier I. where mustelids and cats absent, mortality of males appears higher than that of females, partly because males fight and occasionally kill one another at leks. Some evidence that sex-ratio male-biased in pre-historic times (Trewick 1997). Age of first breeding not known; males appear to reach sexual maturity at 5–6 years old, females when *c.* 9 years old. Two 4-year-old males visited lek at end of booming season and tentatively boomed on several nights; when 5 years old both maintained courts and began booming and displaying sporadically at lek; one of three known-age females bred at 9 years old, another at 11 years and the third, now 5 years old, has not yet attempted to breed (D.V. Merton). **Parental care** Performed solely by female (see Breeding). Young remain within or near natal home-range, and at least occasionally roost with mother, for at least 6 months after fledging. Receive at least some food from female for at least 3 months (Merton 1994).

Breeding dispersion Females nest solitarily within home-range. Home-range of female between 30 and 50 ha and can overlap that of other females or males; tend to be at lower elevation than those of males. Nests of neighbouring females can be 400–1500 m apart. Two nests on Stewart I. were *c.* 600 m and 1200 m from nearest occupied lek.

Roosting During day. Usually roost solitarily; occasionally two or more adult females roost in loose association; adult males and adults of opposite sex not known to roost together, except females visiting leks sometimes roost within 50 m of a male. Reports of up to six birds roosting together (Henry 1895–1908; Best 1942; Gould) likely to be of family parties of female and 2–3 juveniles, or groups of juveniles. Usually roost within home-range. Lekking males roost within *c.* 200 m of their court.

Usually roost on ground in dense vegetation or in natural cavity, such as a tree-trunk or hole in ground; sometimes roost in shrubs or trees, usually <2–3 m above ground. Individuals often display preference for roosting above or on ground. Prefer dark dry sheltered sites large enough to allow bird to move and turn. Roosting sites can be used repeatedly for many days or weeks; some used regularly or irregularly for many years. No obvious difference between sexes in choice of roosting sites or in roosting habits. After prolonged cold wet weather, occasionally roost in direct sunlight in low scrub or in crowns of low trees. For 1–2 months after fledging, juveniles unable to climb well and roost entirely on or very near to ground. When not breeding, normally enter roost *c.* 1 h before sunrise and leave *c.* 1 h after sunset; thus roost between *c.* 07:00 and 18:00 during winter and *c.* 05:00 and 22:00 during summer. Females incubating or with nestlings also often leave nests within *c.* 1 h of sunset and, except when food in short supply, return before sunrise; breeding females with nestlings 1–2 months old or without access to abundant food often leave nest to forage in late afternoon and continue foraging after daylight in early morning. Lekking males roost from 05:30–07:00 to 21:30–23:00, but are occasionally active for short periods by day. At times of low light-intensity (such as when foggy or heavily overcast) courtship activity sometimes continues well into daylight hours. Adults and most juveniles roost in standing, nearly horizontal, posture, with head and bill resting on back above one wing. Nestlings and fledgelings often sleep with head resting on ground in front of body, or lie on side with legs outstretched and head lying on ground (D.V. Merton).

SOCIAL BEHAVIOUR Account prepared by D.V. Merton. Unless stated, all information from published (Merton 1975; Merton *et al.* 1984; Powlesland *et al.* 1992) and unpublished studies by D.V. Merton and colleagues. Main studies are of behaviour at leks in Fiordland, especially courtship behaviour (Merton 1975; Merton *et al.* 1984; Morris & Smith 1995); at nests on Little Barrier and Codfish Is (G.P. Elliott, P. Jansen & D.V. Merton); and first 5 years of life of one captive female (Climo & Ballance 1997). Details of behaviour not well known. Difficult to study because rare, nocturnal, cryptically coloured, solitary, shy, inhabit dense cover in remote and inhospitable country and, except during Booming Displays, seldom call. Highly unsociable; if confined together, will fight and kill one another (Henry 1895–1908, 1903). Have range of visual displays, most of which poorly known but usually observed only in association with lekking. When displaying on lek, often carry objects in bill and whet bill; this behaviour sometimes occurs elsewhere (Climo & Ballance 1997); function not known. Partly hand-raised, captive subadult female observed to skip, hop, often flap wings, run and climb, jump from trees and pick up and throw sticks and leaves in apparent play behaviour (G.A. Climo). When curious about unfamiliar objects or people within enclosure, captive birds first investigate from safe distance, moving quietly with attention focused on object of interest; at such times remain alert and any distraction may cause bird to retreat where it will maintain watch from distant cover before investigating again. Displacement activity includes mock-feeding and grubbing, pulling at vegetation, picking up, and carrying and biting or tossing of twigs and leaves, while partly raising or flapping wings. Three observations of non-breeding females moving hundreds of metres from home-range and remaining 1–2 nights within *c.* 25 m of incubating females. Have not been observed to bathe.

Agonistic behaviour During pre-booming period at lek, males engage in aggressive behaviour, including chasing, screeching and mock and actual fighting; such behaviour continues throughout booming period but at reduced level. Outside breeding season, maintain individual distance by advertising location with loud harsh Skraak Calls given infrequently at night. THREAT DISPLAY: Face opponent, stand erect and raise and hold wings over back till wings almost touching; raise feathers of head and neck and hold neck outstretched with bill partly open, while making low drawn-out growling call. DEFENCE: Stand upright facing opponent with one foot raised ready to strike downward. Bite is main defence, but claws are used during physical conflict. SCREECH-CROWING: In response to high-frequency radio sounds from nearby hide, one male gave series of eight loud screeches interspersed with vigorous, noisy wing-flapping. HUMMING and BILL-CLICKING: Seen to be performed by male on lek; audible only 2–3 m away; probably functions in low-intensity aggression. **Alarm** Usually freeze when danger threatens, or try to run away.

Sexual behaviour Adult males in breeding condition congregate in loose association at traditional leks, typically on ridge-tops, to display at night to attract females. Each displaying male maintains and defends a court or track-and-bowl system, consisting of a series of excavated depressions or bowls, *c.* 60 cm in diameter and *c.* 10 cm deep, linked by tracks *c.* 50 cm wide which are kept clear by bird. Courts can extend for more than 50 m along the crest of ridges or occupy an area 10–20 m in diameter on a hilltop. Courts of neighbouring males separated by 15 m to several hundred metres; variation in dispersion of courts appears related to topography, depletion of population by introduced predators, and possibly a dominance hierarchy. In Fiordland and on Stewart I., leks contained up to 50 associated courts extending over several square kilometres. BOOMING: At lek, males utter low, resonant Booming call, which can be heard up to 5 km away. Standing in or near a bowl, male progressively lowers head and inflates chest while booming quietly, then, at maximum inflation, begins to boom loudly and rhythmically (Fig. 1) (see Voice). While Booming, male holds head low and rhythmic muscular contractions of body can be seen, particularly in lower thorax; muscle contractions cause carpals to flick out immediately after each contraction; at first, wing-tips crossed over uppertail-coverts, but droop lower with each successive Boom and end beneath tail. After Booming sequence, caller stands alert, upright and motionless for 20–30 s before repeating sequence. Booming usually begins *c.* 1 h after dark and stops *c.* 1 h before first light, roughly 7.5–8.5 h each night, but individuals have been recorded Booming continuously for up to 17 h during foggy weather. Neighbouring males often duet. Combined Booming of numerous males can

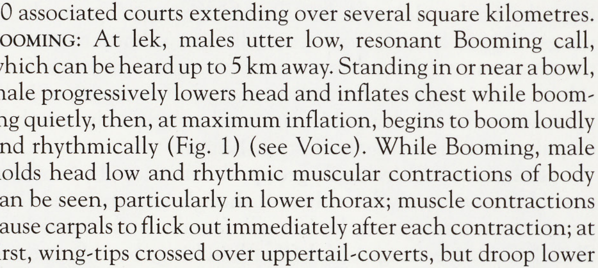


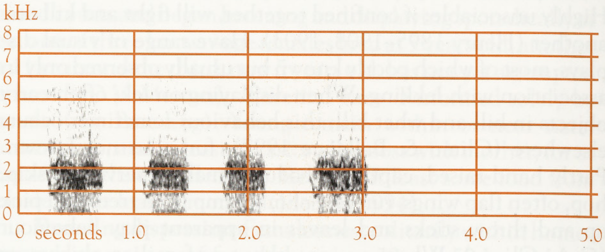
Figure 1 Booming

sound like distant thunder (Buller 1877; Deslongchamps 1880; Henry 1895–1908; see Voice for further details). Booming serves to advertise presence and general location of lek, as well as to stimulate and synchronize sexual activity in both male and female. Males also utter high-pitched, directional Chinging call in sequence similar to that of Booming; advertises precise location of individual males on lek, and probably guides females to specific males. Skraak Call also often uttered at lek, especially during early weeks of display; probably functions in territorial defence and establishment of hierarchy and possibly also in advertising at population and individual levels. Most males occupy a single court, which they maintain and defend season after season; occasionally abandon traditional sites and take over or develop new courts. Males remain on lek for 3–4 months in years when courtship occurs, though little or no courtship activity occurs in some years. Onset of intense display and Booming varies from late Nov. to early Jan.; usually stops in Mar. or early Apr.; copulation occurs in Jan. and Feb. Two 4-year-old males first visited lek at end of Booming season and tentatively Boomed on several nights; at 5 years old they irregularly maintained courts and began Booming and displaying at lek. Subsequently the intensity and duration of their display was identical to that of adult males. **Copulation** Copulation and associated behaviour with a female has not been observed. In response to surrogate females, males on courts observed to perform elaborate ritualized displays including side-to-side rocking, walking backwards while slowly raising and lowering fully extended wings, flapping wings vigorously and uttering various characteristic calls. Copulation with surrogate females has been induced and occurs unprovoked with objects near courts: male crouches on object (equivalent to back of a female) with head held high, tail depressed and wings held partly open by sides and drooping almost to ground; then maintains rhythmic motion involving swaying body from side to side in synchrony with pronounced swinging of half-open wings and rapid, audible panting through partly open bill. Copulation with surrogates lasts 2–14 min.

Relations within family group Vocalizations by female to nestlings have rarely been heard, though known to use low grunt. Soon after young leave nest, female often utters loud Skraak Call. Nestlings vocal from hatching; beg by uttering rapidly repeated grunting. Female often preens nestlings, particularly once feathers sprout. Hostility between siblings or between adults and young not observed. **Anti-predator responses of young** One nestling observed to lunge repeatedly at rat in nest (Rasch 1989) but another nestling showed no apparent reaction to rats. After fledging, young remain motionless when danger threatens. **Parental anti-predator strategies** Incubating female observed to attack Cook's Petrel *Pterodroma cookii* nesting within same cavity: rushed off nest with bill open, neck outstretched, screeching loudly and physically attacking if able to; other Cook's Petrels found dead in or near Kakapo nests probably killed by Kakapo. Female does not cover eggs or young while off nest at night. Females do not perform any display to distract predators from nest.

VOICE Account prepared by D.V. Merton. No detailed studies. Calls associated with lekking behaviour described by Merton *et al.* (1984; see also NZRD), Powlesland *et al.* (1992), and these and other calls also described by Morris & Smith (1995) and Heather & Robertson (1996). Repertoire varied. Seldom call except on lek (see Social Behaviour) when extraordinary Booming call of male most characteristic of vocalizations. Also give a variety of strange squeals, shrieks, growls and a hoarse croak (Henry 1903; Merton 1975; Forshaw & Cooper 1989; NZRD). Outside breeding season, calls heard when birds close together at sources of food or sometimes induced at night by brief loud sounds such as avalanche, earthquake, thunder, a rifle shot or another animal. Booming occurs in most, but not every year. Intense Booming occurs at 2–5-year intervals. Booming continues for 2–4 months, beginning late Nov. to early Jan. and finishing about Apr. It starts *c.* 1 h after dark, and stops *c.* 1 h before dawn; it continues for 6–8 h/night but sometimes, such as in foggy weather, will continue for up to 17 h (Merton *et al.* 1984). Males in groups Boom for longer each night and continue to Boom for longer during a season than do solitary males (Merton 1976b). Only males give Booming and Ching; otherwise female said to have similar repertoire to male. However, available descriptions and examples of call indicate most only given by male or heard from male (see below). Individual and regional variations in Booming calls have been reported (Merton 1976b): Booming of males from Stewart I. more rapid than that from Fiordland. In Sinbad Gully, Milford Sound, Fiordland, males consistently gave double booms. Also, Chinging characteristic of males from Stewart I. and only once heard from birds from NI or SI; in Tutoko Valley, Fiordland, during observation of males displaying on lek in Feb. 1976, one male was heard to give two brief sequences of Chinging (D.V. Merton). Call in response to taped calls. Mimicry not reported. NON-VOCAL SOUNDS: BILL-CLICKING: Mechanical clicking produced by drawing lower mandible across tip of upper mandible. Bill-clicking repeated at 5–10 s intervals. Given at courts, interspersed with Humming (q.v.). Wing-flapping; see Screech, in adult male, below. Audible panting by male when copulating (Merton 1976a).

Adult SKRAAK CALL: A loud high-pitched *skraak* repeated up to four times in rapid succession (sonagram **A**); generally, first call loudest and highest in pitch with rest trailing off (this not shown in example available for sonagram). Given by males on lek, particularly early in courtship period when possession of courts and establishment of dominance important. An identical call seems to be made by both sexes from within home-range throughout year, often in response to call of neighbouring bird or other loud noise. Probably indicates position and functions in territorial defence to maintain individual distance and,



A D. V. Merton; Esperance Valley, Fiordland, NZ, Mar. 1974; priv.

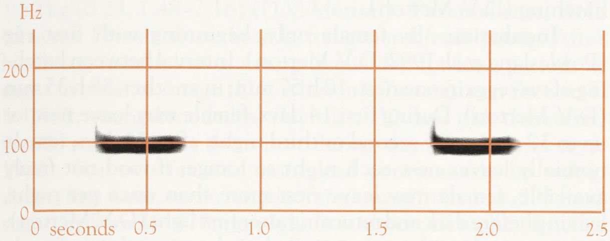
Plate 29

Kea *Nestor notabilis* (page 613)
1 Adult male; 2 Adult female; 3 Juvenile female; 4 Immature male; 5, 6 Adult

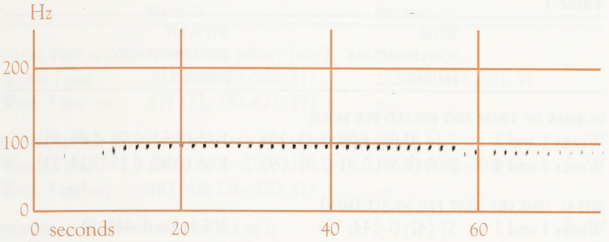
Kaka *Nestor meridionalis* (page 623)
NOMINATE *MERIDIONALIS*: 7–9 Adult
SUBSPECIES *SEPTENTRIONALIS*: 10 Adult; 11 Juvenile; 12 Adult

possibly, as threat; may also serve to deter intruders. Most commonly heard call outside booming periods. Most birds make this call at least once each night, commonly soon after dark when leaving roost. One hand-reared female first gave this call when *c.* 8 month old (Climo & Ballance 1997). Skraak Call of subadults distinctively higher pitched and shorter than that of adults. **Other calls** Throughout year, utter brief isolated calls: hoarse possum-like hisses; screeches; pig-like squeals and grunts; duck-like *wark* sounds; and donkey-like brays. These sounds often heard when birds close together by locally abundant food or in response to brief loud sounds (see above). When handled, males generally silent, though occasionally give low drawn-out Growl (see below); females and subadults usually give low complaining vibrant croaks (see Distress Call).

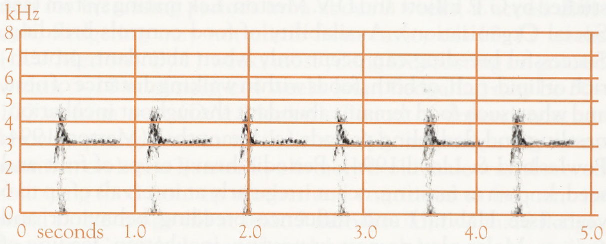
Adult male BOOMING: Very low frequency (generally <100 Hz), foghorn-like, resonant and non-directional boom (two consecutive booms shown in sonagram **B**) given from or near court on lek (see Social Behaviour). In Booming sequence, grossly inflate air-sacs in thoracic region, emitting 3–4 quiet measured grunts on descending scale at *c.* 2 s intervals. At maximum inflation, grunts give way to soft booms with increasing amplitude and reaching maximum intensity after 6–8 booms; booms then repeated 15–20 times at 2 s intervals, after which they decrease in amplitude over further 10–20 booms. Example of complete sequence shown in sonagram **C**. Only loud booms audible at >50 m; in ideal conditions, loud booms audible up to 5 km. Bird stands upright and motionless at end of sequence for 20–30 s before repeating sequence. During those seasons when Booming intense, each male Booms at rate of *c.* 1500 booms/h throughout hours of darkness (roughly 7.5–8.5 h/night) for 3–4 months. Occasionally Boom during day, even in clear weather, in response to disturbance, such as loud noise or person approaching roosting male. On Little Barrier I., attempts at Booming heard at end of season from two 4-year-old males in 1995; calls hardly recognizable as Booming, being significantly higher in pitch, with elements more rapidly delivered (at *c.* 0.5 s intervals) and in shorter phrases. Boom functions to synchronize breeding activity, and to attract females to lek. CHING: High-pitched metallic nasal *ching* (sonagram **D**). Often alternate sequences of Chinging and Booming. Highly directional call of *c.* 1 s duration, repeated at *c.* 1 s intervals, in sequences of 20–50 calls. Sequences of similar structure and duration to Booming, but tempo more rapid. Under ideal conditions, audible up to 1 km. Given at night from in or near court as part of lekking behaviour. May function to assist female to locate calling male after being attracted to lek by Booming (Merton *et al.* 1984; Powlesland *et al.* 1992). HUMMING: Very soft and low-frequency humming sound, audible only within 2–3 m. Humming given at court, and observed only in association with Bill-clicking (see Non-vocal sounds). May continue for several minutes. Function not known. SCREECH: Given during pre-booming period at lek while engaged in aggressive behaviour, such as chasing and mock and actual fighting. SCREECH-CROWING: Heard only once, from one lekking male on its court in Fiordland, late in booming season. Bird screeched loudly, then vigorously and noisily flapped its wings, paused, then repeated sequence eight times; Screech-crowing and associated wing-flapping resembled in structure and timing that of a crowing rooster. Given in response to high-frequency radio sounds from a nearby hide. GROWL: Long drawn-out growl. Given as a threat call and used to drive away intruders that are very close. Also given in distress, e.g. when handled.



B D. V. Merton; Tutoko Valley Fiordland, NZ, Jan. 1976; priv.



C D. V. Merton; Tutoko Valley, Fiordland, NZ, Jan. 1976; priv.



D D. V. Merton; Stewart I., NZ, Feb. 1978; priv.

Adult female Not known to Hum or Screech. DISTRESS CALL: Give series of complaining, long drawn-out, vibrant croak-like calls when handled and occasionally when approached. COUGH: Occasionally give cough-like calls when foraging; described as hoarse cough by Henry (1903).

Young Account mostly based on information supplied by D.V. Merton. Vocal from hatching. FOOD-BEGGING CALL: Monosyllabic grunt-like purring call, given constantly; pitch becomes lower with age. In one hand-reared female, call given in anticipation of being fed described as loud purring (Sibley 1994). Most intense when chick soliciting food and when feeding. By 8 weeks old, call resembles grunt of pig and can often be heard up to several metres from nest. By fledging, call has slowed, and then of *c.* 1 s duration and repeated at *c.* 1 s intervals. From 3 to 7 months old, partly hand-reared female and male gave grunting call when foraging, especially in presence of humans; at *c.* 8 months old, female began to give Skraak Call (Climo & Ballance 1997). DISTRESS CALL: Chicks <2 weeks old appear not to have distress or alarm calls and are silent when approached. Older nestlings have a low-amplitude drawn-out croaking growl similar to Distress Call of female. Fledgelings can often be located from some distance by their constant grunting and, when approached, their croaking and growl-like calls.

Plate 30

Kakapo *Strigops habroptilus* (page 633)
1–3 Adult male; 4 Juvenile female

BREEDING Account prepared by D.V. Merton. Well known. Several detailed studies: early studies by Henry (1895–1908, 1903); long-term studies in Fiordland and on Stewart and Little Barrier Is (Merton *et al.* 1984; Powlesland *et al.* 1992; Powlesland & Lloyd 1994); 1993 breeding event on Little Barrier I. studied by Greene (1993); and 1997 breeding event on Codfish I. studied by G.P. Elliott and D.V. Merton. Lek mating system (see Social Organization). Availability of food controls breeding. Successful breeding can occur only when abundant, protein-rich or lipid-rich, or both, foods within walking distance of nest, and when such food remains abundant throughout incubation, nestling and fledgeling periods (*c.* 8 months) (Merton 1994; Powlesland & Lloyd 1994). Periodic heavy crops of fruit and seed, known as masting, occur irregularly at intervals of up to 6 years (see Habitat) and influence breeding behaviour and success. Males play no part in nesting, incubation, feeding of females, or raising young (Merton *et al.* 1984; Powlesland *et al.* 1992).

Season Laying, late Jan. to mid-Mar.; fledging, late May to mid-June; laying generally confined to 2–3-week period in any locality in a season but may vary from season to season; on Little Barrier I., laying appears to be consistently earlier than on Codfish I. or Stewart I. (*c.*1100 km farther S) (D.V. Merton).

Site In natural cavities; at ground-level. In small caves, under boulders, in holes in banks or rotten trees, under thick vegetation; sites lack screening material at entrance; located within several hundred metres of prime feeding areas and up to several kilometres from leks; two nests on Stewart I., 600 and 1200 m from nearest male arena (Powlesland *et al.* 1992; D.V. Merton). Of 25 nests found since 1980, 10 (40%) were in standing tree-stumps, 4 (16%) in fallen tree-trunks, 9 (36%) in caves or holes in ground and 2 (8%) under grass-tussock or other dense ground-cover (Powlesland *et al.* 1992; D.V. Merton). On Stewart I., two females that nested in successive seasons (1981 and 1985) used different sites, 500 m and 1500 m from previous site (Powlesland *et al.* 1992); one nest-site on Little Barrier I. re-used by same female in 1993 and 1995 (D.V. Merton). Altitude of 25 nests from Stewart, Codfish and Little Barrier Is, 150–400 m asl (D.V. Merton). Female selects site, using an existing cavity (D.V. Merton). MEASUREMENTS: Distance from entrance to nest-bowl, 50 cm (*c.* 20–400+) (D.V. Merton). Of 25 nests, contents of 10 (40%) nests visible from at least 2 m away; entrance of 4 (16%) nests had northerly aspect; 6 (24%) southerly; 6 (24%) easterly and 9 (36%) westerly (D.V. Merton). Nest-platform of six nests on Stewart I. within 20 cm of entrance to cavity; contents of four nests visible 3 m from entrance (Powlesland *et al.* 1992).

Nest, Materials Nest in natural cavity, at or below ground-level (Powlesland *et al.* 1992; Merton 1994). Eggs laid in shallow (<5 cm deep) depression formed in level but deep, dry and well-aerated platform of nesting material, which is constantly worked by female, thus altering shape and position of depression. Egg-platform made from materials on site, including dry rotted wood, bark, wood-chips, soil, peat, clay, and dry leaves; loose bark and decayed wood may be stripped from interior of cavity and added to nest; also crush and break up larger pieces of soil, peat and wood. No material carried to nest. During incubation and nestling stages, female grubs and digs deeply into and turns material of nesting platform, with bill, to a depth of 10 cm or more, at least every few hours day and night. Female also chews and clips coarser items of substrate as well as adding material she strips from walls and roof of chamber. Contents of nest are also constantly moved within cavity, often moving 5–10 cm about once every hour, often in clockwise direction (D.V. Merton). MEASUREMENTS (cm): Diameter of nest-cavity, *c.* 50 (40–200+; 25); height of cavity, *c.* 40 (30–100+; 25) (D.V. Merton). On Stewart I., diameter of six depressions, 250–300, and depth, 2–5 (Powlesland *et al.* 1992).

Eggs Ovate; finely granular; white (Oliver; NZRD). Small relative to female body-weight; each egg 2–3% of female body-weight; a clutch of three, 7–9% of female body-weight (D.V. Merton). MEASUREMENTS: 50.5 (3.74; 18) × 37.2 (1.18; 21); 50.3 (1.81; 46.3–54.0; 29) × 38.1 (0.82; 36.3–39.8) (D.V. Merton); six undamaged eggs, 50.3 (1.13; 48.5–51.8) × 37.9 (0.31; 37.5–38.4) (Powlesland *et al.* 1992). WEIGHT: 35.8 (2.39; 31.6–38.8; 16); a clutch of three incubated for *c.* 16 days, 38.75 (38.25–38.75) (D.V. Merton); a clutch of four infertile eggs removed from a nest after being incubated for 6–7 weeks, 32.8 (30.9–33.7) (Body & Powlesland 1990).

Clutch-size Mean 2.2 (1–4; 25): C/1 × 6, C/2 × 9, C/3 × 9, C/4 × 1; no seasonal or geographical variation (D.V. Merton).

Laying From hatching dates of eggs in two nests: eggs laid at intervals of *c.* 24 h; second eggs in two 2-egg clutches under continuous surveillance hatched within 40 h of first eggs hatching (D.V. Merton).

Incubation By female only, beginning with first egg (Powlesland *et al.* 1992; D.V. Merton). Interval between hatching of two eggs in one nest, 10 h 57 min; in another, 38 h 35 min (D.V. Merton). During first 14 days, female may leave nest for up to 30 min every second or third night; after 14 days, female normally leaves nest each night to forage; if food not freely available, female may leave nest more than once per night, leaving before dark and returning after first light (D.V. Merton). Data on number of times egg rolled per hour, total time female spent off nest per night and maximum time spent off nest per foraging trip for females during incubation period, with and without supplementary feeding, in Table 1. For one female on Stewart I.: average time away from nest per night, 108 min (60–165; 14); increased during incubation from 73 min (60–90; 4) during first 5 days to 139 min (105–165; 4) in last week (Powlesland *et al.* 1992). Will accept foster eggs and artificial eggs of similar size and colour to their own; one incubated a sweet potato placed as food near nest (D.V. Merton). INCUBATION PERIOD: 25 days (n=1) (Powlesland *et al.* 1992); *c.* 30 days; addled clutches may be incubated more than 6 weeks (D.V. Merton). Do not remove eggshells from nest; females chew fragments of eggshell; within 2–3 days, shell fragments reduced in size and have been incorporated into nesting material, and some may be ingested (D.V. Merton).

Table 1

	WITH SUPPLEMENTARY FEEDING	WITHOUT SUPPLEMENTARY FEEDING
NUMBER OF TIMES EGG ROLLED PER HOUR		
Weeks 1 and 2	2.14 (0.68; 1.08–3.15; 19)	1.45 (0.52; 0.78–2.08; 9)
Weeks 3 and 4	2.00 (0.55; 0.91–2.95; 69)	1.66 (0.82; 0.25–3.13; 21)
TOTAL TIME OFF NEST PER NIGHT (MIN)		
Weeks 1 and 2	57 (41; 0–144; 19)	207 (138; 0–440; 9)
Weeks 3 and 4	74 (62; 0–304; 70)	229 (262; 0–913; 22)
MAXIMUM TIME OFF NEST PER FORAGING TRIP (MIN)		
Weeks 1 and 2	50 (38; 0–109; 19)	174 (128; 0–440; 9)
Weeks 3 and 4	67 (56; 0–304; 70)	176 (205; 0–727; 21)

Young Altricial, nidicolous. At hatching, blind and totally helpless, with moderate covering of fine white down (D.V. Merton). Egg-tooth persists for 12 days; at 14–16 days, eyes open; at 18–20 days, a relatively dense coating of greyish second down replaces white down; at *c*. 24 days, quills of secondaries and greater upperwing-coverts appear, emerging at *c*. 29 days; at *c*. 28 days, primaries, contour-feathers, and feathers of facial disc erupt from quills; at *c*. 35 days, quills of rectrices appear. Almost fully feathered at fledging, though tail and wings noticeably short and tufts of down adhere to crown and flanks (D.V. Merton). **Growth** Weight at hatching, *c*. 35 g. Approximate weight of three male, parent-raised chicks from Stewart I. (from growth-curves) (D.V. Merton): at 20 days, 447 g (380–520); 40 days, 1320 g (1260–1380); 60 days, 1787 g (1640–1880); 80 days, 1867 g (1720–1940); 100 days, 2013 g (1900–2110). For a male and female chick in same brood: weight at fledging (*c*. 10 weeks), 2.16 and 1.68 kg; at *c*. 12 weeks, 2.35 and 1.74 kg (Powlesland *et al*. 1992). Growth and weight-gain rapid till *c*. 8 weeks old, when it slows, and may plateau at *c*. 10 weeks; if food not limiting, weight may continue to increase till 14–16 weeks old; fledging weights vary with sex and availability of food; usually equal to or exceed normal weight of adult female (D.V. Merton); fledging weight for seven males at *c*. 10 weeks, 1.80 kg (0.23; 1.48–2.16) (D.V. Merton). **Parental care, Role of sexes** Female alone broods, forages and feeds young. After hatching, female leaves young unguarded for long periods at night in order to forage (D.V. Merton). Two nests on Stewart I. in 1981: young brooded by day till *c*. 30 days old; thereafter, female roosted away from nest during day (Powlesland *et al*. 1992). For two females monitored continuously by video: during first week, mean length of time away from nest, 305 min/night; by 5 weeks, 478min/night (i.e. almost all night); females remained in nest during day up till fledging (D.V. Merton). For total time female spent off nest per night, maximum time spent off nest per foraging trip and number of times young fed per hour during nestling period, for females with and without supplementary feeding, see Table 2. Female feeds young by regurgitation, bill to bill (D.V. Merton). For two nests on Stewart I.: during first 5 weeks, young fed and brooded twice per night; brooded throughout day and fed 4–6 times; at 3–5 weeks, female returned at about 23:00 and 02:00, with visits lasting 10–40 min; at 8–10 weeks, female spends day away from nest; young fed 1–2 times per night and again at dawn; for one female, feeding sessions consisted of several regurgitations of *c*. 20 s duration, with 2–3 s between each (Powlesland *et al*. 1992).

Table 2

	WITH SUPPLEMENTARY FEEDING	WITHOUT SUPPLEMENTARY FEEDING
TOTAL TIME SPENT OFF NEST PER NIGHT (MIN)		
Weeks 1 and 2	303 (158; 29–565; 31)	222 (50; 156–291; 9)
Week 3 and on	475 (73; 350–671; 27)	–
MAXIMUM TIME SPENT OFF NEST PER FORAGING TRIP (MIN)		
Weeks 1 and 2	150 (65; 29–290; 31)	125 (39; 85–207; 9)
Week 3 and on	183 (48; 116–320; 31)	–
NUMBER OF TIMES YOUNG FED PER 24 H		
Weeks 1 and 2	23 (9; 10–50; 31)	21 (5; 15–33; 9)
Week 3 and on	19 (11; 8–53; 26)	–
TOTAL TIME PER 24 H SPENT FEEDING YOUNG (MIN)		
Weeks 1 and 2	120 (38; 57–192; 31)	69 (18; 27–84; 9)
Week 3 and on	132 (52; 76–242; 27)	–

Young defecate round periphery of nest; droppings desiccate quickly; constant digging of nest-substrate by female results in many droppings being incorporated into nest; brushing action of female's tail as she turns her body in nest serves to spread accumulations of droppings from area round nest (D.V. Merton).

Fledging to independence FLEDGING PERIOD: *c*. 10 weeks; fledging often protracted; young may move a few metres from nest for increasing periods from about 9 weeks; if access difficult, fledgeling may not climb from cavity till 10–12 weeks (D.V. Merton). By 11 weeks most young are roosting on ground within 5–10 m of nest; c. 4 weeks later, fledgeling may be 50–100 m from nest (D.V. Merton). Period of dependence not known; young remain in their natal home-ranges for many months; on Little Barrier I., a 6-month-old male was observed soliciting food from its mother and continued to frequent its natal home-range till at least 9 months old; two male fledgelings on Codfish I. stayed within natal home-ranges till 9 months old (left late Nov.–Dec.) (D.V. Merton).

Success From Stewart, Codfish and Little Barrier Is, between 1981 and 1997: from 58 eggs in 26 nests, 33 (56.9%) fertile, 25 (43.1%) hatched, 11 (18.9%) fledged, 9 (15.5%) reached independence; young fledged from six (23%) nests; mean number of young fledged per successful nest, 1.16 (1–2) (D.V. Merton). Pacific Rat eats eggs and young (Merton 1994). Seven of nine young raised to independence since 1980 would not have survived without human intervention; three were partly hand-raised and rest received food supplementation via mother (D.V. Merton).

PLUMAGES Prepared by A.M. Dunn. Fledge in juvenile plumage. Little known of post-juvenile moult or sequence of moults to adult. Probably attain adult plumage in either complete post-juvenile moult or first immature post-breeding moult if post-juvenile moult partial. Thereafter one complete post-breeding moult each cycle produces successive adult plumages without change in appearance. Sexes differ only slightly. No subspecies.

Adult male (Definitive basic). HEAD AND NECK: Forehead and lores, light grey-brown (119C). Crown, nape and hindneck appear mostly green (60) with dark-brown (219) mottling; feathers, dark brown (219) with broad green (60) tips and concealed cream (54) to straw-yellow (56) crescent-shaped patch in middle of feathers. Chin bare. Cheeks, throat and foreneck, very pale yellow (ne). Feathers of lores, cheeks and ear-coverts have long bristle-like spines that extend well past rest of feather and radiate outward from eye forming a pale facial disk. Feathers of sides of neck, brown (28) with pale-yellow (c157) shaft-streaks and green (60) or greenish-yellow (ne) edges. UPPERPARTS: Appear mostly green (60) with dark-brown (219) and straw-yellow (c57) spotting or mottling; feathers straw-yellow (c57) with broad green (60) tips and irregular dark-brown (219) spotting, mottling or barring. UNDERPARTS: Breast and belly appear mostly yellow-olive (c52) to yellow (c55) with brown (119B) and very pale yellow (ne) mottling; feathers mostly very pale yellow (ne) with yellow-olive (c52) to yellow (ne) fringes and irregular brown (119B) to dark-brown (121) spotting or barring; brown barring becomes fainter toward vent. Vent and undertail-coverts similar but without brown markings. Flanks similar to breast and belly but more boldly marked with brown, and showing a green suffusion. Concealed bases to all feathers, brown (28). TAIL: Brown (123) with thick black-brown (119) vermiculations. Underside slightly paler. UPPERWING: Primary and secondary coverts and alula appear mostly green (60) with dark-brown (219) and straw-yellow (c57) spotting or mottling; feathers, straw-yellow (c57) with broad green (60) tips and irregular dark-brown (219) spotting, mottling or barring. Primaries, dark brown (219) with rows of large squarish straw-yellow (56) spots or thick half-bars along outer edge and narrow straw-yellow (c56) half-bars along inner edge that broaden toward base of feather; bars on inner edge may appear as faint speckling or smudged bars near tips of feathers. Yellow spots and half-bars on primaries usually speckled with dark brown (219). Primaries have rounded tips. Secondaries similar to primaries though bars become larger and more heavily speckled toward innerwing; innermost secondaries and tertials have complete barring, heavy speckling and green (60) suffusion along outer web and tip. UNDERWING: Secondary coverts, pale yellow (ne) with dark-brown (121) blotches and yellow (c55) tips; amount of blotching on feathers varies individually. Lesser and median primary coverts, dark greyish-brown (c121) with one or two pale-yellow (ne) bars and yellow (c55) tip. Greater primary coverts, greyish brown (c28) with large pale-yellow (ne) spots along shafts. Remiges patterned as upperwing.

Adult female (Definitive basic). Similar to adult male, but appear to have less yellow in plumage and also differ slightly in underparts and patterning of primaries. Differences from adult male: UNDERPARTS: Barring and mottling paler. UPPERWING, UNDERWING: Pattern on tips of outer five primaries slightly different: no barring on tip of inner web of outer primaries from about one-third below tip of feather; much reduced compared with male (see Powlesland 1989).

Downy young At hatching, covered in thick white or creamy-white first down (Buller 1888; Westerskov 1980; Forshaw & Cooper 1989; Merton & Empson 1989; Oliver; D.V. Merton). Second down develops at 3 weeks old; long and grey; paler on head, darker on body (D.V. Merton).

Juvenile male Differ from adult in having slightly darker colours, with less yellow in plumage, particularly on upperparts; retain short strand of grey down at tip of each primary and tail rachis till 3–6 months old (Williams 1956; Westerskov 1980; D.V. Merton; skins [NMNZ]). Differences from adult: HEAD AND NECK: Facial disk not so extensive as in adult, though lower portion obvious and protrudes forward; streaked radially with yellow. Face paler and greyer with prominent dark-grey lores, but lower facial area may become stained tobacco-brown by food, as in some adults (D.V. Merton). UPPERPARTS: Green parts of feathers appear slightly darker, dark green (c160). Dark barring, mottling and spotting also tends to be finer, more uniform and more pronounced (D.V. Merton). UNDERPARTS: Appear much browner than adult, with pale indistinct barring. Indistinct broad pale-yellow band or longitudinal streaks extend across upper breast (D.V. Merton). Breast varies between individuals and usually contains a mixture of differently patterned feathers: some feathers mottled dark brown (121) and pale yellow (pale 157), appearing almost barred, and with dark-green (c260) tips; some mostly dark brown (121) with partial pale-yellow (pale 157) barring and dark-green tips; some have wriggly dark-brown (121) lines over olive-brown (30) ground-colour; in others, feathers have pale-yellow (pale 157) shaft-streaks and pale-yellow (pale 157) half-bars. TAIL: Like that of adult but often have downy projections on tip of rachis. UPPERWING: Greater primary coverts and primaries appear much darker than in adult; outer web of feathers mostly black-brown (119) with narrower, more widely spaced pale-yellow barring. Tip of inner web of outer primaries similar to adult male. Rest of inner web of primaries have more complete barring than in adult male; bars extend along most of feather. Primaries have relatively pointed tips (cf. rounded in adults).

Juvenile female Similar to juvenile males, but tip of inner web of outer primaries similar to that of adult female.

Aberrant plumages Many colour variations have been observed (Buller 1888; Westerskov 1981; Oliver), mostly involving yellow replacing green in plumage. In some, only small areas of plumage are affected, resulting in yellow patches; others appear mostly yellow with brown barring, some appear entirely canary-yellow (e.g. skin at CM). One skin (MV) had very pale plumage with an extensive blue suffusion.

BARE PARTS Based on photos (Merton & Empson 1989; Moon 1992; Temple 1996; NZRD; unpubl.: D.V. Merton) and published information as cited. **Adult** Bill, light blue-grey (grey 168C) to creamy grey (ne) with off-white tip and cutting edges; in live birds, described as blue-grey, with ivory tip and cutting edge; and lower mandible often becomes heavily stained brown by food (D.V. Merton). Cere, blue-grey (c88), pinkish brown (ne) or cream (c92); in live birds, described as blue-grey, with a pale-grey bloom, which is less obvious, or lacking, in female (D.V. Merton). Iris, black-brown (119) or dark chocolate-brown (D.V. Merton). Orbital ring, bluish grey (bluish 87), dark grey (83) or grey-black (82). Legs and feet, bluish grey (bluish 87), pale grey (c86) or light brown-grey (c45); in live birds described as grey, with pink tinge in females (D.V. Merton). Soles, cream or pale yellow-flesh (D.V. Merton). **Downy young** Bill and cere, grey-black (82) or glossy dark grey-brown (D.V. Merton). Iris, brown; lighter than adults (D.V. Merton). Skin, pink (D.V. Merton). Legs and feet, pink at hatching, changing to dark pinkish-grey at c. 14 days (D.V. Merton). Soles, pale pinkish-grey (D.V. Merton). **Juvenile** Based on examination of two frozen skins (NMNZ), published information (Forshaw & Cooper 1989) and some information from D.V. Merton. Bill, off-white with a pink tinge (NMNZ); also described as pale yellowish-white (Forshaw & Cooper 1989); or, in live birds, like bill of adult (D.V. Merton). Orbital ring, paler grey than adult (D.V. Merton). Cere, light brown (c25) or brown (c28); in live birds, said to be like adults (D.V. Merton). Legs and feet, dark greyish-brown (ne) with a fleshy tinge, darkest toward tips of toes.

MOULTS Based mostly on information supplied by D.V. Merton. Most specimens examined did not have reliable collection dates. **Adult post-breeding** (Definitive, probably third and subsequent pre-basic). Very little information. Probably complete. Moult protracted; in non-breeding adults, begins Apr.–May and finishes Oct.–Nov. In breeding females, moult does not start till after young fledge; begins in June–Sept. or later; of two females that bred successfully in 1981, one began in Sept. and had not finished moult by following Mar.; the other had not begun moult in Sept. Holyoak (1973) suggested moult of primaries can begin with any primary, but usually starts between p5 and p8 and proceeds inward and outward from that point. Conversely, data from other sources suggests that sequence of moult of primaries appears more haphazard. Sequences of moult of primaries recorded by Stresemann & Stresemann (1966) difficult to interpret and are slightly different in each wing: one bird had a sequence of $O^3 1^1 O^1 N^1 O^1 1^1 O^2$ in left wing and $O^4 N^1 O^1 N^1 1^1 O^2$ in right wing. Furthermore, sequences of primary-moult recorded from c. 40 live adults (D.V. Merton) showed no obvious patterns; moult began with any primary and each primary replaced was not necessarily adjacent to the last. The number of primaries growing at once also varied greatly; some were only moulting one or two primaries but many were moulting about half their primaries at once, and, in three birds, all primaries were still growing (sequences $1^1 3^1 4^4 3^2 4^2$; $4^4 1^1 4^1 1^1 4^3$; 4^{10}). These unusual patterns of replacement of primaries probably occur because Kakapo is flightless. **Post-juvenile** (First basic). Poorly known. Apparently partial, involving only feathers of body (but further study needed); moult when roughly 7–8 months old (i.e. Oct.–Nov.). **First immature post-breeding** (Second pre-basic). Little information. Apparently complete. One captive female began its first full moult in May, when *c.* 14 months old, and finished in Oct., at *c.* 19 months old. Moult began with feathers of body; followed by moult of wing and tail in July–Aug. Dropped all but one rectrix over 17 days from late July, with final rectrix dropped on 7 Sept., 45 days after losing first; in late Aug., many new rectrices, *c.* 5 cm long, apparent. Moult slowed in Sept. and was finished by early Oct. In next year, when 2 years old, moult began earlier than in previous year, Mar., and finished earlier, late Sept. (G. Climo).

MEASUREMENTS (1–2) SI and Stewart I., NZ, but locality data on labels not precise; skins; sexed using label data or plumage or both (AIM, AM, CM, MV, NMNZ): (1) Adults; (2) Juveniles. (3) Stewart I., NZ, live adults (D.V. Merton). CLAW = length of claw on longer fore-toe.

		MALES	FEMALES	
WING	(1)	276.0 (8.63; 257–290; 35)	272.5 (9.10; 252–290; 25)	ns
	(2)	266.4 (11.02; 248–283; 12)	248, 258, 280	
	(3)	268.5 (12.46; 240–280; 19)	266.2 (14.51; 250–285; 13)	ns
TAIL	(1)	223.5 (9.62; 205–241; 34)	228.8 (9.76; 214–257; 23)	*
	(2)	210.7 (18.88; 172–233; 12)	208.2 (25.34; 190–245; 4)	ns
	(3)	224.5 (21.75; 195–272; 17)	222.5 (9.72; 210–240; 13)	ns
BILL	(1)	38.7 (2.30; 35.1–48.2; 40)	35.9 (0.97; 33.7–37.6; 25)	**
	(2)	37.0 (2.90; 30.5–40.9; 13)	36.3 (2.69; 33.7–39.8; 4)	ns
	(3)	40.2 (1.15; 38.8–43.1; 20)	37.3 (0.86; 36.2–38.9; 12)	**
BILL W	(3)	23.7 (0.95; 22.0–25.7; 20)	20.6 (0.43; 19.9–21.4; 13)	**
TARSUS	(1)	52.8 (3.08; 46.7–58.4; 37)	48.9 (2.36; 43.4–52.4; 24)	**
	(2)	52.5 (2.70; 48.5–55.8; 13)	51.0 (2.23; 47.7–52.5; 4)	ns
	(3)	60.1 (2.02; 56.8–63.8; 17)	54.1 (1.34; 51.9–56.7; 12)	**
TOE C	(1)	62.6 (4.16; 56.9–70.1; 19)	59.7 (4.80; 52.8–65.7; 12)	ns
	(2)	64.1 (1.96; 61.6–66.0; 4)	–	
TOE	(3)	56.9 (2.09; 52.1–61.5; 20)	50.3 (3.01; 44.3–54.1; 12)	**
CLAW	(3)	21.7 (1.08; 19.5–24.1; 19)	20.4 (0.96; 19.1–21.9; 13)	**

Adult males have significantly longer and wider bill and longer tarsus than females, but significantly shorter tail (in skins). Juvenile males have significantly shorter wing ($P<0.01$), tail ($P<0.01$) and bill ($P<0.05$) than adult males; juvenile females had significantly shorter tail ($P<0.01$) than adult females. Additional measurements in Forshaw & Cooper (1989).

WEIGHTS (1) SI, NZ, adults, from museum labels; sexed using label data or plumage or both (NMNZ). (2) NZ, adults (Powlesland *et al.* 1992). (3) NZ, adults (Merton *et al.* 1984).

	MALES	FEMALES	
(1)	1601.2 (205.60; 1425–1890; 4)	–	
(2)	2000 (410; 1600–3000; 28)	1500 (140; 1300–1900; 28)	**
(3)	2060 (1500–3000; 39)	1280 (950–1640; 18)	

Maximum weights for birds not receiving supplementary food, 1.9 kg for female, and 3.6 kg for male (D.V. Merton).

STRUCTURE Plumage unusually soft in texture. Rudimentary keel to sternum. Wing short, broad and rounded. Usually ten primaries (one had 11): p6 longest; p10 40–58 mm shorter, p9 9–25, p8 5–17, p7 1–4, p5 1–6, p4 6–20, p3 11–33, p2 22–39, p1 40–52. No emargination of primaries. About 13 secondaries, including about five tertials; tips of longest tertials fall between p3 and p4 on folded wing. Tail short, rounded and curved slightly downwards, with pointed feathers; rachis projects past end of feather and has broad flattened tip; 12 rectrices; t1 longest, t6 37–50 mm shorter. Cutting edges of upper mandible sharp; tip rounded, inside flattened with small transverse grooves. Lower mandible broad and scoop-like with longitudinal ridges running from base to tip; adults have five primordial ridges and juveniles have three (D.V. Merton). Cutting edge of lower mandible straight. Broad fleshy bare cere along base of upper mandible, in which nostrils situated close to top. Nostrils large and crescent-shaped in males and >4 mm in length; in females, smaller and oblong (D.V. Merton). Tarsus short and strong; scaling granulate. Tibia fully feathered. Outer toe directed backwards. Outer hindtoe 84–99% of outer front, inner front 72–80%, inner hind 44–61%. Breeding females develop large, obvious brood-patches (D.V. Merton).

GEOGRAPHICAL VARIATION None. Several subspecies have been described, but none currently recognized (NZCL). At least one of these (*greyi*) considered a colour variant only (Buller 1888). However, there are some subtle differences in coloration of plumage between Stewart I. and SI populations (D.V. Merton). Furthermore, Triggs *et al.* (1989) examined genetic variation by estimating level of allozymic variation in blood, and noted that level of variation appeared to be higher in Stewart I. population than in that of SI. However, differences not significant, at least in part because sample sizes small.

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Volume 4, Plate 30

Kakapo *Strigops habroptilus* (page 633)
1–3 Adult male; **4** Juvenile female