

Order PASSERIFORMES

The largest and most diverse order of birds, commonly called passerines or perching birds, and comprising some 5712 species in 45 families (based on Sibley & Monroe 1990; Sibley & Ahlquist 1990), and well over half the world's known bird species. In the HANZAB region, Passeriformes represented by some 382 species in 39 families. Tiny to large: smallest passerine is Pygmy Tit *Psaltria exilis* of Java, with a total length c. 8 cm; largest is Greenland Raven *Corvus corax principalis*, with a total length c. 64 cm and weighing up to 1.7 kg. Superb Lyrebird *Menura novaehollandiae* of e. Aust. probably second largest in Order, with a total length (in adult male) of c. 103 cm, including tail of c. 70 cm, and weight up to c. 1.1 kg. Cosmopolitan except Antarctica and some oceanic islands; and occupying all terrestrial habitats.

Overall, Passeriformes are characterized by (based on Raikow 1982; Sibley & Ahlquist 1990; and DAB [=Schodde & Mason 1999]): Palate aegithongnathous (except Conopophagidae [gnateaters]). Intestinal caeca rudimentary. Single left carotid artery (except paired in *Pseudocalyptomena* and possibly other broadbills [Eurylaimidae]). Aftershaft reduced or absent. Neck short, with 14 cervical vertebrae in most, but 15 in Eurylaimidae (broadbills); atlas perforated; metasternum usually two-notched (rarely four-notched). Bicep slip absent. Expansor secundariorum often present (Berger 1956; Raikow 1982; *contra* Beddard 1898; Ridgeway 1901). Pelvic muscles AXY (AX in *Dicrurus* [drongos]). Ambiens absent. Iliofemoralis externus usually absent, but present in some groups as 'developmental anomaly' (Raikow 1982). Tensor propatagialis brevis tendon present. Hypocleideum present (except Menuridae [lyrebirds]). Wings eutaxic. Usually ten primaries, but p10 often reduced or absent; 11 primaries in Menuridae (lyrebirds), most Eurylaimidae (broadbills), most Furnariidae (ovenbirds), and some Passeri (oscines [see below]). Usually nine secondaries (ten in Menuridae [lyrebirds]). Usually 12 rectrices, but from six (*Stipiturus* [Maluridae]) to 16 (Menuridae). Lesser primary and secondary coverts usually reduced or absent (Zeidler 1966; Morlion 1985; Winkler & Jenni 1996), but a few well-developed lesser primary coverts are present in Superb Lyrebird (Morlion 1985). Uropygial preen glands naked. No basipterygoid process. Nasal glands minute. Foot anisodactyl. Hallux incumbent, large and directed backwards; toes 2, 3 and 4 directed forward; digital formula 2-3-4-5. Deep plantar tendons usually of type VII (lacking vinculum), but often type I in Eurylaimidae (broadbills). Spermatozoa bundled with coiled head and large acrosome.

The DNA-DNA hybridization studies of Sibley & Ahlquist (1985a, 1990) revealed much about the relationships within the Passeriformes and resulted in fundamental changes to the higher level taxonomy of passerines, not least to the taxonomy of the Australo-Papuan oscine passerines. Importantly, these studies showed that many elements of the Australo-Papuan avifauna (e.g. the A'asian wrens [Maluridae], robins [Petroicidae], babblers [Pomatostomidae], and so on), represent an endemic radiation of forms that bear an external resemblance to Eurasian families. Many of the findings of DNA-DNA hybridization studies regarding the Australo-Papuan oscines have since been broadly corroborated by studies using protein allozymes (e.g. Christidis 1991; Christidis & Schodde 1991) and microcomplement fixation (e.g. Baverstock *et al.* 1991, 1992), though there are also many points that remain uncertain and many familial relationships within the Passeriformes are unresolved (Christidis & Boles 1994). (For discussion of historical taxonomic arrangements preceding results of DNA-DNA hybridization studies, see BWP, and Sibley & Ahlquist [1985a,b, 1990]).

The Passeriformes divide into two main groups:

SUBORDER TYRANNI (SUBOSCINES): The distribution of the suboscines is centred in the American and Afro-asian Tropics, with a massive radiation in South America (Sibley & Ahlquist 1990; DAB). Suboscines characterized by mesomyodian syrinx, with or without a single pair of intrinsic syringeal muscles (van Tyne & Berger 1976; Campbell & Lack 1985; DAB). Suborder sometimes named Oligomyodi (e.g. Sibley & Ahlquist 1985a,b), Deutero-Oscines (e.g. Morony *et al.* 1975; Voous 1977), or Clamatores (Campbell & Lack 1985). Poorly represented in the HANZAB region: only TYRANNIDAE (tyrant-flycatchers), with two species, both accidental to South Georgia; ACANTHISITTIDAE (NZ wrens), with four species (one extinct) in three genera, endemic to NZ; and PITTIDAE (pittas), with four species in one genus in HANZAB region (three breeding, one accidental). Tyranni formerly included the Menuridae and Atrichornithidae (e.g. Wetmore 1960; Storer 1971), though subsequently shown that these two families should be included in Passeri (e.g. Sibley 1974; Sibley & Ahlquist 1985, 1990).

SUBORDER PASSERI (OSCINES OR SONGBIRDS): Cosmopolitan in distribution. Within the HANZAB region there are 36 families of Passeri. The Australo-Papuan Passeri can be subdivided into several supra-familial groups, but those recognized differ between authors (for further information, see Sibley & Ahlquist 1985, 1990; DAB). Oscines are

characterized by acromyodian syrinx, with three or four pairs of intrinsic syringeal muscles (van Tyne & Berger 1976; Campbell & Lack 1985; Sibley & Ahlquist 1990; DAB).

Suborder Passeri comprises the major element of the Aust. and NZ passerine avifauna. The families recorded in the HANZAB region, and the representatives in the region, are (following Christidis & Boles [1994] for Aust., with additional species for wider region added as appropriate):

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- MENURIDAE (lyrebirds): two species in one genus; endemic to Aust.;
- ATRICHORNITHIDAE (scrub-birds): two species in one genus; endemic to Aust.;
- CLIMACTERIDAE (A'asian treecreepers): six species in two genera breeding in Aust.;
- MALURIDAE (Australopapuan fairy-wrens, emu-wrens and grasswrens): 22 breeding species in three genera in Aust.;
- MELIPHAGIDAE (honeyeaters and Aust. chats): 76 species in 26 genera in Aust. and NZ, all breeding;
- PARDALOTIDAE (pardalotes, scrubwrens, thornbills and allies): 51 species (one extinct) in 15 genera in HANZAB region, all breeding;
- PETROICIDAE (A'asian robins): 23 species in eight genera in HANZAB region, all breeding;
- ORTHONYCHIDAE (logrunners): two breeding species in one genus in Aust.;
- POMATOSTOMIDAE (A'asian babblers): four breeding species in single genus in Aust.;
- CINCLOSOMATIDAE (whipbirds, wedgebills, quail-thrushes and jewel-babblers): eight breeding species in two genera in Aust.;
- NEOSITTIDAE (sitellas): single species breeding in Aust.;
- PACHYCEPHALIDAE (whistlers, shrike-thrushes and allies): 17 species in seven genera in HANZAB region, all breeding;
- DICRURIDAE (monarchs, flycatchers, fantails and drongos): 19 species in seven genera in HANZAB region, all breeding;
- CAMPEPHAGIDAE (cuckoo-shrikes, trillers and minivets): eight species (one extinct) in two genera in HANZAB region, all breeding;
- ORIOLIDAE (Old World orioles and figbirds): three species in two genera in Aust., all breeding;
- ARTAMIDAE (woodswallows, butcherbirds and currawongs): 14 species in four genera in HANZAB region, all breeding;
- PARADISAEIDAE (birds of paradise): five breeding species in two genera in Aust.;
- CORVIDAE (crows and jays): six breeding species in single genus in Aust. and NZ, including one introduced to NZ;
- CORCORACIDAE (Aust. mudnesters): two species in two monospecific genera, endemic to Aust.;
- CALLAEIDAE (NZ wattlebirds): three species (one extinct) in three monospecific genera, endemic to NZ;
- LANIIDAE (shrikes): two species in HANZAB region, one accidental to Prince Edward Is, the other accidental to Christmas I.;
- PTILONORHYNCHIDAE (bowerbirds): ten species in seven genera in Aust. (nine species) and NZ (one species), all breeding; Piopio of NZ probably extinct (Heather & Robertson 1997);
- ALAUDIDAE (larks): two breeding species in HANZAB region (including one successfully introduced to Aust. and NZ);
- MOTACILLIDAE (wagtails and pipits): eight species in two genera in HANZAB region, only two breeding (one on South Georgia), the rest non-breeding visitors or accidentals;
- PRUNELLIDAE (accentors): one species successfully introduced to NZ;
- PASSERIDAE (Old World sparrows and A'asian finches): 22 species in nine genera (including four successful introductions) in HANZAB region, all breeding;
- FRINGILLIDAE (Old World finches): seven species in four genera in HANZAB region, all introduced except one naturally occurring vagrant to South Georgia;
- EMBERIZIDAE (buntings, cardinals, tanagers and allies): two successfully introduced species, occurring NZ and Lord Howe I.;
- NECTARINIIDAE (sunbirds and spiderhunters): single breeding species in Aust.;
- DICAEDIDAE (flowerpeckers): single breeding species in Aust.;
- HIRUNDINIDAE (swallows and martins): eight species in four genera in HANZAB region, including four breeding species in Aust. and NZ, one non-breeding visitor and three accidentals;
- PYCNONOTIDAE (bulbuls): one successfully introduced species in Aust.;
- SYLVIIDAE (Old World warblers): 13 species in eight genera in HANZAB region, including ten breeding species (one extinct) in Aust. and NZ, and three accidental to region;
- ZOSTEROPIDAE (white-eyes): seven species (one extinct) in single genus in HANZAB region, all breeding;
- MUSCICAPIDAE (Old World flycatchers, thrushes and chats): eight species in six genera in HANZAB region, including five breeding species (two introduced), and four accidentals (including one on Prince Edward Is);
- STURNIDAE (starlings and mynas): five species in four genera, four breeding in HANZAB region (including two species successfully introduced, and one species now extinct), and one accidental.
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The Aust. oscines fall into two distinct clusters, each with at least three major supra-familial lineages (DAB): One cluster is the Passerida, comprising the Muscicapoida (including true thrushes and allies), Sylvioidea (true warblers and babblers, and swallows, and others), and Passeroidea (including larks, pipits, sunbirds, flowerpeckers and all finches and their allies). The other cluster is the Corvida, which is centred on the Australo-Papuan region (though its origins are not certain) and which also comprises three main lineages: Menuroidea (lyrebirds, scrub-birds, treecreepers and bowerbirds), Meliphagoidea (A'asian wrens, pardalotes, acanthizid warblers, and honeyeaters), and Corvoidea (A'asian robins, logrunners, A'asian babblers, whipbirds and quail-thrushes, sitellas, whistlers, fantails and monarchs, birds of paradise, butcherbirds and woodswallows, cuckoo-shrikes, Old World orioles, crows and mudnesters).

Throughout this volume, arrangement of families follows that of Christidis & Boles (1994) except that the Meliphagidae precedes the Pardalotidae. This change was made to ensure the Meliphagidae were dealt with in a single volume, rather than split between volumes, and because the switch meant no change to the positioning of Meliphagidae relative to the Pardalotidae (including Acanthizidae), one another's closest relatives, and because there is little overriding evidence of the exact taxonomic positioning of all families within the Meliphagoidea; Sibley & Monroe (1990) also placed the Meliphagidae between the Maluridae and Pardalotidae. However, DAB points out that based on structure of humeral fossa, positioning of Meliphagidae between the Maluridae and Pardalotidae is not correct.

DAB, however, varies from the familial arrangement of Christidis & Boles (1994) in several ways. The main differences are: (1) recognition of Pardalotidae and Acanthizidae as separate families (combined in Pardalotidae in Christidis & Boles); (2) minor rearrangement of the sequence of the families Paradisaeidae–Artamidae–Campephagidae–Oriolidae between the Dicuridae and Corvidae (cf. Dicuridae–Campephagidae–Oriolidae–Artamidae–Paradisaeidae–Corvidae in Christidis & Boles); (3) and use of the more traditional muscicapoid (flycatcher) – sylvioid (warbler) – passeroid (finch) sequence of Sibley *et al.* (1988), Sibley & Ahlquist (1990) and Sibley & Monroe (1990) and much contemporary literature of n. hemisphere, with families in the sequence Muscicapidae–Sturnidae–Hirundinidae–Pycnonotidae–Zosteropidae–Sylviidae–Alaudidae–Dicaeidae–Nectariniidae–Passeridae–Motacillidae–Estrildidae–Fringillidae and noting recognition of the Estrildidae as a separate family (cf. the reversed sequence of Christidis & Boles, as given above, and which submerges the Estrildidae within the Passeridae). For discussion of the reasons for these changes, see DAB (and discussion under these families in future volumes of HANZAB).

Arrangement of genera and species within families also follows Christidis & Boles (1994), which was in turn largely based on Schodde (1975) unless there were specific reasons for change. Lastly, with few exceptions, which are discussed in individual species accounts, taxonomy of subspecies follows DAB.

Passerines are extremely diverse in body form and plumage, and vary greatly in rates of maturation. Some attain adult plumage within months or weeks of fledging; others can take up to 9 years to attain adult plumage (e.g. Superb Lyrebird). Degree of sexual dimorphism also varies greatly: some monomorphic, others vary in either size, plumage or both. Common pattern of annual moult is a single complete post-breeding (pre-basic) moult, but some groups (e.g. Maluridae) or species (e.g. Banded Honeyeater *Certhionyx pectoralis*) also undergo a partial pre-breeding (pre-alternate) moult annually. Moult of primaries usually outward. Secondaries moult from innermost and outermost toward s5. Moult of tail usually centrifugal (outward from centre). Young altricial, nidicolous and dependent on adults for food; usually hatch with sparse to very sparse covering of down, mainly on dorsum; Menuridae (lyrebirds) have heavy natal down. Juvenile plumage usually duller than adult, and in many sexually dimorphic species, often similar to that of adult female.

There are few common features of food, feeding behaviour, social organization and behaviour, voice or breeding in such a large and diverse group of birds.

Volant; extinct Stephens Island Wren *Traversia lyalli* probably the only flightless passerine (Millener 1988). Movements vary greatly: some species long-distance migrants (e.g. Barn Swallow *Hirundo rustica*, Nightingale *Luscinia megarhynchos* and many Old World warblers, such as *Acrocephalus* and *Locustella*, breed in temperate Palaearctic and migrate to Africa or Indian subcontinent [BWP]; Acadian Flycatcher *Empidonax virescens* breeds North America and migrates to South America [Ridgely & Tudor 1994]), others sedentary in small territories (e.g. Cactus Wren *Campylorhynchus brunneicapillus* of sw. USA and Mexico [Ricklefs 1975; Ehrlich *et al.* 1988]). In HANZAB region, movements also vary widely: e.g. Yellow-faced Honeyeater *Lichenostomus chrysops* regular annual migrant in parts of e. Aust.; Rifleman *Acanthisitta chloris* of NZ sedentary in small territories. In Aust., movements often poorly known and unstudied; many species often said to be nomadic, with such claims often based on no or very poor knowledge of actual movements and based only on apparently irregular occurrence in an area (see General Introduction [Movements] for fuller discussion of this point).

Arboreal or terrestrial or both; some strictly arboreal (e.g. Hirundinidae), others strictly terrestrial (e.g. Menuridae, Pittidae); most combine both arboreal and terrestrial foraging to varying degrees, but usually with one predominating. Feed on almost all known food, from plant material to vertebrate animals, but most show some specialization for certain food, such as feeding on nectar (Nectariniidae), seeds (Passeridae), fruit (Zosteropidae), small vertebrates (Artamidae) and, commonly, insects (e.g. Maluridae, Pardalotidae, Petroicidae and others). Mostly feed by gleaning

and probing, including probing flowers for nectar; and other substrates for invertebrates; also feed by sallying, including various sallying techniques (sally-hovering, sally-striking and sally-pouncing), each suited for one group of prey, particularly moving animals.

In passerines, parental care in both sexes is well developed. However, a few species are parasitic, e.g. cowbirds *Molothrus* (Campbell & Lack 1985). Young are dependent on parents for food. Young beg by gaping, typically exposing brightly coloured inside of mouth, often with contrasting pale or dark spots; in non-passerines, bright gape present only in hoopoes (Upupidae), mousebirds (Coliiformes) and cuckoos (Cuculiformes) (BWP). See Boles & Longmore (1985) for descriptions of colours and markings inside the mouths of some Aust. passerines.

Anting is a highly specialized behaviour: ants are held in the bill and applied to the plumage, usually to the underside of the wing-tip (direct or active anting, or ant-application), or ants are allowed access to the plumage (indirect or passive anting, or ant-exposure), or both, e.g. anting recorded in Regent Honeyeaters *Xanthomyza phrygia* in HANZAB region, with bird then seen eating ant. Thought to be unique to Passeriformes (e.g. Simmons 1966; Campbell & Lack 1985; BWP). Suggested this may be comfort behaviour related to maintenance of feathers, by perhaps reducing ectoparasite load, removing stale or excess lipids, or adding supplementary essential oils (Campbell & Lack 1985); some secretions of ants are antibiotic, inhibiting growth of both fungi and bacteria, and the secondary acquisition of these antibiotic secretions would be an important advantage of anting (Ehrlick et al. 1986).

Other behavioural characters include head-scratching indirectly (or over the wing) in most families, with the foot brought up above the lowered wing. Head oiled indirectly, as seen in most taxa, but passerines also oil head by head-scratching, in which bird oils the bill directly, then transfers the oil first to one foot by scratching the bill, and then to the head by scratching the head with foot. To oil the undersurface of the wings, use bill or bill and head together, extending one wing at a time sideways and forward, carpus uppermost, and often alternating rapidly from one wing to the other. The stretching of one wing as a comfort movement seems common to all birds, but in passerines it is often accompanied by sideways fanning of tail. After both wings are stretched, passerines often give a two-leg stretch as they straighten the tarsal joints and lift the body. Heat is dissipated by gaping and panting (not by gular-fluttering, so far as known) (Campbell & Lack 1985; BWP). Bathing widespread, mainly by standing in shallow water, but some groups jump into and out of water repeatedly, or flight- or plunge-bathe, while others bathe only or mainly in rain or among wet foliage; for further details of bathing, see Campbell & Lack (1985). Passerines do not flap wings in the manner of non-passerines to dry, but perform various shaking movements, as well as preening (Campbell & Lack 1985). Dusting confined to only a few groups, but sunning, both for gaining heat (sun-basking) and other purposes (sun-exposure), is widespread, and of two distinct types: (1) lateral posture, in which sunning bird squats or sits down, usually on ground, and leans to one side exposing the flank or the 'sun-wing', which has been lowered and partly unfolded, and the fanned tail, which has been brought round to the same side; and (2) spread-eagle posture, in which bird squats or lies flat with both wings open and tail fanned (details in Campbell & Lack 1985; Simmons 1986).

There is a high incidence of co-operative breeding in Aust. and NZ, and it is especially common and well-studied in the Maluridae but is more widely recorded, including within the Acanthisittidae, Meliphagidae, Petroicidae, Pomatostomidae and Corcoracidae (see Dow 1978, 1980; Brown 1987; Ford 1989; Rowley & Russell 1997).

In vocal abilities, species of Passeriformes are more accomplished than those of any other order, but songs may be simple or highly complex, and repertoires small or large. Mimicry of calls of other species is practised by many species; c. 15% of Australian passerine species have been reported to mimic (Marshall 1950). The Superb Lyrebird and the Tui *Prosthemadera novaeseelandiae* have been classed among the best seven of the world's songsters (Hartshorne 1973). Oscines, or songbirds, have specialized forebrain song nuclei, and, through auditory feedback, learn their songs from those of adults, in much the same way as human young learn their spoken language from adults. In contrast, the songs of suboscines are relatively simple (like the non-learned call-notes of songbirds), repertoires are small, geographical variation is minimal, and development of song appears to take place without any imitative or feedback process. Some oscine species use vocal learning to generate large song repertoires and may vary them geographically, even locally. Other oscine species forgo these possibilities and have song repertoires more like those of suboscines; how the learning process maintains stereotypy of song over the range of such species is a mystery (Kroodsma 1996).

Apart from the five families discussed hereunder, syringeal structure of passeriform species of our area is similar, there being four pairs of intrinsic muscles. Pittidae have no intrinsic muscles (Ames 1971); calls are mostly loud strong whistles (Pizzey 1980). Acanthisittidae also have no intrinsic muscles, but the presence of a well-developed drum (fusion of posterior tracheal elements) suggests they may have once been present; vocal repertoire is not great (Ames 1971). Menuridae and Atrichornithidae have similar syringeal structures, with three pairs of intrinsic muscles; songs are highly developed, and there can be much mimicry (Ames 1971). Climacteridae, with four pairs of intrinsic muscles, exhibit gross asymmetry of the extrinsic muscles, unusual directions of muscle fibre in the intrinsic muscles, and an exceptionally robust sternotracheal muscle (Ames 1987); calls are brisk, sharp and piping (Pizzey 1980).

Extended tracheae are found in the genus *Manucodia* (Paradisaeidae), the calls of which are deep, loud or far-carrying (Frith 1994). In the only species occurring in our area, the Trumpet Manucode *M. keraudrenii*, the trachea forms a flat coil between the skin and the pectoral muscles, sometimes extending over the abdominal muscles as well,

and may be up to 828 mm in length, compared with body-length, from bill to pygostyle, of c. 150 mm (Ames 1971; Clench 1978).

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Family PACHYCEPHALIDAE whistlers, shrike-thrushes, pitohuis and allies

A large and diverse group of small to medium-sized passerines, many of which have loud, complex whistled songs. Within HANZAB region, smallest is Brown Creeper *Mohoua novaeseelandiae* (length c. 13 cm, weight c. 13 g), and largest Grey Shrike-thrush *Colluricincla harmonica* (length 23–25 cm, weight 60–75 g); range of sizes of extralimital species not known, but probably within range of those in HANZAB region. The Pachycephalidae comprises some 57–59 species in 11–12 genera, centred in Aust. and New Guinea, but extending across se. Asia and parts of s. Asia, and to islands in sw. Pacific Ocean, including Palau, Loyalty Is, Vanuatu, New Caledonia, Tonga, Samoa and Fiji (Sibley & Ahlquist 1987, 1990; Coates 1990; Bregulla 1992; Coates *et al.* 1997; Coates & Peckover 2001; DAB; also see species accounts). Within the HANZAB region there are 17 species in five genera:

<i>Mohoua</i>	three species, endemic to NZ;
<i>Falcunculus</i>	monotypic Crested Shrike-tit <i>F. frontatus</i> , endemic to Aust.;
<i>Oreoica</i>	monotypic Crested Bellbird <i>O. gutturalis</i> , endemic to Aust.;
<i>Pachycephala</i>	whistlers; eight species in HANZAB region; extralimitally, some 32–34 additional species, occurring mostly in New Guinea, Wallacea and islands in sw. Pacific, with species in se. Asia and parts of s. Asia;
<i>Colluricincla</i>	shrike-thrushes; four species in HANZAB region (two of which, <i>C. harmonica</i> and <i>C. megarhyncha</i> , extend to New Guinea); extralimitally one in New Guinea and one in Palau.

Other genera include: monotypic *Rhagologus* (New Guinea), monotypic *Hylocitrea* (Sulawesi; sometimes included within *Rhagologus*), monotypic *Coracornis* (Sulawesi), monotypic *Aleadryas* (New Guinea), monotypic *Pachycare* (New Guinea), *Pitohui* (six species, New Guinea), and monotypic *Eulacestoma* (New Guinea).

The composition and taxonomic placement of this group has varied over time and remains unclear. Traditionally, the group has been placed with the Petroicidae (A'asian robins) and placed within or linked with the Old World flycatchers Muscicapidae (e.g. Schodde 1975; Boles 1979; see DAB). Recent molecular evidence shows they are part of the Australo-Papuan corvid radiation, though the relationships of the Pachycephalidae within the Corvoidea is not clear; molecular evidence suggests they are only rather distantly related to the Petroicidae (Sibley & Ahlquist 1982, 1985, 1990; Christidis & Schodde 1991; see DAB); Sibley & Ahlquist (1990) suggested that the whistlers and allies are most closely related to the crows and jays (Corvidae) and fantails, drongos and monarchs (Dicruridae). The group has also been considered a subfamily, Pachycephalini, of the Corvidae, which also included sittellas *Daphoenositta*; and the subfamily subdivided into four tribes: Neosittini (*Daphoenositta*), Mohouini (*Mohoua*), Falcunculini (*Falcunculus*, *Oreoica*), and Pachycephalini (*Pachycephala*, *Colluricincla*, *Pitohui*, *Rhagologus*, *Hylocitrea*, *Coracornis*, *Aleadryas*, *Pachycare*, *Pitohui*, and *Eulacestoma*) (Sibley & Ahlquist 1990; Sibley & Monroe 1990). However, studies of protein electrophoresis indicate that the sittellas should be placed in a separate family Neosittidae (Christidis & Schodde 1991; DAB; see elsewhere in this volume). Sibley & Ahlquist (1990) and DAB included the Piopio *Turnagra capensis* of NZ within this family, but it is treated in HANZAB (Volume 7) as part of Ptilonorhynchidae (bowerbirds) following Olson *et al.* (1983) and Christidis *et al.* (1996).

Robust birds with rather large and thick heads (hence former vernacular name of 'thickhead' for *Pachycephala*) with well-developed and more or less distinctly hooked bills (which gave rise to the group-name shrike-thrush for *Colluricincla*). The Pachycephalidae are characterized by (after DAB): Pocock's (1966) process 'D' present on carpo-metacarpus; fossa at head of humerus, single and trabeculated; internasal septum lightly and varyingly ossified; nasal bars usually slender (not in *Aleadryas* and some *Pitohui*); palantines generalized with narrow medial shelves and acute, nipple-like transpalatine processes; maxillopalatine processes usually broad and flat but tip of vomer varies more; usually lack lachrymals (except *Rhagologus* and some *Pitohui*); ectethmoid plate large with broadly flared, laterally rounded wing reaching jugal bar; ectethmoid foramen reduced to single small aperture in mesethmoid region; temporal fossa usually rather small and oblatly rounded (*Pachycephala* and *Colluricincla*); processes flanking temporal fossa attenuate, especially postorbital, which sometimes directed downward (*Aleadryas*, *Oreoica* and *Falcunculus*), but directed upward in *Eulacestoma*. Feet strong; tarsi usually booted (holothecal). Bills vary but often rather short, stout, heavy and slightly hooked, usually with a well-developed tomial notch; range from short, wedge-shaped, laterally compressed and powerful (e.g. *Falcunculus*, *Eulacestoma*),

to short and rather stubby (e.g. many *Pachycephala*), to medium-long and rather heavy (e.g. *Colluricincla*, *Pitohui*). Wings generally rather short, broad and rounded with ten primaries and usually nine secondaries (ten in some *Pitohui*). Tails vary in length, but usually square-cut; 12 rectrices.

Adult plumage mostly rather dull tones of grey, brown or olive, though often with brighter yellow or rufous on underparts and, in some, on dorsum. Many have distinct patterning or colouring on head and neck, often of black and white, yellow or rufous, or streaking on parts of underbody. Many are sexually dimorphic in plumage, with males brightly coloured and females rather nondescript; in some species, both sexes rather plain, while in others, both sexes brightly coloured. Juveniles tend to have rufous edges to feathers of wings, and often have reddish-brown tinge to rest of plumage. Bristles at base of bill poorly developed. All appear to undergo a partial post-juvenile (first pre-basic) moult shortly after fledging, to adult female-like first immature plumage; males tend to show delayed plumage maturation and, in many species, do not attain adult plumage till third year (e.g. Rufous Whistler *Pachycephala rufiventris*); some attain adult male plumage in second year (e.g. Crested Shrike-tit). Adults undergo a single complete post-breeding (pre-basic) moult annually, with no change in appearance. Primaries moult outward.

Throughout range, occupy most wooded habitats, from shrublands to rainforests and mangrove associations, in most bioclimatic zones; use all heights from ground to canopy. In Aust., widespread in dry and wet sclerophyll forests and woodlands, primarily those dominated by eucalypts, in temperate, subtropical, tropical and arid and semi-arid regions (e.g. Crested Shrike-tit, and Golden *Pachycephala pectoralis* and Rufous Whistlers); also widely recorded from arid and semi-arid shrublands and woodlands, including mallee eucalypt woodland (e.g. Crested Bellbird, Gilbert's *P. inornata* Whistlers), temperate (e.g. Olive Whistler *P. olivacea*), subtropical and tropical rainforests (Little *Colluricincla megarhyncha* and Bower's *C. boweri* Shrike-thrushes), and mangroves (White-breasted *Pachycephala lanoides* and Mangrove Golden *P. melanura* Whistlers). In NZ, *Mohoua* occur in all types of native forest, including beech *Nothofagus* forest; Whitehead *M. albicilla* and Brown Creeper *M. novaeseelandiae* also inhabit plantations of exotic pines and regrowth, though Yellowhead *M. ochrocephala* does not (Rand & Gilliard 1967; Watling 1982; White & Bruce 1986; Coates 1990; Coates *et al.* 1997; Coates & Peckover 2001; see species accounts).

Usually considered resident or sedentary, with usually local or dispersive movements, usually in non-breeding season. Movements, mainly local, during non-breeding season and possibly undertaken mainly by immatures; such movements may result in seasonal patterns of occurrences. Some apparently migratory movements noted in Aust., e.g. some populations of Rufous Whistlers move N in autumn and S in spring, though extent of migration not clear. Altitudinal movements undertaken in some populations in se. Aust. (e.g. Golden Whistler) and in ne. Qld (e.g. Grey Whistler *Pachycephala simplex*) (Aust. Atlas; see species accounts). In some whistlers that move regularly, sexes appear to travel separately (Lawrence 1952; Bridges 1994); and in e. NSW, migrate either singly or in a succession of small flocks (Frith 1969; Morris *et al.* 1981). See reviews of movements of Aust. species in Chan (2001) and Griffioen & Clarke (2002).

Arboreal and terrestrial, and nearly all insectivorous; some species take fruit as well as arthropods (e.g. Yellow-flanked Whistler *Hylocitrea bonensis* of Sulawesi); and some larger species, such as shrike-thrushes, known to take small vertebrates such as frogs, lizards and nestling birds. Mostly forage singly or, less often, in twos, which often pairs; *Mohoua* and *Falcunculus* are gregarious and mostly forage in groups. Many species forage in mixed-species feeding flocks at times, and can form nucleus of such flocks (e.g. *Mohoua*). Height of foraging varies with species, and some forage at all heights from ground to canopy. Many arboreal, foraging in canopy and subcanopy, among foliage, on branches and trunks of trees, especially eucalypts; other species forage mostly in lower canopy or understorey (e.g. most shrike-thrushes *Colluricincla* and Olive Whistler) or mainly on ground (e.g. Crested Bellbird, Sandstone Shrike-thrush *Colluricincla woodwardi*, Crested Pitohui *Pitohui cristatus*). Catch prey mainly by gleaning, and less often by pulling, sallying or hanging. Several species specialized, e.g. Crested Shrike-tit has massive, wedge-shaped and laterally compressed and heavily muscled bill, and specializes in stripping bark from branches and taking exposed insects; and Wattled Ploughbill *Eulacestoma nigropectus* also has a thick wedge-shaped and laterally compressed bill, and digs into bark and strips wood from twigs in search of prey, as well as gleaning from surfaces (Coates 1990; Coates *et al.* 1997; Coates & Peckover 2001; DAB; see species accounts).

Social organization and behaviour well known for a few species, including Whitehead, Yellowhead and Brown Creeper of NZ, and Golden and Rufous Whistlers of Aust.; most species poorly known. Usually occur singly or in pairs throughout year; occasionally recorded in small family parties after breeding. Often join mixed-species

feeding flocks, especially in non-breeding season. *Mohoua* are gregarious, more so outside breeding season; Crested Shrike-tits also forage gregariously in non-breeding season; Golden Whistlers may also form loose congregations in temperate zone in winter. Subadults of some species associate in groups outside breeding season, e.g. Golden Whistler and Brown Creeper. Most species are monogamous and breed as simple pairs, though co-operative breeding reported in *Falcunculus* and all three *Mohoua* (and, in latter, is common in Whitehead and Yellowhead). Pair-bond appears to be maintained long term in some well-studied species (e.g. Rufous Whistler) and is re-established on return to breeding site in migratory populations, but data lacking for most species. Most species considered to be territorial, but breeding dispersion and size of territories known for only a few. Most species have loud and complex songs, which are used to advertise ownership of territory and in defence of territory, as well as in courtship. Roosting not well known; Grey Whistler recorded roosting in open at night, while Rufous Whistler usually roosts among foliage, often near nest or round centre of territory. Crested Shrike-tit seen roosting in hunched posture with crest flattened (see species accounts). Of maintenance behaviour, anting recorded in two species of shrike-thrush. Agonistic displays include threat and bowing displays (e.g. in Golden and Rufous Whistlers); most species can be pugnacious in defending nests or young. Mobbing behaviour recorded in *Mohoua*. Courtship chases, courtship feeding or courtship displays recorded in some species; sexual behaviour of most poorly known. Distraction displays reported in Gilbert's and Red-lore'd *Pachycephala rufogularis* Whistlers and two of the shrike-thrushes, but apparently not in well-studied Golden and Rufous Whistlers. Crested Bellbird nestlings appear to mimic action of hairy caterpillars placed in nests by parents, which seems to be a noteworthy, and perhaps unique, anti-predator behaviour.

Vocalizations usually powerful and distinctive, with most species uttering complex and often quite beautiful whistled or bell-like songs, which are one of the distinctive characteristics of the group and place them among the most outstanding avian songsters. Songs of most species highly characteristic. Some whistlers utter long sequences of varying and complex songs, often involving loud whipcracks as components, particularly at end of songs; other whistlers utter shorter and quieter songs, described as pensive, small voices, of a curiously indrawn quality. Vocalizations of shrike-thrushes *Colluricincla* are strong, mellow and beautiful whistles, with sequences of notes often shorter than those of whistlers. Vocalizations of pitohuis *Pitohui* are often loud, melodious whistles, with downslurred or upslurred elements, and Crested Pitohui also has a loud continuous throbbing bell-like call. Songs of *Mohoua* are canary-like trills, whistles and warbles. Song of Crested Bellbird clear and bell-like and distinctly ventriloquial. Many whistlers, and possibly other species, often call in response to sharp sounds, such as a loud, quick handclap, thunder or an explosion (e.g. Gilbert's Whistler). Song can be given in long bouts, e.g. lasting up to 15 min. Most species also utter harsher notes in contact or alarm, e.g. Grey Shrike-thrush (Jack 1949; Falla *et al.* 1979; Pizzey 1980; Ford 1989; Coates 1990; Coates *et al.* 1997; Gould).

Most species breed in simple pairs, though co-operative breeding reported in a few species (see above), and Whitehead sometimes polyandrous. In Aust., season usually from June–July to Jan.–Feb., but recorded at other times if conditions suitable; in NZ, season mainly Sept.–Feb. Extralimitally, in New Guinea, breeding of pitohuis largely undescribed, though season probably extends from late dry season to mid-wet season, roughly Oct. to mid-Feb. (Coates 1990). Most build nest in a fork in a branch or trunk of tree or shrub, usually in a well-concealed site among foliage; some species also recorded nesting in hollows in trunk or stump or other tree-cavities (e.g. Yellowhead), while others occasionally nest on ground (e.g. Grey Shrike-thrush), or on tussock of spinifex *Triodia* (e.g. Red-lore'd Whistler); some species nest on ledges of cliffs, quarries or steep banks (e.g. Sandstone Shrike-thrush). All species build a cup-shaped nest, usually of twigs, grass, bark, and sometimes leaves, often bound together with spider web, and lined with grass, plant-fibre or feathers. Crested Bellbirds unique in that they place hairy caterpillars, often alive but paralysed by adults, in and on rim of nest. Both sexes usually build, though only female builds in Brown Creeper and Yellowhead. Eggs usually oval to elliptical; white, yellowish white, pinkish flesh or bluish white, with light-brownish, inky or blackish markings; eggs of many species have zonation of markings at large end. Eggs usually laid on consecutive days, though last egg of clutch sometimes laid after an interval of 48 h (e.g. Crested Bellbird). Clutch-size usually two or three, though some species (e.g. Crested Bellbird and Brown Creeper) often lay four eggs. Both sexes usually share incubation, but in Whitehead and Yellowhead, only female incubates. Eggs hatch after 15–19 days. Usually both sexes brood, though in Whitehead and Brown Creeper, and presumably Yellowhead, only female broods. Both sexes feed nestlings. Fledge at 11–21 days old. Fledgelings continue to be fed by both parents for up to 9 weeks, sometimes longer.

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Mohoua albicilla Whitehead

COLOUR PLATE FACING PAGE 1025

Fringilla albicilla Lesson, 1830, In Duperrey, L.I., *Voy. Coquille, Zool.* 1, livr. 15: 662 — Bay of Islands, North Island, New Zealand.

This genus echoes the Maori names *mohuahua* and *momohua* for the Yellowhead. The specific name perpetuates the erroneous use of Modern Latin *-cilla*, the tail, instead of Latin *capillus*, the hair (Latin *albus*, white, and *-capillus*, headed, capped).

OTHER ENGLISH NAMES None.

MONOTYPIC

FIELD IDENTIFICATION Length c. 15 cm; wingspan c. 18 cm; weight: male 18 g, female 15 g. Distinctive small NZ passerine with short, sturdy bill and medium-length tail, tip of which appears slightly rounded when fresh but rather scruffy and spiky when worn; intermediate in size between Brown Creeper *Mohoua novaeseelandiae* and Yellowhead *M. ochrocephala*. Adult mostly light brown above and off-white below, washed light grey-brown on flanks and lower underbody, with contrasting off-white head and black bill, iris, legs and feet. Sexes differ slightly in adults, with males usually showing bright-white head and neck and glossy black legs, and females a varying brown wash on crown, hindneck, sides of neck and ear-coverts, and slightly paler legs (see Plumages); sexes alike in juveniles and immatures. Juvenile similar to adult female but more extensively washed brown below and much browner on top and sides of head and neck, with pale gape and paler greyish legs and feet. Immature very similar to adult female, but sometimes separable by pale gape. No seasonal or geographical variation. **Adult male** Head and neck usually uniform, off-white, though some have faint light grey-brown wash on hindneck and still fainter wash on crown. Rest of upperbody, light brown, sharply demarcated from white head and neck and grading to slightly darker brown on uppertail-coverts and uppertail; tips of rectrices often worn down to spine-like shafts, giving rather scruffy, spiky appearance to tip of tail. Folded wing mostly brown, with slightly darker brown

alula, primary coverts, greater secondary coverts and remiges; outer primaries have paler light grey-brown edges, forming diffuse pale panel, and greater secondary coverts show hint of similar pale panel, both becoming paler (almost whitish) and more obvious with wear. Underbody, off-white, washed light grey-brown on flanks, vent and undertail-coverts. Undertail, brown. Bill and gape, black. Iris, black-brown or black, prominent in whitish head. Legs and feet, glossy black or duller black, with paler greyish soles. **Adult female** Very similar to male but often more strongly washed light grey-brown on crown, nape and hindneck, and legs are dark but never black. Some overlap in pattern of head and neck with male, but these areas never as clean white as palest males and pairs usually separable when seen together by combination of differences in typical pattern of head and neck and colour of legs. **Juvenile** Broadly similar to adult female, differing by: brown of upperbody extending forward over hindneck and crown to forehead, with sides of head and neck also strongly washed brown, giving much darker-headed appearance overall; underbody slightly duller, off-white or cream, with more extensive and buff-tinged light grey-brown wash along sides, vent and undertail-coverts. Gape prominent and fleshy, and legs and feet are pale grey and paler than in any adult. **Immature** Very similar to adult female though some separable by outwardly adult female appearance coupled with obvious pale fleshy gape and juvenile begging behaviour.

Similar species None; in adult and immature plumages, combination of brown upperparts and whitish underbody with contrasting whitish head, diagnostic among NZ passerines. Juvenile Whitehead bears superficial resemblance to juvenile **Brown Creeper** but Brown Creeper does not occur on NI. Singing birds possibly confused with **Common Chaffinch** *Fringilla coelebs*, but Whitehead has more varied Song: starts with several chirps, followed by string of clear, canary-like chimes or *peek-o, peek-o, peek-o* calls and descending slurs, and ends with a chuckle (Song of Chaffinch is a more constant series of short notes ending in a terminal flourish *chip chip chip tell tell tell cherry-erry-erry tissi cheweeo*).

Gregarious; in breeding season seen singly, in pairs or, more usually, in small family groups and noisy flocks of 8–10 birds moving quickly through canopy; in autumn and winter often form loose foraging flocks of up to 30, and occasionally up to 70, birds, and often form mixed-species feeding flocks with other forest birds such as Yellow-crowned Parakeets *Cyanoramphus auriceps*, Saddlebacks *Philesturnus carunculatus* and Grey Fantails *Rhipidura fuliginosa*. Foraging flocks restless, noisy and inquisitive; move through canopy in short, almost hopping flights. Forage at all levels in vegetation, from ground to canopy, though mainly in middle and upper strata of forest. Feed mainly by gleaning insects from foliage, twigs and branches, but also by searching for prey under loose bark on trunks and large branches; less often snatch insects from foliage or air while hovering, and rarely feed on ground. Work hurriedly up tree-trunks and climb acrobatically among foliage, sometimes hanging upside-down to reach food; use stiff tail as a prop when clinging to bark. Calls distinctive, including loud chiming Song (see above), harsh single-note contact calls, and loud alarm calls (see Voice).

HABITAT Mainly confined to forest and dense shrubland, including regrowth, from coastal to subalpine areas (Wilkinson 1927; Moncrieff 1929; Challies 1962, 1966; Stidolph 1977; CSN 30); occur at elevations of up to c. 1300 m asl (Sibson 1958; Challies 1966; St Paul 1976).

Mainly inhabit tall open native forest dominated by Kanuka *Kunzea ericoides*, Manuka *Leptospermum scoparium*, Tawa *Beilschmiedia tawa* and Tawhera *Weinmannia silvicola*, usually with shrubby understorey and, sometimes, grassy ground cover (McLean 1907, 1912; Turbott 1947; Gravatt 1969; Stidolph 1977; McLean & Gill 1988; Gill & McLean 1992; Oliver; CSN 5, 31, 41). Also occur in mixed podocarp–broadleaf forest (Hilton 1969; Fitzgerald *et al.* 1989; CSN 31, 32) and beech *Nothofagus* forest (Sibson 1958; Challies 1966; St Paul 1976; CSN). Said to often inhabit edge of forest and low riparian vegetation (Turbott 1967). Also occur in shrubland (Sibson 1947; Stidolph 1977; Heather & Robertson 1997; Oliver); recorded in tall, subalpine scrub of Leatherwood *Olearia colensoi* and *Senecio eleagnifolius* (Challies 1966); also, on Kapiti I., occur mainly in low Tauhinu *Cassinia leptophylla* scrub (Wilkinson 1927). **MODIFIED HABITATS:** Often occur in plantations of exotic conifers, such as Monterey Pine, Beech Pine *Pinus contorta*, fir *Pseudotsuga* and larch *Larix*, occurring in plantations varying in age from young (5 years old) to mature (Weeks 1949; Falla *et al.* 1975; St Paul 1976; Innes *et al.* 1982; Gaze 1985; Heather & Robertson 1997; CSN). Sometimes occur in other exotic and modified habitats, such as gardens, farmland and orchards (Stidolph 1933; Sibson 1947; Gill 1990; CSN 41).

In **KAINGAROA FOREST**, recorded in pine and fir plantations at densities of 0.15–3.1 birds/ha (Gibb 1961).

DISTRIBUTION AND POPULATION Endemic to NI of NZ.

NI Occur on Little Barrier I. On mainland, recorded S of line joining Te Aroha, Hamilton and Pirongia. **BAY OF PLENTY:** Scattered, mainly in W, round Kaimai Ra. and Tauranga, and more sparsely scattered in s. subcoastal areas, E to Kereru and Raukokore Rs. **EAST COAST:** Recorded at a few scattered sites, in Raukumara Ra., and from Mangaheia R. S to Gisborne. **VOLCANIC PLATEAU:** Widespread. **HAWKES BAY:** Recorded at scattered sites in N, E to Putorino; widespread in Ruahine Ra. **WAIRARAPA:** Occur at scattered sites in SE and E, from near Flat Pt S to Haurangi Forest Park, and more widespread in Aorangi Mts and e. Rimutaka Ra. **WELLINGTON:** Widespread in Rimutaka and s. Tararua Ras. Also occur on Kapiti I. **MANAWATU:** Widespread in Tararua Ra. **WANGANUI:** Widespread in N, especially in Tongariro and Whanganui NPs. Occur S to Hihitahi (S of Waiuru) in E, and near Nukumarū (E of Waverley) in W. **TARANAKI:** Widespread in E, W to line joining sites near Waverley and Awakino. Farther W, recorded in Egmont NP, extending N through Kaitake Ra. to Oakura and New Plymouth. **WAIKATO:** Widespread; in W, widespread N to Pirongia Forest Park; also widespread in S and SE, N to Waikato R., upstream from L. Arapuni. Farther N, single NZ Atlas record near Hamilton (NZ Atlas; CSN).

Introductions Forty birds successfully introduced to Tiritiri Matangi I. from Little Barrier I. in Sept. 1989, and another 40 in May 1990 (Gill 1990; Armstrong *et al.* 1995); also introduced to Mokoia I. in L. Rotorua (Heather & Robertson 1997).

Breeding Throughout range.

Change in range, populations Formerly widespread throughout NI. Occurred round Auckland till mid- to late



Plate 29

(P. Marsack)

Varied *Sittella daphoenositta chrysoptera* (page 1000)
NOMINATE CHRYSOPTERA: 1 Adult male; 2 Adult female;
 3 Juvenile male; 4 Immature male (first basic); 5, 6 Adult male
SUBSPECIES STRIATA: 7 Adult male; 8 Adult female
SUBSPECIES PILEATA: 9 Adult male; 10 Adult female;
 11 Juvenile male
SUBSPECIES LEUCOCEPHALA: 12 Adult
SUBSPECIES LEUCOPTERA: 13 Adult male; 14 Adult female;
 15 Adult male

1870s but declines noted there and in Waikato round that time (Hutton & Drummond 1904; Turbott 1967; Oliver); no longer recorded in n. NI, and not recently recorded round Hamilton (I.G. McLean). Extinct on Great Barrier I., where formerly common (though recorded on nearby Arid I. [Rakitu I.] till at least 1957; Bell & Brathwaite 1964), Kawau I. and Hen and Chickens Is and islands in Hauraki Gulf by late 1880s (Turbott 1967; Bell 1976). Formerly common in Raukumara and Huiarau Ras but only present in scattered pairs by 1960s (CSN 19 Suppl.). Populations in Whakarewarewa and Kaingaroa Forests said to have increased in 1940s (Weeks 1949), but round Mt Holdsworth 1940–68 (Stidolph 1977). Numbers in Egmont NP increased noticeably in 1980s (CSN 37, 39).

Populations RECORDED DENSITIES: c. 50–60 birds/ha, Little Barrier I. (Gill 1990); 0.15–3.1 birds/ha, Kaingaroa Forest (Gibb 1961; see Habitat).

THREATS AND HUMAN INTERACTIONS Disappeared over large areas after clearing of forests, and survive mainly in areas of extensive and less modified forest (Turbott 1967; Falla *et al.* 1975; Innes *et al.* 1982; Oliver). However, have adapted to exotic pine plantations in some areas, where reportedly increasing in numbers (Oliver).

Eggs and young taken by rats (Wilkinson & Wilkinson 1952).

MOVEMENTS Little known. Probably resident (Moncrieff 1929; see below); may make local seasonal movements (Moncrieff 1929) though records possibly biased by changes in conspicuousness.

Present throughout year on Little Barrier I. (Gill & McLean 1992), at Whakarewarewa (Weeks 1949), in Kaingaroa Forest (Weeks 1949; Gibb 1961), Minginui (St Paul 1976; CSN 9), Orongorongo Valley, near Wellington (Gibb 1996) and on Kapiti I. (Wilkinson & Wilkinson 1952). At Minginui and in Orongorongo Valley, recorded most often in spring and summer, possibly because of movement in winter by part of population, but more likely because birds less vocal, and thus less conspicuous, during winter (St Paul 1976; Gibb 1996; CSN 7, 8).

Banding Total of 363 banded in NZ, 1950–96 (Cossee 1998); total number of retraps not known but only single recovery 1988–93 (Cossee 1989, 1992, 1993, 1995, 1998; Cossee & Wakelin 1991); of 40 banded 1964–73, 19 recoveries (47.5%) (Robertson 1972, 1974). In study on Little Barrier I., 1984–89 (Gill & McLean 1992), 195 colour-banded, and 158 resighted in study area. Some juveniles dispersed, but many remained in natal area: overall, 31 juveniles banded, and, of 26 resighted, all remained within 350 m of natal area in first year, after which some dispersed and some stayed near natal

area; ten stayed within 200 m of natal area for up to 40 months, while rest moved up to 650 m from natal area in second or third year. **LONGEVITY:** Adult male banded on Little Barrier I., Aug. 1984, recaptured 8 years later (Gill 1993).

FOOD Invertebrates, mainly insects; also fruit and seeds. **Behaviour** Mostly arboreal. Gregarious; usually forage in noisy flocks in tops of trees and vegetation in understorey; forage among foliage, under bark of branches and tree trunks, in moss on branches or logs and very occasionally on forest floor. Food mostly obtained by gleaning, but also by hanging upside-down, pulling, probing flowers and bark, and sallying, either sally-hovering to pick prey from foliage or sally-striking flying insects (Hutton & Drummond 1904; McLean 1912; Wilkinson & Wilkinson 1952; Turbott 1967; Gravatt 1971; Falla *et al.* 1975; Heather & Robertson 1997; Oliver; CSN 24, 29, 31, 34). **DETAILED STUDIES:** On Little Barrier I., 1967–1968 (Gravatt 1969, 1971); and in pine plantations in Kaingaroa Forest, 1958–59 (Gibb 1961). **SIZE OF FEEDING FLOCKS:** Forage in small flocks throughout year (Heather & Robertson 1997); feeding flocks most common during winter (St Paul 1976; Oliver), and usually comprise 8–10 birds, though sometimes up to 40, and, once, at least 70 (McLean 1912; Andersen 1926). On Kapiti I., foraged in pairs or singly in breeding season and in flocks outside breeding season (Wilkinson & Wilkinson 1952). On Little Barrier I., often forage in flocks, especially in winter; flocks may contain 15–20 birds, and become more common as winter progresses, and are most conspicuous in July, when food least available (Gravatt 1969). Often forage in mixed-species feeding flocks with Yellow-crowned and Red-crowned *Cyanoramphus novaeseelandiae* Parakeets, Saddlebacks, Grey Fantails, Silver-eyes *Zosterops lateralis*, Grey Warblers *Gerygone igata*, Bellbirds *Anthornis melanura*, Stitchbirds *Notiomystis cincta* and Common Chaffinches (McLean 1907; Andersen 1926; Gravatt 1969; St Paul 1976; McLean *et al.* 1987; Gill 1990; CSN 8). Usually most abundant species within flock, foraging in tight-knit groups at front of flock, determining direction of movement of flock (McLean 1907; McLean *et al.*). **FORAGING HEIGHTS:** Forage in crowns of trees and in understorey (McLean 1912; Wilkinson & Wilkinson 1952; Turbott 1967; Gravatt 1971; Falla *et al.* 1975; Heather & Robertson 1997; Oliver). On Little Barrier I., foraged at all levels of vegetation, from ground to canopy, though foraged more often in upper and middle levels of understorey than in other strata; of 1314 observations of foraging: 0.9% were on ground; 8.9% in lower understorey; 27.1% in understorey; 30.4% in upper understorey; 24.0% in subcanopy; and 8.7% in canopy; of 1837 observations of foraging, actual heights of feeding were: 3.4% on ground; 8.1% up to 1.5 m above ground; 16.4%, 1.6–3 m; 17.7%, 3.1–4.5 m; 16.8%, 4.6–6.0 m; 14.0%, 6.1–7.5 m; 13.4%, 7.6–9.0 m; 6.3%, 9.1–11.5 m, and 4.2%, >11.6 m. In Kaingaroa Forest, of 451 observations of foraging (figures estimated from graph), foraged mainly in middle levels of forest: none recorded on ground; c. 20%, 1.1–5 m above ground; c. 34%, 5.1–10 m; c. 27%, 10–15 m; c. 14%, 15.1–20 m; and c. 5%, 20.1–25 m. **FORAGING SITES:** Forage mostly among foliage; also on branches and trunks of trees where probe under bark; occasionally on ground (Wilkinson & Wilkinson 1952; Turbott 1967; Gibb 1961; Gravatt 1969, 1971; St Paul 1976; Gill 1990; Heather & Robertson 1997; Oliver). On Little Barrier I. (n=1718 observations of foraging), mostly foraged among foliage of trees and shrubs (39.5%); also among twigs (24.2%), on branches (22.9%), on

Plate 30

(D. Onley)

Brown Creeper *Mohoua novaeseelandiae* (page 1041)
1 Adult; 2 Juvenile; 3 Adult

Whitehead *Mohoua albicilla* (page 1023)
4 Adult male; 5 Adult female; 6 Juvenile

Yellowhead *Mohoua ochrocephala* (page 1032)
7 Adult male; 8 Adult female; 9 Juvenile

trunks (12.7%) and on ground (0.7%); not seen feeding in air. In Kaingaroa Forest, of 451 observations of foraging, mostly foraged among foliage (needles) of pine trees: 52% among live needles; 20% among dead needles; 22% on branches and among pine-cones; 4% on tree-trunks; 1% in vegetation in understorey; and 1% on ground. **FORAGING METHODS:** Forage mostly by gleaning. In Kaingaroa Forest, mostly foraged by gleaning, and sometimes by hanging upside-down or sallying for prey, including both sally-striking in air and sally-hovering to take prey from tips of pine-needles (Gibb 1961). Also often seen probing *Metrosideros* flowers, extracting either nectar or insects (Turbott 1967). Sometimes hover in air to examine tips of leaves; occasionally cling to tree-trunks, with tail pressed against trunks, tearing off chunks of moss and lichen with bill, in search of insects; sometimes hang upside-down when feeding (McLean 1912). Bill used to prise off pieces of bark and break up dead wood, and feet used to pull foliage to within reach, and to hold large insects while dismembering them (Gibb 1961; Gill 1990). Also use feet to hold fruit against branch to prevent it from rolling away (CSN 23).

Detailed studies In ORONGORONG VALLEY (19 faecal samples from adults mist-netted, Oct. 1973–Aug. 1976; Moeed & Fitzgerald 1982): **Plants** (fru., sds) Unident. 32% freq. **GYMNOSPERMS:** Podocarpaceae: *Dacrydium cupressinum* 16. **MONOCOTYLEDONS:** Pandanaceae: *Freycinetia baueriana* 11. **DICOTYLEDONS:** Cornaceae: *Griselinia lucida* 25; Epacridaceae: *Cyathodes fasciculata* 5; Escalloniaceae: *Carpodetus serratus* 11; Loganiaceae: *Geniostoma ligustrifolium* 16; Violaceae: *Meliccytus ramiflorus* 5. **Animals** MITES 32. **SPIDERS** 84. **INSECTS:** Blattodea 11; Coleoptera larv. 21, ads 79; Curculionidae 32; Elateridae 16; Diptera 11; Hemiptera 42; Cicadellidae 21; Hymenoptera 5; Lepidoptera: ads 32, larv. 58; Neuroptera 1; Orthoptera: Anastrostomatidae or Rhophadophoridae 16.

Other records **Plants** Fruit⁵, seeds^{1,4}. **DICOTYLEDONS:** Araliaceae: *Pseudopanax crassifolium* fru.³; Cunoniaceae: *Weinmannia racemosa* sds¹⁰; Escalloniaceae: *Ixerba brexioides* sds^{1,2,7}; Icacinaceae: *Pennantia corymbosa* fru.³; Loganaceae: *Geniostoma ligustrifolium* fru.³; Myrsinaceae: *Myrsine australis*³; Pittosporaceae: *Pittosporum* sds⁷, *P. crassifolium* sds²; *P. tenuifolium* sds²; Onagraceae: *Fuchsia excorticata* fru.³; Violaceae: *Meliccytus ramiflorus* fru.^{3,7,8}. **Animals** **SPIDERS**^{3,6}. **INSECTS**^{1,3,4,5}; Coleoptera⁶; Lepidoptera: ads^{5,6}; larv.^{6,9}.

REFERENCES: McLean¹ 1907,² 1912; ³ Wilkinson & Wilkinson 1952; ⁴ Turbott 1967; ⁵ St. Paul 1976; ⁶ Heather & Robertson 1997; ⁷ Oliver; CSN⁸ 23, ⁹ 29, ¹⁰ 32.

Young Fed by both parents and any helpers present (see Social Organization, Breeding). Contribution of helpers varied: at nests with no helpers (nine watches of >1 h at six nests) female made 46%±13.3 of feeding visits and male 53%±13.25; at nests with up to four helpers (12 watches at eight nests), primary female made 43%±18.1 of feeding visits, primary male 37%±17.7 and helpers 20%±18.5 (McLean *et al.* 1987; McLean & Gill 1988). At two nests on Little Barrier I., nestlings fed only by parents at one nest and by parents and one male helper at other; at first nest (n=124 min feeding obs.), nestling fed by female three times and male six times, and, combined, adults made 4.4 feeding visits/h; at other nest (n=255 min feeding obs.), three birds made total of 48 feeding visits at rate of 11.3 visits/h (Gill 1993). Also on Little Barrier I., adults and helpers carried food in throat-pouch as well as in bill; up to 1 h elapsed between feeds; and not all members in group fed young, as some only accompanied feeding birds (McLean 1987b).

SOCIAL ORGANIZATION Well known; several studies of colour-marked birds on Little Barrier I. (McLean & Gill 1988; Gill & McLean 1992; Gill 1993). Usually gregarious, occurring in small flocks of up to 10 or so birds (Oliver 1922; Moncrieff 1929; St Paul 1976; McLean & Gill 1988; Heather & Robertson 1997; CSN), comprising breeding pair and progeny from previous years (Heather & Robertson 1997); sometimes occur singly or in pairs during breeding season (Wilkinson & Wilkinson 1952). Outside breeding season, form larger flocks, including one of at least 70 birds (McLean 1912; St Paul 1976; McLean 1982; McLean & Gill 1988; CSN). Flock-size usually increases towards end of winter, when home-ranges of breeding groups overlap and groups may coalesce into larger flocks. Flocks break down into pairs and small flocks in spring (McLean 1912; Turbott 1947; McLean & Gill 1988). Form nucleus of mixed-species feeding flocks, especially in non-breeding season (see Food).

Bonds Often breed co-operatively (McLean & Gill 1988; Gill 1990; Gill & McLean 1992) but at least sometimes breed as simple pairs (Gill 1993). Apparently monogamous (Gill & McLean 1992). Of 75 birds, 43 were males; sex-ratio not significantly different from 1:1; of 11 helpers, nine were male and two female, a significant bias (Gill & McLean 1992). On Little Barrier I., where population density is high, usually do not breed till 2–3 years old, but on Tiritiri Matangi I., where introduced, breed in first season after hatching (Gill & McLean 1992). **MATE-GUARDING:** Male sings near nest during construction of nest (McLean 1912) and always guards female during building and laying (Gill & McLean 1986).

Co-operative breeding, Care of young From McLean & Gill (1988) unless otherwise stated. When breeding co-operatively, breeding unit usually comprises primary pair and up to six helpers, some of which sometimes help at nest; some groups contain two breeding pairs (McLean & Gill 1988; Gill 1990). Helpers are progeny from previous broods. Sometimes, two adult males appear to have similar status, but not known whether both copulate with primary female. Some females are polyandrous, with or without helpers; breeding units sometimes have more than one primary female. Suggested that within breeding unit, helper males may compete with primary males for copulation. One male nested successfully one year, lost his mate in winter and remained unmated in following breeding season. Helper male copulated with unbanded female, but copulation broken up by primary male of group. Helpers accompany primary female when she is off nest, and sometimes feed her; also associate with flock, giving alarm calls (McLean & Gill 1988). Primary female does all incubation and brooding (Gill & McLean 1986; McLean & Gill 1988; Gill 1993; see Breeding). Young fed by both parents or co-operatively by primary pair and one or more helpers (Guthrie-Smith 1925; Blanshard 1966; McLean *et al.* 1986, 1987; McLean & Gill 1988; Gill & McLean 1992; Gill 1993); see also Breeding. **TRANSLOCATED BIRDS:** In experiment involving groups of birds familiar with each other and taken from Little Barrier I. to Tiritiri Matangi I., groups largely disbanded and tended to form smaller breeding groups (Armstrong *et al.* 1995). Five of seven breeding groups formed on Tiritiri Matangi I. comprised unfamiliar pairings, and only two groups had helpers in first breeding season, compared with all of eight groups studied in high-density population on Little Barrier I. (Armstrong *et al.* 1995). **Dependence of young** Dependent for several weeks (Wilkinson 1927); often fed for 4–6 weeks after hatching, when young beg loudly and follow adults persistently, with almost continuous trilling if

adult is nearby (McLean 1982; McLean & Waas 1987; McLean & Gill 1988). Some juveniles continue to be fed in first winter, when 8–9 months old (McLean & Gill 1988). Young sometimes remain on natal territory with parent for up to 31 months, as helpers (Gill & McLean 1992).

Breeding dispersion, Territories, Home-range On sw. Little Barrier I., density of 1.6 primary pairs/ha much higher than density usually recorded on mainland NI (McLean & Gill 1988). On Little Barrier I., males and females occupy home-range of same size, crudely estimated to cover 7.0 ha (2.7; 3.8–14.1; 55) (Gill & McLean 1992); later and finer estimates showed home-range of up to 3.5 ha before breeding and as small as 1.3 ha in breeding season, range expanding again in fledgeling period (Allen 1988). Breeding group occupies all-purpose territory, but contribution to defence by helpers poorly known (Gill & McLean 1992). In non-breeding season, flocks often c. 1.6 km or more apart (St Paul 1976), though home-ranges of groups may overlap and groups may coalesce and form larger flocks (Heather & Robertson 1997).

Roosting No information.

SOCIAL BEHAVIOUR Reasonably well known from studies on Little Barrier I. (see Social Organization for references). Noisy and inquisitive (McLean 1912; Oliver), though also said to be shy (Secker 1960). Use chattering call or sharp notes to communicate with members of flock while foraging (McLean 1912). **MAINTENANCE BEHAVIOUR:** Parents reported bringing young to bathe in creek; birds jumped into water and splashed it over themselves till soaked; group then preened and dried out on branch (Wilkinson 1927).

Agonistic behaviour Two birds seen chasing each other through tree-tops; when another bird joined in, chase ended (McLean 1912); may have been part of courtship (see below). Male seen displacing another male (Gill & McLean 1992). A male sometimes prevents breeding female from returning to nest, once for 12 min; thought that female was subordinate in hierarchy of breeding group (McLean *et al.* 1986). **THREAT BEHAVIOUR, DEFENCE OF TERRITORY:** During nest-building and laying periods, male spends long periods singing from song-posts (McLean & Gill 1988); claim that not strongly territorial (NZRD) incorrect. A vigorous slurring call believed to be used in defence of territory (Secker 1958). Near nest, sometimes chase or mob other birds, e.g. Long-tailed Cuckoo *Eudynamis taitensis*, Grey Warbler and Saddleback (McLean *et al.* 1986; CSN 29, 31). Once attacked a Tui *Prosthemadera novaeseelandiae* caught stealing nest-material from White-head's nest during incubation; later, Whitehead abandoned nest (McLean *et al.* 1986).

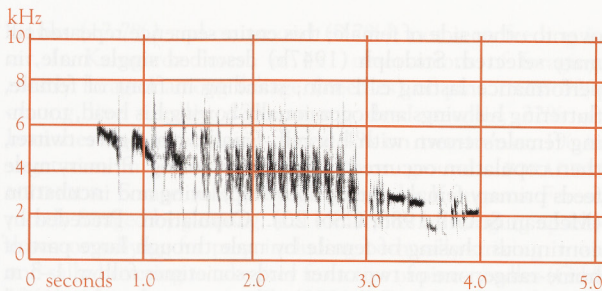
Sexual behaviour Lasts for several weeks before nesting begins. Male stays close to female and chases her (McLean & Gill 1988). A fluttering flight-display by two males in front of female, lasting several minutes, sometimes forms part of courtship (McLean 1912). **COURTSHIP DISPLAY** (from McLean 1912): Several groups of three, comprising two males displaying to a female, have been recorded; other males sang overhead, while others in understorey said to twitter at female to gain her attention. Female sat on sunlit branch, 1.5–2 m above ground, flanked by two males within 10–12 cm. With wings lowered and quivering, and tail fanned, each male slowly advanced towards female from either side, with body bowed and tail elevated, and birds twisting and turning. When female about to select one male, other may gently pull at her wing and bow. Other male then positions himself between female and rival male; in response, rival male skips

over to other side of female; this entire sequence repeated till mate selected. Stidolph (1947b) described single male, in performance lasting c. 1 min, standing in front of female, fluttering his wings and occasionally bowing his head, touching female's crown with his bill. Finally, male gave twitter, then copulation occurred. **Courtship feeding** Primary male feeds primary female during courtship, laying and incubation (McLean & Gill 1988; CSN 20). **Copulation** Preceded by continuous chasing of female by male through large part of home-range; one or two other birds sometimes follow, 1–3 m behind (McLean & Gill 1988). Chasing may last for several hours, during which copulation occurs several times. Copulation itself takes only a few seconds (McLean & Gill 1988) and may also be preceded by Courtship Display (see above).

Relations within family group Adults approach nest quietly and alone (Stidolph 1947a; McLean & Gill 1988). **Anti-predator responses of young** If disturbed, young may fledge, but vulnerable to predation when on ground (McLean *et al.* 1986). **Parental anti-predator strategies** In presence of intruder, one bird utters Chirrt, then rest of flock approaches. They gather with wings lowered and tails spread, uttering scolding calls till threat has passed (McLean 1912). Agitated male may scold intruders (McLean 1912). Once incubation advances, female sits tightly and low in nest, such that only tip of bill and tail visible at short range (Wilkinson 1927); she may utter alarm calls in presence of avian intruders without leaving nest (McLean *et al.* 1986). When young bathe in presence of person, parents attempt to drive them out of water (Wilkinson 1927).

VOICE Quite well known. Account largely follows observations of McLean (1912); descriptions of vocalizations in Allen (1988) not available for inclusion. Sonagram of begging trill of dependent fledgeling in McLean & Waas (1987). Many calls in musical notation given by Andersen (1918, 1926), and one, the trill component of Song, by McLean (1911). Noisy; heard much more often than seen; thought to give fewer Songs in winter (McLean 1907, 1912; St Paul 1976; Oliver). At Maunga-Haumia, in winter, vocalizations mostly short and harsh; Song first heard in July, but not heard often before flocks break up in late Aug. (McLean 1907, 1912). During nest-building and laying periods, male spends much time singing from song-posts; male helpers (see Social Organization) utter some Song (McLean & Gill 1988). Only male utters Song (McLean 1912). Respond to imitation, e.g. to shrill whistle, imitation of Chirrt or Swerre, or squeaking of cork on bottle (Reischek 1887; McLean 1907, 1912; St Paul 1976; CSN 36).

Adult SONG: Various described as: three *viu* notes, followed by four *zir* notes (Reischek 1887); a pleasant trill of six rapid bell-like notes, the sixth of higher pitch and sometimes omitted (McLean 1912); a continuous strain of various phrases, with portions of a canary-like character, as well as whistles, warbles and slurs (Andersen 1926); a very strong, high-pitched descending warble (St Paul 1976); and several chirps, followed by a series of clear canary-like chimes or *peek-o*, *peek-o*, *peek-o* notes and descending slurs, concluding with a chuckle (Heather & Robertson 1997). Sonagram A shows a Song described as three *viu* chirps, followed by a trill comprising a large number of *zir* notes, a few softer notes, a loud *peek-o* and some final softer notes (T. Howard). Suggestion that although Songs are all constructed from the same phrases, the same Song is never sung twice (Andersen 1926) is not



A L.B. McPherson; Puerora SF, NI, Jan. 1988; P106

supported by recordings, which show that Songs sometimes very similar or identical (T. Howard). Songs described as six-note trills (see above) said to be repeated from vantage point at intervals of c. 1 min, linked by soft notes, which may be barely audible (McLean 1912). Only males sing (McLean 1912). **CHIRP**: A chirp, given during communication within a group (McLean 1987a). A short *cheet* (sometimes *ter-cheet*), in an enquiring tone, heard continually from groups (McLean 1912); a hard single *zit* (Falla *et al.* 1975) and quick slurred *tsuit* uttered almost incessantly when foraging (sound of flock described as a twitter) (Andersen 1926) may describe same call. **CHIRRT**: A sharp *chirt* often taken up by other members of flock (McLean 1912). Louder and of higher pitch than Chirp (McLean 1987a). Uttered when young removed for banding, when mobbing owls and when attacked by honeyeaters. **CHE-CHE-CHE-CHE**: Rapid *che-che-che-che*, uttered when very excited (McLean 1912). **SWERRE**: Whistled hissing *swerre* given by male when very excited (McLean 1912). **CHATTER**: Various reported: a chattering call, thought to be a contact note (Secker 1958); chattering when foraging (McLean 1912); harsh chattering '*tche-tche ch-ch-ch-ch*' from female in breeding season (McLean 1912); much chattering and excitement when crowding round intruder (Oliver 1922). **TWITTER**: By males when courting (McLean 1912). Little twitter just before copulation (Stidolph 1947b). **Other calls** Vigorous slurring call, thought to be territorial threat (Secker 1958), may correspond to Chirrt. Give undescribed alarm call in presence of intruders (McLean *et al.* 1988).

Young Dependent fledgelings give trills constantly when parents nearby; rate of calling and length of trill increase as parent approaches. Main frequency of trills 7.94 kHz, and frequency range 2.7–9.84 kHz, with minimum frequency low because of descending tail on individual elements; begging trill contains 51.3 elements/s (McLean 1982; McLean & Waas 1987).

BREEDING Fairly well known, with studies of individually marked birds on Little Barrier I. (McLean *et al.* 1986; McLean & Gill 1988; Gill 1993). Breed in simple pairs or groups comprising primary pairs with helpers or polyandrous females with or without helpers (McLean & Gill 1988; see Social Organization, Behav-iour). Sometimes double-brooded (McLean & Gill 1988).

Season Eggs usually Oct.–Dec. (Oliver; CSN 20). On Kapiti I., eggs, Nov. and Dec., and young, Dec. and late Feb. (Wilkinson 1927); on Little Barrier I., eggs, first half of Sept. to second half of Dec., with peak in early Nov. (McLean & Gill 1988).

Site Usually well concealed among foliage of dense shrub or in canopy of tree (Wilkinson 1927; Weeks 1949); in fork, in intermeshed twigs or small branches, between trunk

and two branches or on frond of fern; once on accumulated leaf-litter along mid-rib of upright frond of Nikau *Rhopalostylis sapida*; said to prefer small-leaved plants, such as Kaikomako *Pennantia corymbosa*, Mahoe *Melicoytus ramiflorus*, Mapou *Myrsine australis*, Ramarama *Myrtus bullata*, Tauhinu *Cassinia leptophylla* or tea-tree (McLean 1912; Wilkinson 1927, 1936; Sibson 1947; Turbott 1947; Wilkinson & Wilkinson 1952; McLean & Gill 1988; Gill 1993; CSN 20). Round Urewera, on Volcanic Plateau, usually build on frond of tree-fern, 30–60 cm from trunk (Oliver). On Kapiti I., usually in dense, low-growing, small-leaved trees and shrubs, especially Tauhinu (Wilkinson 1927; Wilkinson & Wilkinson 1952); on Little Barrier I., of 72 nests, 50 (69.4%) were in Kanuka, the dominant species in the canopy (McLean & Gill 1988). Also nest in pine plantations (Gibb 1961). **MEASUREMENTS** (m): Height of nest, 2.5 (1.57; 1.2–5.5; 7) (Wilkinson 1927, 1936; Sibson 1947; Gill 1993; CSN 20); on Little Barrier I., 2–30 (McLean & Gill 1988); on Kapiti I., usually c. 1.8 (Wilkinson 1927).

Nest, Materials Nest a neat, deep cup with smooth, well-finished sides and rim; made of grass, twigs, leaves, leaf skeletons, plant-fibre, bark, rootlets, moss and sometimes wool, bound together with spider web; and lined with fine grass, tree-fern fibres and small feathers of other birds, such as parakeets *Cyanoramphus* and New Zealand Pigeon *Hemiphaga novaeseelandiae* (McLean 1912; Wilkinson 1927; Wilkinson & Wilkinson 1952; Gill 1993; Oliver). On Kapiti I., camouflage nest with lichen (Wilkinson & Wilkinson 1952). Only primary female builds (McLean & Gill 1988; *contra* Oliver). Building takes up to 4 days (Wilkinson & Wilkinson 1952); 4–7 days (McLean & Gill 1988). One female in group with primary male and four helpers built a second nest before young of first nest had fledged; other females began new nests while other birds fed their fledgelings (McLean & Gill 1988). On Little Barrier I., if more than 10 days elapsed between completion of nest and initiation of laying, nest abandoned and new nest built, or birds stopped breeding for that season. **MEASUREMENTS** (cm): For dimensions of nests, see Table 1.

Eggs Conical-oval to elliptical; finely textured; almost transparent; whitish to pink or fleshy, most speckled with minute, faint yellowish-brown spots or blotches, mostly on large end; some lack markings (Wilkinson 1927; Wilkinson & Wilkinson 1952). On Little Barrier I.: eggs vary from white with a few orange-brown spots, through being well spotted, to solid orange-brown with no spots (McLean & Gill 1988). Colour of eggs within a clutch usually similar (McLean & Gill 1988), though in one clutch of three, first egg different colour to second and third eggs (Wilkinson 1927). **MEASUREMENTS**: On Little Barrier I.: 20.1 (19.8–20.6; 4) × 14.7 (14.5–14.9; 4) (McLean & Gill 1988); on Kapiti I.: three eggs, 22 × 17, 23 × 17 and 24 × 17 (Wilkinson 1927). **WEIGHT**: Five eggs close to hatching, 2.18 (2.1–2.3) (McLean & Gill 1988).

Clutch-size On Little Barrier I., 2.82 (0.53; 2–4; 17): C/2 × 4, C/3 × 12, C/4 × 1 (McLean & Gill 1988); on Kapiti I.,

Table 1. Dimensions of nests.

External diameter	External depth	Internal diameter	Internal depth	N	Ref.
10.9 (10–11.4)	8.1 (7.6–9.0)	5.5 (5.0–6.4)	3.8 (2.9–4.5)	3	1, 3
10.2–12.7	c. 7.6	c. 5.1	2.5+	1	2

REFERENCES: ¹ Wilkinson 1927; ² Wilkinson & Wilkinson 1952; ³ Gill 1993.

usually three (Wilkinson & Wilkinson 1952); one clutch of one (Wilkinson 1927). Claimed that usually two, but in nests shared by two females, clutch-size is three (Oliver).

Laying Eggs laid on consecutive days (Wilkinson & Wilkinson 1952; McLean & Gill 1988). Laying usually begins a few days after completion of nest (Wilkinson & Wilkinson 1952), but can begin immediately (McLean & Gill 1988). Appear to need favourable weather during pre-laying period; in one season, squalls passed across island weekly and all completed nests that had not been laid in were abandoned (McLean & Gill 1988). Suggested that only one female lays in a nest (McLean & Gill 1988; *contra* Oliver). Primary male feeds primary female during laying (McLean & Gill 1988). Sometimes multi-brooded, and can raise two broods in a season; in one season, six (28.6%) of 21 groups laid two clutches, as did two (13.3%) of 15 groups in following season (McLean & Gill 1988). One female in a group built a second nest before young of first nest had fledged; second nest failed and female re-laid in first nest c. 2 weeks after first brood fledged (McLean & Gill 1988).

Incubation By primary female only (Gill & McLean 1986; McLean & Gill 1988; Gill 1993) *contra* claim that incubation by both sexes (Wilkinson & Wilkinson 1952; NZRD). During 362 min of observation at one nest, mean length of stints of incubation, 28.6 min (7.95; 17.5–40.0; 8); mean length of period off nest, 8.8 min (1.91; 6.0–13.0; 9) (Gill 1993). Incubating bird sits very low in nest so that only tip of bill and tip of tail visible (Wilkinson 1927). Incubating female fed mostly by primary male, and occasionally by helpers, either on or off nest (McLean & Gill 1988; Gill 1993; CSN 20). Settle onto nest by landing on rim with feet apart, then moving both feet forward on each side of nest and falling forward into nest, landing with bill digging into far side of nest; feet then moved farther forward to about halfway along nest and body lowered till tail rests on rim and bill lifted clear of nest (Blanshard 1966). When observer placed egg of Long-tailed Cuckoo in an unparasitized nest of Whitehead, egg was found undamaged on ground below nest 6 h later; when placed back in nest, it was found smashed on ground below nest next morning (Wilkinson & Wilkinson 1952). **INCUBATION PERIOD:** 18 days (17–19; 5) (McLean & Gill 1988); c. 17 days (Wilkinson & Wilkinson 1952).

Young Altricial, nidicolous. Newly hatched young have patches of grey down on top of head, back, top of wings, tibia and abdomen (Gill 1993). **Parental care** Only primary female broods (McLean & Gill 1988); during 124 min of observation at nest with young c. 4 days old, three bouts of brooding occurred, lasting 17, 28 and 15 min, with inattentive periods of 11, 17 and 18 min; during 255 min of observation at another nest with young c. 12 days old, bouts of brooding 11.9 min (8.0; 1.0–24.0; 10) with periods of inattentiveness 8.7 min (3.87; 5.0–18.5; 10) (Gill 1993). Both sexes feed young (Gill 1993; see Food). Sometimes helpers undertake most feeding of young, allowing primary female to re-nest (McLean & Gill 1988; see Laying, above). Adult removes faecal sacs from nest during feeding visit, while other adult may be waiting to feed nestlings (Blanshard 1966). **Growth** Weight of two nestlings: 1–2 days old, 2.4 and 3.3; 1 day later, 2.7 and 4.0; 2 days later, 3.0 and 4.1; 14 days later, 13.5 and 19.0; in another nest, three young, at c. 10 days old weighed 9.4, 11.4 and 13.0 (Gill 1993); and in another nest, chick 4–5 days old weighed 7 (McLean *et al.* 1986).

Fledging to independence **FLEDGING PERIOD:** 17.4 days (16–19; 5) (McLean & Gill 1988); 16 or 17 days (Wilkinson

& Wilkinson 1952). Young liable to leave nest early if disturbed; a Tui foraging round a nest caused two young, 16 days old, to leave nest; observer placed both young in tree near nest; next day, a Tui attacked and killed one of them (McLean *et al.* 1986). Fledgelings barely able to fly when leave nest; begin feeding themselves after c. 10 days, but still fed by parents at 4–6 weeks, and sometimes fed till 9 months old (McLean & Gill 1988).

Success On Little Barrier I., of 64 active nests, 21 (32.8%) fledged one or more young. Outcome of nests in 1984–85 (31 nests from 21 groups) and 1985–86 (20 nests from 15 groups): total number of clutches, 25 and 15; number of nests to fledge at least one young, 16 (51.6%) and six (30%); mean number of fledgelings per group, 1.38+ and 0.73; largest number of fledgelings produced by a group in either season (including groups which re-nested) in one season, four (McLean & Gill 1988). On Kapiti I., in one season, only one of eight nests was successful (Wilkinson 1927). Rats and Long-tailed Cuckoos take eggs and young (Wilkinson & Wilkinson 1952; McLean *et al.* 1986); one nest with eggs was deserted after observer twice placed egg of Long-tailed Cuckoo in nest (Wilkinson & Wilkinson 1952); once, a Saddleback plucked a 4–5-day-old chick from a nest and dropped it nearby (McLean *et al.* 1986). Rate of survival of young that leave nest early reduced because adults continue to feed any young left in nest (McLean *et al.* 1986). Parasitized by Long-tailed Cuckoo (Wilkinson 1927, 1936; HANZAB 4).

PLUMAGES Prepared by A.M. Dunn. Fledge in juvenile plumage. Post-juvenile moult results in adult-like first immature (first basic) plumage; timing and extent uncertain, but probably begins a few months after fledging. Thereafter, complete post-breeding (pre-basic) moults each cycle produce successive adult plumages without change in appearance. Sexes average slightly different in adult plumage. No subspecies. Descriptions based on examination of skins of 22 adult males, 11 adult females, five juveniles and four first immatures (AIM, NMNZ).

Adult male (Definitive basic). **HEAD AND NECK:** Mostly off-white (ne) with concealed dark-grey (83) bases to feathers. Sometimes have brown (c119B) suffusion to tips of feathers of nape and hindneck, and occasionally have weak brown (c119B) suffusion to tips of feathers on crown. **UPPERPARTS:** Mantle, back, scapulars and rump, light brown (c25). Uppertail-coverts, brown (c119B). All feathers have concealed dark-grey (83) bases. **UNDERPARTS:** Breast and belly, off-white (ne). Flanks, light grey-brown (119C). Vent, undertail-coverts and thighs, light grey-brown (119D). All feathers have concealed dark-grey (83) bases. **UPPERTAIL:** Rectrices, brown (119B). **UNDERTAIL:** Rectrices, brown (119B) with off-white (ne) shafts. **UPPERWING:** Marginal and median secondary coverts, brown (119B). Greater secondary coverts and alula, dark brown (121) with brown (119B) outer webs; outer webs can become very pale with wear. Most marginal and median primary coverts, brown (119B); marginal coverts near alula, off-white (ne). Greater primary coverts, dark brown (121) with brown (119B) edge to outer webs. Tertiaries, brown (119B). Primaries and secondaries, dark brown (121) with narrow brown (119B) edge to outer webs and concealed off-white (ne) edge to inner webs; on p4–p10, edge to outer webs grades to light grey-brown (c119D) distally. **UNDERWING:** Secondary coverts, off-white (ne) with concealed dark-grey (83) bases. Marginal and median secondary coverts, brown

(119B) with broad off-white (ne) tips. Greater primary coverts, light grey-brown (45). Tertiaries, dark brown (121). Primaries and secondaries, dark brown (121) with off-white (ne) edges to inner webs.

Adult female (Definitive basic). Very similar to adult male, but usually browner on crown, nape and hindneck. Feathers of nape and hindneck usually have strong brown (119B) suffusion to tips, and feathers of crown often also suffused with brown (c119B). Head never as white as whitest males, but there is some overlap in appearance between sexes. Rest as adult male.

Nestling Down, grey, and distributed in eight main patches: ocular, coronal, occipital, dorsal, humeral, secondary, femoral and abdominal (Gill 1993).

Juvenile Similar to adult, but with much browner top of head and slightly browner underparts. **HEAD AND NECK:** Forehead, crown, nape and hindneck, almost uniform brown (c119B) with partly visible off-white suffusion to middle of feathers, and concealed dark-grey (c83) bases to feathers. Lores, ear-coverts and sides of neck, off-white (ne) with weak brown (c119B) suffusion to tips of feathers. Chin and throat as adult. **UPPERPARTS:** Coloured as adult, but feathers softer and more loosely textured. **UNDERPARTS:** Breast and belly, off-white (ne) to cream (c92) with light grey-brown (c119D) to buff (c124) suffusion to feathers at sides. Flanks, light brown (c239) with greyish (ne) wash. Vent and undertail-coverts, light grey-brown (c119D) with weak buff (c124) wash. Thighs, light grey-brown (c27). **TAIL:** Mostly as adult, but rectrices average slightly narrower and more pointed at tips. **WING:** As adult.

First immature (First basic). Mostly as adult female, from which difficult to distinguish, but appears to average slightly browner head, and rectrices average slightly narrower and more pointed at tips. Remiges and rectrices probably retained from juvenile plumage.

BARE PARTS Based on photos (Moon 1992; NZRD) and published information. **Adult male** Bill, black (89). Gape, black (89). Iris, black-brown (119); or black (Oliver). Orbital ring, black (89). Legs, glossy black (89); sometimes dark but not black (Gill & McLean 1986). Feet, grey (84); or black (Oliver). Claws, brown (Oliver). **Adult female** Mostly as adult male, but legs slightly paler (Gill & McLean 1986). **Nestling** When newly hatched: gape, yellow; inside mouth, deep yellow (Gill 1993). No further information. **Juvenile and first immature** Little information. Gape, fleshy (Gill & McLean 1986; Heather & Robertson 1997; AIM); some still had fleshy gape in July after fledging (Gill & McLean 1986). Legs, pale grey (Heather & Robertson 1997); paler than both adult male and adult female (Gill & McLean 1986).

MOULTS Based on examination of skins of 25 adults and nine juveniles and immatures (AIM, NMNZ), and published information as cited. **Adult post-breeding** (Second and subsequent pre-basic). Complete; primaries outward. Few data. Moulting of primaries probably starts Feb. or Mar. and probably finishes in Apr.; from skins, active moult recorded: Mar. (3 of 4; PMS 5, 19, 25); no skins for Apr.; all had finished by May (n=7), and none recorded with active moult of primaries June–Feb. (n=10). Active moult of tail recorded only in Mar., when one was moulting all rectrices, and another moulting t1. Active moult of body recorded Mar. (3 of 4), May (2 of 7) and June (1 of 1), and appeared most active in Mar. when moult was heavy in both upperparts and underparts. On Little

Barrier I., moult of wing and tail recorded only in mid-Feb. (Gill & Veitch 1990). **Post-juvenile** (First pre-basic). Few data. Extent uncertain; probably partial, involving feathers of body and most wing-coverts. Active moult of body was recorded in Mar. (n=3), May (n=2) and June (n=1).

MEASUREMENTS (1–2) NI, skins (AIM, NMNZ): (1) Adults; (2) Juveniles and first immatures. (3) Little Barrier I., adults, live, sexed by behaviour (Gill & McLean 1986). (4) Little Barrier I., adults and first immatures, live (Gill & Veitch 1990). (5–6) Orongorongo Valley, adults, live (Robertson *et al.* 1983): (5) Sexed by plumage; (6) Sexed by principal components analysis. Wing U = minimum chord of flattened but unstraightened wing; Bill N = length of bill from anterior edge of nostril to tip; Tarsus B = length of tarsus from ankle-notch to edge of bent-over foot.

		MALES	FEMALES		
WING	(1)	72.5 (2.11; 68–77; 22)	67.7 (3.10; 63–73; 11)	**	
	(2)	71, 74	66, 66, 67		
WING U	(3)	71.5 (2.4; 67–77; 19)	65.8 (2.2; 62–70; 20) ¹	**	
	(4)	70.6 (1.90; 67–74; 42)	65.1 (1.76; 62–69; 25)	**	
	(5)	72.5 (1.93; 67–76; 19)	68.5 (2.91; 64–74; 27)	**	
	(6)	71.7 (1.70; 67–75; 24)	66.3 (1.10; 64–68; 15)	**	
	TAIL	(1)	66.3 (3.60; 60–74; 21)	66.1 (3.36; 62–72; 8)	ns
		(2)	66, 71	61, 63, 66	
(3)		64.3 (3.5; 59–72; 19)	59.6 (2.7; 56–67; 19) ¹	**	
(4)		64.1 (3.19; 57–72; 41)	60.4 (2.39; 57–66; 24)	**	
(5)		67.7 (3.04; 60–71; 15)	65.2 (3.40; 60–71; 21)	*	
(6)		67.8 (3.02; 60–71; 21)	64.3 (2.94; 60–69; 15)	**	
BILL S	(1)	13.9 (0.66; 12.1–14.7; 20)	12.9 (0.47; 12.4–13.9; 11)	**	
	(2)	13.2, 13.7	11.5, 12.7, 12.8		
BILL N	(3)	7.3 (0.29; 6.6–7.9; 19)	6.6 (0.35; 5.8–7.0; 19) ¹	**	
	(4)	7.8 (0.37; 7.0–9.0; 42)	7.0 (0.31; 6.5–7.7; 25)	**	
BILL F	(5)	10.7 (0.46; 10–11; 15)	9.9 (0.53; 9–11; 22)	**	
	(6)	10.4 (0.51; 10–11; 22)	9.7 (0.59; 9–11; 15)	**	
TARSUS	(1)	26.8 (0.83; 25.0–28.4; 20)	25.6 (0.40; 25.2–26.3; 11)	**	
	(2)	25.6, 27.3	23.6, 25.1, 25.8		
	(3)	27.7 (0.62; 27–29; 12)	25.9 (1.49; 23–28; 21)	**	
	(4)	27.6 (0.68; 26–29; 21)	25.1 (0.96; 23–36; 15)	**	
	TARSUS B	(3)	27.2 (0.87; 25.1–28.4; 19)	25.4 (0.87; 23.6–27.0; 20) ¹	**
		(4)	27.9 (0.95; 25.4–29.7; 42)	26.2 (0.90; 24.6–27.5; 25)	**
TOE C	(5)	17.6 (1.35; 14–19; 15)	16.7 (1.45; 14–20; 22)	*	
	(6)	17.9 (0.95; 16–20; 22)	16.0 (1.00; 14–17; 15)	**	

¹ Includes one incorrectly sexed female, subsequently found to be male based on behavioural observations (Gill & Veitch 1990).

There may be some overlap of samples (3) and (4).

WEIGHTS (1) NI, NZ, adults, from museum labels (AIM, NMNZ). (2) Little Barrier I., adults, live, sexed by behaviour (Gill & McLean 1986). (3) Little Barrier I., adults and first immatures, live; sexed using measurements (Gill & Veitch 1990). (4–5) Orongorongo Valley, adults, live (Robertson *et al.* 1983): (4) Sexed by plumage; (5) Sexed by principal components analysis.

	MALES	FEMALES
(1)	13.6 (1.88; 10.5–15.9; 7)	11.0
(2)	18.0 (0.72; 16.6–19.3; 19)	14.0 (1.11; 12.3–16.4; 18) ¹
(3)	18.3 (1.05; 16.1–20.6; 42)	14.1 (0.90; 12.3–15.9; 25)
(4)	18.3 (1.27; 16–21; 20)	17.0 (2.42; 12–20; 27)
(5)	18.5 (1.12; 16–21; 24)	15.2 (1.79; 12–19.5; 15)

¹ Female with weight 16.4 g incorrectly sexed; subsequently found to be male based on behavioural observations (Gill & Veitch 1990).

There may be some overlap of samples (2) and (3). One adult female with egg in oviduct weighed 18 g (Gill & McLean 1986). One adult female weighed 1.9 g more in Aug. than in Nov. (Gill & McLean 1986). One immature female from Mt Bruce weighed 14 g (from museum label; NMNZ).

STRUCTURE Wing moderately long and broad. Ten primaries: p5 and p6 longest, p7 sometimes equal; p10 30–34 mm shorter, p9 13–16, p8 3–6, p7 0–1, p4 1–3, p3 5–7, p2 9–11, p1 12–13. P5–p8 slightly emarginated on outer webs; no emargination on inner webs. Nine secondaries, including three tertials; tips of longest tertials do not reach tips of secondaries on folded wing. Tail moderately long with rounded tip and slight downward (concave) curve; 12 rectrices. Bill rather short and straight; about half length of head. Tarsus moderately long and rather strong; partly fused scutes on front and fully fused to rear. Tibia fully feathered. Middle toe with claw 16.3 (1.59; 14.4–18.5; 6). Outer toe 79–93% of middle, inner 75–87%, hindtoe 89–106%. Claws rather strong, and rear claw quite long.

SEXING Sexes overlap in plumage, but measurements can be used to separate sexes (Robertson *et al.* 1983; Gill & McLean 1986; Gill & Veitch 1990). Robertson *et al.* (1990) used a principal component analysis of seven different measurements to separate sexes. This analysis found that weight and wing-length were especially good indicators of sex. A plot of wing-length against weight resulted in a total separation of sexes into two separate clusters. Robertson *et al.* (1990) also found that attempts to identify sex on the basis of plumage characteristics resulted in some incorrectly sexed individuals. In an attempt to develop sexing criteria, Gill & McLean (1986) identified the sex of individuals using behavioural observations and compared the results with sexing based on plumage characters and measurements. They found that all birds with bright-white head and black legs were males, but that browner-headed birds and those with slightly paler legs were either sex. They found that within a pair, male was always whiter-headed and larger than female. They also confirmed that a plot of wing-length against weight resulted in separation of sexes into two separate clusters. In their initial analysis, one bird identified as female by plumage was clustered with males, but subsequent behavioural observations showed that it was in fact a male (Gill & Veitch 1990).

GEOGRAPHICAL VARIATION None.

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Volume 6, Plate 30

Brown Creeper *Mohoua novaeseelandiae* (page 1041)
1 Adult; 2 Juvenile; 3 Adult

Whitehead *Mohoua albicilla* (page 1023)
4 Adult male; 5 Adult female; 6 Juvenile

Yellowhead *Mohoua ochrocephala* (page 1032)
7 Adult male; 8 Adult female; 9 Juvenile