

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 some 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 ochrocephala **Yellowhead**

COLOUR PLATE FACING PAGE 1025

Muscicapa ochrocephalus Gmelin, 1789, *Syst. Nat.* 1(2): 944 — Queen Charlotte Sound, South Island, New Zealand.

The specific name is based on Latham's (1783; *Gen. Synop. Birds* II: 342) 'Yellow-headed Fly-catcher' (Greek ὠχρός, pale yellow, and κέφαλος, headed).

OTHER ENGLISH NAMES Yellow-headed Flycatcher, Bush Canary.

MONOTYPIC

FIELD IDENTIFICATION Length c. 15 cm; wingspan unknown; weight male 30 g, female 26 g. Largest *Mohoua*, noticeably larger than Whitehead *Mohoua albicilla* or Brown Creeper *M. novaeseelandiae*. Distinctive small NZ passerine with sturdy bill and medium-length tail, tip of which appears rather scruffy and spiky when worn. Adult, olive-brown above, with strikingly bright-yellow head, neck and underbody, and black bill, legs and feet. Sexes differ slightly in adults, with head and neck often cleaner yellow in males, and hindneck, crown and nape usually mottled with olive-brown in females; however, much overlap and sexes not reliably separable in field; sexes alike in juveniles and immatures. No seasonal variation. Juvenile similar to adult, but head and underparts paler yellow with stronger brown tinge. Immature indistinguishable from adult in field. **Adult** Head and neck, bright yellow, with olive-brown wash or mottling on centre of hindneck, and finer mottling over crown, strength and extent of which varies, with males usually showing cleaner yellow head and neck, and females more strongly marked with olive-brown, but much overlap with male in pattern of head and neck. Rest of upperbody, olive-brown, grading to olive on uppertail-coverts and yellowish olive on uppertail; tips of rectrices wear down to spine-like shafts, giving rather scruffy, spiky appearance to tip of tail. Folded wing mostly olive, with outer primaries edged paler, forming faint diffuse paler panel. Underbody mostly bright yellow, as head and neck, merging to off-white on lower belly and vent; undertail-coverts, off-white with yellow suffusion; and flanks and extreme sides of breast and belly often washed olive-brown. Undertail, dark yellow-olive. Bill, gape, legs and feet, black, with paler greyish-yellow soles. Iris, black-brown, prominent in bright-yellow head. **Juvenile** Poorly known. Broadly similar to adult but possibly distinguished by: top of head and neck, almost uniform olive-brown, as rest of upperbody, and sides of head and neck also strongly suffused olive-brown, giving much less yellowish appearance. Further differ by: paler yellow underbody; duller, yellow-brown undertail-coverts; yellow gape in recently fledged birds; and paler legs and feet with yellower soles.

Similar species Unlikely to be confused: within tall native forest, combination of olive-brown upperparts with contrasting bright-yellow head, neck and underbody, diagnostic. In darker-headed juvenile, combination of olive-brown upperparts and duller olive-yellow underbody and sides of head equally distinctive. Among NZ passerines, only adult male **Yellowhammer** *Emberiza citrinella* shares predominantly bright-yellow head, neck and underbody, but inhabits more open country (rarely within native forest); usually has lateral crown-stripes and dark-framed ear-coverts; olive-brown and boldly dark-streaked saddle; uniform reddish-brown rump;

obvious white edges to tail; diffuse reddish-brown breast-band and dusky flank-streaking; short finch-like bill; and very different calls. Calling Yellowheads could be confused with **Brown Creeper**; Song has some resemblance to Song of Brown Creeper, but readily distinguished with experience: consists of loud penetrating series of 6–8 rapidly repeated notes, described as a trill or rapid shivering rattle with many variations, louder and more mechanical than Song of Brown Creeper.

Usually seen in pairs, threes or small family parties during breeding season. More gregarious in autumn and winter, when family groups amalgamate to form large, noisy feeding flocks of up to 40 birds. In autumn and winter often occur in mixed-species feeding flocks of Brown Creepers, Grey Warblers *Gerygone igata* and other small passerines, and, especially, foraging Yellow-crowned Parakeets *Cyanoramphus auriceps*. Feeding flocks restless, noisy and inquisitive, moving quickly through forest in short, almost hopping flights. Forage mainly in or just below upper canopy of forest and in trees of sub-canopy, but occasionally also on logs and among litter on ground; feed mainly by gleaning insects from foliage, twigs, branches and trunks of trees, pulling bark and moss from trees, or by probing cracks and crevices of trees, and occasionally also take insects by sally-hovering. Agile and acrobatic when foraging in canopy, often hanging upside-down to reach prey on leaves and twigs, and clinging to bark and using stiff tail as a prop while scratching vigorously with one foot among leaf-litter that has accumulated in forks and crevices of trees. Calls distinctive; include loud musical canary-like trilling Song of male, and varied loud rapid staccato Rattles, slurring and buzzing notes (see Voice).

HABITAT Mainly large tracts of native beech forest (Turbott 1967; Falla *et al.* 1975; Gaze 1985; Elliott 1986), often dominated by Red Beech *Nothofagus fusca* or Silver Beech *N. menziesii*, and less often Mountain Beech *N. solandri*; forests usually have an open understorey (Elliott & Ogle 1985; Gaze 1985; Elliott 1986; Read & O'Donnell 1987; Read 1988a; Elliott & Rasch 1995; Elliott *et al.* 1996; O'Donnell 1996a; Heather & Robertson 1997; Dilks 1999; Oliver; CSN). In Dart and Rees R. Catchments, Mt Aspiring NP, recorded mainly in low-altitude valleys with tall, low-density Red Beech forest, and least often at high altitudes in low, dense Silver and Mountain Beech forests on steep slopes (Elliott 1992). Preference for tall forests probably because diameter of trees larger and provide suitable nest-cavities (Elliott 1990, 1992); also selectively forage in large trees (Read 1988a; Elliott 1990). Many historical records in podocarp-hardwood forests, but species disappeared from most by early 1900s (Gaze 1985; Elliott 1986; O'Donnell

1993; Heather & Robertson 1997; C.F.J. O'Donnell). Absent from modified habitats, such as regrowth vegetation and exotic pine plantations (Turbott 1967).

DISTRIBUTION AND POPULATION Endemic to SI of NZ.

SI (Based on Gaze [1985] and references therein.) **NELSON:** Few recent records, mainly on Nukuwaiata I. in Marlborough Sounds, where introduced (see below); before 1990s, recorded at edge of Pikikiruna Ra. 'above' Abel Tasman NP, Flora Stream and Cobb Valley; single bird recorded in hills near Nelson. **MARLBOROUGH:** No records in NZ Atlas. Recent records include: L. Chalice, Richmond Ra., in 1973; Whangamoia Saddle, Richmond Ra., in 1975–76; and Mt Stokes in Queen Charlotte Sound in 1985. **CANTERBURY:** Largely confined to Arthurs Pass NP, especially in E round tributaries of Waimakariri R., with records extending N to Hurunui R. **OTAGO:** Recorded in Blue Mts and downstream along Clutha R. to near Evans Flat; also much farther W, along Rees, Caples and Dart Rs. **SOUTHLAND:** Recorded at scattered sites in Catlins State Forest Park, and scattered sites from Longwood Ra. N to Eyre Mts; farther W, widespread throughout Fiordland. **WESTLAND:** Few recent records; NZ Atlas shows records from Mt Aspiring NP N to Paringa; in Westland and Mt Cook NPs; at a few sites on w. slopes of Southern Alps adjacent to Arthurs Pass NP; at a few sites in Paparoa Ra.; and at Little Wanganui Saddle on Wangapeka Track. However, since mid-1970s, despite several extensive surveys, recorded at very few sites: Okarito, Hunts Beach SF and Landsborough Valley (Gaze 1985; O'Donnell 1993; NZ Atlas; CSN).

Breeding Few recent records; possibly throughout range.

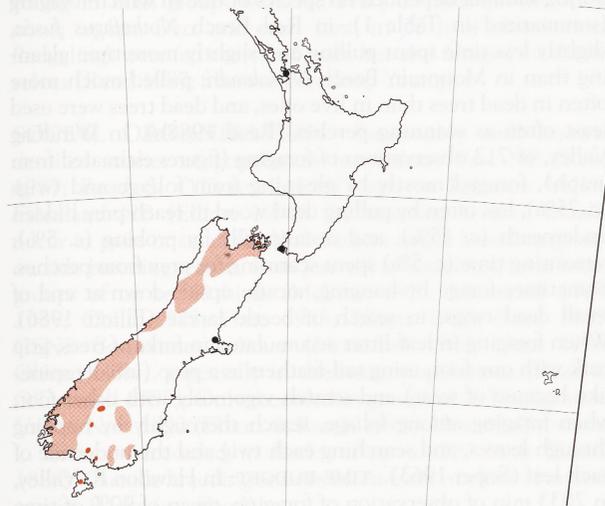
Introductions In 1999, four birds from Mt Stokes were released onto Nukuwaiata I. in Marlborough Sounds; a further 27 from Dart R., Otago, released in 2001 (M. Avis).

Change in range, populations Based on Gaze (1985) unless stated. Formerly widespread and abundant (Turbott 1967; Elliott & O'Donnell 1988; Oliver) but overall range declined dramatically in late 19th and 20th centuries, with much of reduction in range having occurred since late 1960s, probably largely as a result of clearance of forests, though other influences such as introduced predators probably also involved (Gaze 1985; Elliott 1986; Elliott & O'Donnell 1988;

C.F.J. O'Donnell). Currently absent from c. 75% of former range (O'Donnell 1996a). In Nelson and Marlborough, formerly recorded from C. Farewell to Queen Charlotte Sound. Apparently plentiful round Nelson till 1920s and 1930s, though said to have disappeared from round the city by mid-1920s. Regularly recorded at sites N of Buller R. till 1950s; not recorded s. Big Bush 1962–73; regularly recorded Flora Stream and Cobb Valley till 1975, but recorded only once since then, in 1984. Recorded near Nelson in 1978. In Marlborough, formerly widespread and common; disappeared from D'Urville I. by 1930, and by early 1940s no longer present in parts of Richmond Ra. or in inner Sounds. However, large flocks still recorded at some sites in 1950s and in mid-1960s, but rarely recorded since 1970s. Formerly plentiful in Canterbury, with breeding recorded on Banks Pen., but disappeared from most areas by early 1900s. Last recorded on Banks Pen. in 1910. Once common in Otago, round Dunedin and Taieri, but said to have gone by early 20th century, though still reported in vegetated valleys near Dunedin till 1946. Formerly present round Invercargill and on Stewart I. in Southland, but gone by 1930s (Elliott 1986). Populations in Eglinton Valley increased rapidly after Stoats *Mustella erminea* systematically poisoned and trapped after 1990 (Dilks 1999) but numbers have since declined greatly after populations of Stoats increased again in late 1990s (D.J. Onley). Said to have been common in Westland in 1860s, but few historical records between Paringa and Taramakau R.; recorded at Franz Josef and Fox Glaciers in early 1900s but gone by 1930. Population in Landsborough Valley declined from c. 350 birds in 1985 to <30 birds after two irruptions of Stoats (O'Donnell 1993). Total population in Fiordland and Mt Aspiring NPs said to be several thousand birds (O'Donnell 1993).

Status Threatened. Populations At Mt Stokes, Marlborough Sounds, population estimated at c. 15 birds in early 1990s (O'Donnell 1993); increased to 90 birds by 1999, but gone by summer 2000 after plague of Black Rats *Rattus rattus* (M. Avis). In Hawdon R. Valley, Arthurs Pass NP, recorded at: 0.06 birds/ha in 1983, 0.07 birds/ha in 1984, 0.08 birds/ha in 1985, 0.07 birds/ha in 1986, 0.04 birds in 1987 and 0.03 birds/ha in 1988 (Read & O'Donnell 1987; Elliott & O'Donnell 1988); overall population in Arthurs Pass is <200 birds (Elliott & O'Donnell 1988) or <50 birds (O'Donnell 1993). In 1993–94, 30 territories recorded along 2.5-km transect (CSN 42). In Eglinton Valley, recorded at: 0.9 birds/ha in 1984–85, 1.4 birds/ha in 1985–86, 1.1 birds/ha in 1986–87 and 1.0 birds/ha in 1987–88 (Elliott & O'Donnell 1988). In s. branch of Hurunui R., estimated at c. 150 birds; in Blue Mts estimated at several thousand birds (O'Donnell 1996a).

THREATS AND HUMAN INTERACTIONS Population has declined and range contracted since 1880s (Gaze 1985; Read & O'Donnell 1987; Elliott & Rasch 1995; see above). Major cause of decline on e. coast is probably clearance of forest, though disappeared from large areas of uncleared forest in Nelson and n. Westland; other factors, such as modification of forests by possums and deer, and disease, also possibly partly responsible for decline (Gaze 1985; Elliott 1986; O'Donnell 1993; Oliver). Continued logging of forests considered a major threat to survival of the species (Elliott 1986, 1992); especially adversely affected by removal of large trees which are used for feeding and breeding (Elliott 1986). In Waitutu SF, w. Southland, absent from logged areas (Elliott & Ogle 1985).



Populations decline dramatically during eruptions of introduced Stoats and Black Rats that occur after abundant seeding of beech *Nothofagus* (Elliott & O'Donnell 1988; O'Donnell 1993; Elliott 1996; O'Donnell *et al.* 1996); e.g. population in Hawdon Valley, Arthurs Pass NP, declined from 60–80 birds to 12–14 birds after irruption of Stoats and House Mice in Nov. 1987 (CSN 36). Incubating females are especially vulnerable to predation by Stoats, with no escape from nest-hollow for adult bird (Elliott & O'Donnell 1988; O'Donnell 1993; Elliott 1996). Also killed by Black Rats, which occasionally occur in plagues, and possibly by Cats (Elliott 1986; O'Donnell 1993; M. Aviss; C.F.J. O'Donnell). Possibly vulnerable to competition for nest-hollows with introduced wasps (O'Donnell 1993).

MOVEMENTS Very little known. Described as resident in Eglinton Valley, Fiordland NP (Dilks 1999) and present throughout year in Windbag Valley, s. Westland (O'Donnell & Dilks 1994). Also make local seasonal movements in search of food (Moncrieff 1929); and mobile flocks occur in winter (Elliott 1986); in winter in Hawdon Valley, adjacent territorial groups form into larger flocks and range over 60–100 ha, often moving from valley floors up mountainsides to c. 900 m asl (C.F.J. O'Donnell).

Banding Total of 149 banded in NZ, 1950–96; no recoveries, 1988–93 (Cossee 1989, 1991, 1993, 1995, 1997, 1998a,b; Cossee & Wakelin 1991). **LONGEVITY:** In Eglinton Valley, Fiordland NP, 1990–98, of 39 colour-banded pairs, oldest individual was at least 16 years old, and six birds were ≥ 12 years old (Dilks 1999).

FOOD Invertebrates, mainly insects; occasionally fruit and nectar. **Behaviour** Mainly arboreal. Forage from foliage, branches and trunks of trees, mostly in canopy, searching crevices and crotches in large trees; sometimes forage among lichen and moss on bark of trees and on ground, or among leaf-litter (Hutton & Drummond 1904; Andersen 1926; Soper 1963; Turbott 1967; Child 1978; O'Donnell & Dilks 1994; Heather & Robertson 1997; Oliver; CSN). **DETAILED STUDIES:** In Hawdon River Valley, Arthurs Pass NP (Read 1988b) and in Windbag Valley, s. Westland (O'Donnell & Dilks 1989, 1994). **SIZE OF FEEDING FLOCKS:** Usually forage in flocks of from three birds up to 40 or so (Andersen 1926; Lambert 1970; Child 1978; Oliver; CSN 25, 32). Feeding flocks common outside breeding season (mid-summer to late winter) and mostly comprise congregations of family parties (Heather & Robertson 1997). During breeding season, when female incubating, male feeds either alone or with conspecifics (Soper 1963). Often accompanied by parakeets *Cyanoramphus* while feeding, and occur in mixed-species feeding flocks, often containing Brown Creepers, Grey Warblers, New Zealand Tomtits *Petroica macrocephala*, Grey Fantails *Rhipidura fuliginosa*, Rifleman *Acanthisitta chloris*, Silvereyes *Zosterops lateralis* and Bellbirds *Anthornis melanura* (McLean 1911; Lambert 1970; Read & McClelland 1984; Elliott 1986; Read 1987; Oliver; CSN); also formerly followed by Saddlebacks *Philesturnus carunculatus* that fed on insects disturbed by Yellowheads (Andersen 1926). In Arthurs Pass NP, Yellowheads usually determined the direction of movement of feeding flock; such flocks common from mid-Jan. till late Feb. 1983 (Read 1987; Read & McClelland 1984). **FORAGING HEIGHTS:** Forage mostly in canopy and upper levels of understorey; in Hawdon R. Valley, during summer, in observations of foraging over 2033 min, foraged in upper understorey and

shaded lower part of canopy, spending most foraging time in these strata (height of canopy not given, but estimated at mean of 10–15 m): 0.4% of time spent on ground, 10.6% in lower understorey, 33.9% in upper understorey, 41.1% within canopy and 14.2% in top of canopy. In Windbag Valley, of 712 observations of foraging, most foraging was in upper levels of forest (heights not specified): 4% on ground, 14% in lower understorey, 18% in upper understorey, 34% in canopy and 30% in top of canopy. **FORAGING SITES:** Forage among foliage and on branches, mostly in canopy of trees; occasionally on ground, on logs and in saplings beside tracks (Lambert 1970; CSN 23, 25). Selectively forage in large beech *Nothofagus* trees (Read 1988b; Elliott 1990), often in forks (Soper 1963; CSN 25, 32). In Hawdon R. Valley, in observations of foraging over 1321 min, foraged mostly among foliage of trees: 46.5% of time was spent foraging among foliage; 17.4% on tree-trunks; 14.3% on dead wood; 11.9% among small branches; 9.3% on large branches; and 0.6% in crotches between branches and trunk. Substrates used as scanning perches differed from those used as foraging surfaces; in observations of foraging over 414 min (figures estimated from graph), scanned from small branches (c. 65%), foliage (c. 20%), large branches and trunks of trees (c. 10%) and dead wood (c. 5%). In Windbag Valley, of 712 observations of foraging, foraged from 11 species of plants, including two species in canopy and nine shrubs and other plants in understorey; mostly foraged in Silver Beech *Nothofagus menziesii* and plants associated with this species (79%); also in moss (10%); dead trees (7%); mistletoe (2%); and on ground (2%). Of 119 observations of foraging, invertebrates were captured almost exclusively from Silver Beech (96.6%); nectar was taken only from flowers of mistletoe *Peraxilla colensoi*; and fruit taken only from *Griselinia littoralis*. At Routeburn Falls, seen feeding on fruit of *Astelia fragrans* (Liliaceae); fruit swallowed whole (Child 1978). **FORAGING METHODS:** In Hawdon R. Valley, in foraging observations over 1756 min, spent 23.9% of time scanning for prey from perches, and rest of time attacking prey, mostly by gleaning (68.1%), pulling (7.1%), probing (0.6%) and sally-hovering (0.5%); sally-striking in air was seen only once. Proportion of time spent using each method changed significantly over time; during summer, time spent gleaning was inversely proportional to that spent scanning; in Apr., an increase in time spent pulling coincided with a decline in gleaning. Time devoted to each foraging method during summer depended on species of tree in which foraging (summarized in Table 1): in Red Beech *Nothofagus fusca*, slightly less time spent pulling and slightly more time gleaning than in Mountain Beech *N. solandri*; pulled much more often in dead trees than in live ones, and dead trees were used least often as scanning perches (Read 1988b). In Windbag Valley, of 712 observations of foraging (figures estimated from graph), foraged mostly by gleaning from foliage and twigs (c. 75%), less often by pulling dead wood to reach prey hidden underneath (c. 15%), and occasionally by probing (c. 5%); remaining time (c. 5%) spent scanning for prey from perches. Sometimes forage by hanging, mostly upside-down at end of small dead twigs, in search of beetle larvae (Elliott 1986). When foraging in leaf-litter accumulated in forks of trees, grip bark with one foot, using tail-feathers as a prop (usually spine-like because of wear) and scratch vigorously with other foot; when foraging among foliage, search thoroughly by hopping through leaves, and searching each twig and the underside of each leaf (Soper 1963). **TIME-BUDGET:** In Hawdon R. Valley, in 2033 min of observation of foraging, mean of 90% of time

Table 1. Foraging methods used by adult Yellowheads in different species of trees. Values are proportion of total number of foraging observations (after Read 1988b).

	GLEAN	HOVER	PROBE	PULL	SCAN	N
MOUNTAIN BEECH	65.1	0.4	0.3	6.9	27.3	783
RED BEECH	67.7	0.4	0.1	3.0	28.8	701
STANDING DEAD TREES*	50.8	0	3.4	35.6	10.2	59

* Including dead Mountain Beech and Red Beech.

spent foraging; proportion of time spent foraging increased as day-length decreased. When feeding nestlings, females spent significantly greater proportion of time foraging than males (females 94.2%, males 82%; $n=329$ min); there was no difference in time spent foraging by males and females immediately after young fledged. **FOOD-HANDLING:** Adults use their feet to place prey in bill, by holding prey in claws and raising it, parrot-fashion, to bill; also use feet to change position of prey already held in bill (Moncrieff 1925; DNFC 1947; Oliver). Female once observed catching large insect larva, then pulling it into two pieces and feeding each piece to two accompanying juveniles (CSN 23).

Detailed study In WINDBAG VALLEY (712 obs. of foraging in 11 species of plants; O'Donnell & Dilks 1994): 16.7% of observations identified as feeding on invertebrates (mostly insects), 0.4% fruit, 0.8% nectar, and remaining 82.1% were unidentified items of food, probably invertebrates.

Other records. FUNGI⁵. **Animals** INSECTS^{2,3}: Coleoptera³; Diptera: Tipulidae⁴; Lepidoptera: larv.^{1,4}, ads²; Orthoptera: Anastomatidae or Rhophadophoridae⁴. Also said to eat spiders and bugs (Hemiptera) (NZRD).

REFERENCES: ¹ Moncrieff 1925; ² Soper 1960; ³ Turbott 1967; ⁴ Read 1988b; ⁵ CSN 24.

Young Fed by both parents and any helpers present (see Social Organization, Breeding). In Eglinton Valley, chicks fed by regurgitation from adults' crops for 5 or 6 days after hatching, then fed insects and their larvae (Soper 1963). In Arthurs Pass NP, at two nests watched for 5 h in mid-Dec., nestlings fed by males every 11.5 min (8–18) and by females every 14 min (8–22). Both parents foraged up to 150 m from nest, and usually arrived to feed young within 2 min of each other. Fledgelings fed near nest, by both parents, and one group of fledgelings was also fed by a helper; newly fledged young in both groups were fed every 23 min (2–64; 9.5 h obs.); in late Dec. and early Jan., in 20 h of observation, fledgelings were fed every 2–6 min, but also foraged for themselves (Read 1987; also see Breeding: Young).

SOCIAL ORGANIZATION Reasonably well known; detailed studies of population in Arthurs Pass NP (Read 1987; Read & O'Donnell 1987) and in Eglinton Valley, Fiordland NP (Elliott 1990). In breeding season, usually occur in pairs or small flocks, based on single breeding group; outside breeding season, from Jan. till at least May, form larger groups of up to 40 birds (McLean 1911; Moncrieff 1929, 1935; Child 1978; Gaze 1985; Elliott 1986; Read 1987; CSN). Sometimes solitary (Moncrieff 1925; Gaze 1985; Oliver; CSN), especially in declining populations (Read & O'Donnell 1987). Only recorded in groups of 1–3 in Eglinton Valley, Nov. 1992 (Elliott & Rasch 1995). Historically, round L. Brunner, recorded in flocks of up to 200 birds (Smith 1888). Outside breeding season, often form nucleus of mixed-species flocks (see Food).

Bonds Apparently monogamous; pairs remain together for many years (Elliott 1986). **Co-operative breeding** Often breed co-operatively (Soper 1960, 1963; Read 1987; Elliott 1990; CSN 24). Breeding unit consists of primary pair, sometimes with a helper (Read 1987). In Arthurs Pass NP, 1983–84, 70% of birds occurred as breeding pairs, and rest were helpers or itinerants (Cunningham & Holdaway 1986). Of 11 pairs in Arthurs Pass NP, at least three had a helper (Reid 1987), and two of five breeding pairs in Eglinton Valley had helpers (Soper 1963). Of 63 breeding groups in Eglinton Valley, all but one had a male helper (Elliott 1990). However, of three helpers in Arthurs Pass NP, two were females and the third was unsexed (Read 1987). At a nest attended by three birds, two, claimed to be females, shared incubation; one relieved the other by entering nest-hole and offering food (Soper 1960; see Breeding). **Care of young** Both sexes and any helpers present feed nestlings and fledgelings (see Breeding: Young).

Breeding dispersion Information from Read & O'Donnell (1987) unless stated. In Hawdon Valley, Arthurs Pass NP, in 1983, 11 pairs recorded in c. 500 ha (1 pair/45.5 ha) and in 1984, 21 pairs in c. 2900 ha (1 pair/41.7 ha); mean distance between pairs was 650 m, and pairs no closer than 300 m. As population density quite low, home-ranges probably not contiguous. In Catlins SF, 1981–82, pairs were 50–200 m apart. In Eglinton Valley, Fiordland NP, one pair per 2.85 ha. At various other sites in Fiordland, mean density was one breeding pair per 3.7 ha; at specific sites: L. Monk, two pairs in c. 8.1 ha; mouth of Spey R., four pairs in c. 20.2 ha; Jeanie Burn, three pairs in c. 7.3 ha (Kikkawa 1966). Historically, home-ranges estimated at 3.2–4.0 ha in Pukikirunga Ra. (Guthrie-Smith 1936). In 1983–84, in Arthurs Pass NP, one pair ranged over 7 ha, though when breeding, usually remained within 150 m of nest (Read 1987). One family group stayed in breeding territory for 2.5 days after fledging, then ranged throughout forest, and was recorded moving 1.0–1.5 km within 6 h. After breeding, leave territory and disperse more widely, with mobile groups often ranging up to 1.5–2 km in a day (Read 1988a). In Otago, 44 territories recorded along 3 km of track at Garden Gully; 62 territories along 4 km of track at Rankleburn; and 30 territories along 2.5 km of Cattle Spur track (CSN 42).

Roosting No information.

SOCIAL BEHAVIOUR Some aspects reasonably well known from study in Arthurs Pass NP (Read 1987). Time-budgets for classes of social behaviour observed are shown in Read (1988b), though behaviour not described in detail. As length of day decreases, spend greater proportion of time foraging and less time on social activities; time spent foraging increases sharply when feeding fledgelings (Read 1988b; see Food). Male noisier and more conspicuous than female (Elliott & Rasch 1995). Only male utters Rattle, from tops of trees for several minutes at a time (Elliott 1990; see Voice). Young more

inquisitive than adults, often perching within 1 m of observer (Read 1987). In flocks, maintain contact by calling frequently (Read 1987).

Agonistic behaviour Once, when feeding, one bird seen aggressively preventing another from gaining access to food (Child 1978). Rarely chase each other in non-breeding flocks, though occasionally aggressive towards other species (Read 1987). Males display by facing each other with wings raised (C.F.J. O'Donnell). Male Song used in territorial defence; males sing for long periods from regular perches within territory and in territorial conflict hop within few centimetres of opponent and sing very loudly (Elliott 1990).

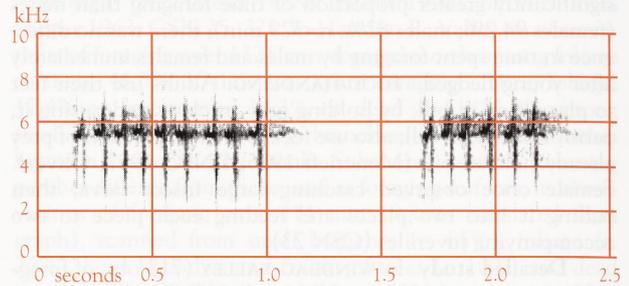
Sexual behaviour **Courtship feeding** Early in breeding season, female crouches and flutters her wings to solicit courtship feeding by male, who gives her food held inside his mouth or in bill (Soper 1963; NZRD); continues less regularly throughout breeding season (C.F.J. O'Donnell). Male feeds female for c. 2 weeks before laying (Elliott 1990) and during incubation; female sometimes called off nest and fed nearby, or fed in nest after both birds have returned from a brief absence; early in incubation period, male brings food at intervals of c. 30 min (Guthrie-Smith 1936). **Copulation** Male landed beside female and waved his wings back and forth at rate of 3 flaps/s. With every sixth or seventh flap, he leant over and pecked female on nape. After five or six pecks, female crouched and pair copulated (NZRD).

Relations within family group Fledgelings trill continuously when begging if adult nearby, and follow adults constantly while dependent (McLean & Waas 1987). **Parental anti-predator strategies** Usually stay near dependent young; once observed >100 m away from young, when mobbing Southern Boobook *Ninox novaeseelandiae* (Read 1987).

VOICE Quite well known. Sonagram of Begging Trill of dependent fledgeling in McLean & Waas (1987). One call in musical notation in Andersen (1915, 1926). Sonographic study by Harper (1988) not available for inclusion in this account. Heard much more often than seen (Soper 1976) with male much noisier than female (Elliott & Rasch 1995). In Fiordland NP, in Nov., rate of singing peaks in morning and evening (Elliott & Rasch 1995). At L. Rotoroa, near Murchison, in late Nov., family groups of parents and fledgelings very noisy (Moncrieff 1925). In Arthurs Pass NP, from mid-Jan., family groups briefly form noisy flocks, with much calling and singing; amount of calling by an individual is related to size of flock: individuals call more often in large flocks than when in family group; flocks less noisy in autumn, and by May could sometimes be located only by sound of debris, disturbed while foraging, hitting forest floor (Read 1987). Only male utters Song, and Buzz given only by female (see below). Vocalizations said to be louder than those of Whitehead, and Song more varied and musical (Buller 1888). **RESPONSE TO PLAYBACK, IMITATION:** Discharge of gun, snapping of stick or cry of wounded bird attracts a noisy flock (Buller 1888).

Adult SONG: An attractive and musical canary-like trill (Soper 1976); loud and penetrating series of 6–8 notes repeated rapidly, with much variation (Falla *et al.* 1975). Only male sings (Elliott 1990). **RATTLE:** A series of rapid staccato notes, often added as long trill at end of Song (Soper 1976); sound likened to that of coin spinning on hard surface (Moncrieff 1925) or a pneumatic drill (Falla *et al.* 1975). Males whose mates are incubating utter Songs interspersed with occasional weak Rattles, which become louder and

change in timbre and quality when joined by mate (Soper 1976). Two Rattles are shown in sonagram A. Possibly analogous to interlude in Song of Brown Creeper and zir notes in Song of Whitehead (T. Howard). Given by both sexes (Elliott 1990). **SCOLDING:** A scolding note in alarm, e.g. when mobbing potential predator (Soper 1976). **BUZZ:** Buzzing call given only by female (Elliott 1990). Also described as *zurz* call (Harper 1988). Associated with male Song (Elliott 1990); and usually given at end of male Song (M. Aviss). **Other calls** Harsh *lukaart*, *lukaart* from female, starting a few days before eggs hatch (Soper 1976). A pleasant upslurred note, uttered once (Andersen 1915, 1926).



A C.F.J. O'Donnell; Arthurs Pass NP, SI, Feb. 1988; P106

Young BEGGING TRILL: Dependent fledgelings constantly trill when parents nearby; older fledgelings call continually while following adults; rate of calling and length of trill increase as parent approaches. Main frequency of Trill, 7.94 kHz; range of frequencies, 6.67–8.25 kHz; and Trill composed of 43.1 elements/s (McLean & Waas 1987; Read 1987). By Feb., juveniles give adult calls, as well as Begging Trill (Read 1987). Attempted Song of juvenile males easily distinguished from adult Song; rhythm similar to adult male Song, but pitch often different (Elliott 1990).

BREEDING Well known from detailed studies in Eglinton Valley, Fiordland NP, Oct. 1984–Mar. 1988 (Elliott 1990), and then till 1993 (Elliott *et al.* 1996); notes from an earlier study in Eglinton Valley (Soper 1960, 1963); and small study in Hawdon R. Valley, Arthurs Pass NP (Read 1987). Breed either in simple pairs or co-operatively in groups comprising a primary pair and a helper (see Social Organization).

Season Breed Oct.–Feb. (Moncrieff 1957). Laying from early Oct. to early Feb., with peak in early Nov., and second, smaller peak late Dec. to early Jan., corresponding to second clutches laid after successful first ones (Guthrie-Smith 1936; Soper 1960, 1963; Read 1987; Elliott 1990). Young, early Nov. to early Mar. (Read 1987; Elliott 1990).

Site In cavity in trunk, large branch or stump of large beech *Nothofagus*, including Red Beech *N. fusca*, Silver Beech *N. menziesii* and Mountain Beech *N. solandri*; often high in canopy (Soper 1960, 1963; Elliott 1986, 1990; Read 1987; Elliott *et al.* 1996; CSN 34). In Eglinton Valley: of 95 nests, 42 (44.2%) were in Silver Beech, 34 (35.8%) in Red Beech, four (4.2%) in Mountain Beech and 15 (15.8%) in dead beech trees (Elliott 1990); of 166 nests, 76 (46%) were in Red Beech, 53 (32%) in Silver Beech, two (1%) in Mountain Beech, three (2%) in Red Beech × Mountain Beech hybrids and 32 (19%) in dead beech trees (Elliott *et al.* 1996). At unknown site, single report in Manuka *Leptospermum scoparium* (NZRD). In Eglinton Valley, of 95 nest-sites, 64 (67.4%) were in tree-trunks, and rest in large

branches (Elliott 1990); of 166 nests, 118 (71%) were in tree-trunks and 48 (29%) in large branches, 22 (13%) of which were dead but in live trees (Elliott *et al.* 1996); and of 15 nests, 12 (80%) were in a dead tree or dead rotting limb in a living tree, and three (20%) were in a rotting stump (Soper 1960). Of 95 nests, 78 (82.1%) were in knotholes and 17 (17.9%) in holes formed by rotten wood crumbling away (Elliott 1990). Of 166 nests, 139 (84%) were entered through a knothole, 18 (11%) through hole formed by rotting wood crumbling away, seven (4%) through a slit and two (1%) were in a cavity where branch rejoined above a crook (Elliott *et al.* 1996). Two reports of nests in open, in beech and Manuka *Leptospermum scoparium* (NZRD). Nest-site selected by male, and shown to female by male flying repeatedly back and forth between her and hole for up to 90 min, till female investigates and accepts it (Soper 1963). Sites sometimes used more than once; in Eglinton Valley, of 149 sites, 12 (8.1%) were used twice, one (0.7%) was used three times and one (0.7%) four times; re-use of a site ranged from re-use of hole by same pair in same season, to use of same hole by a different pair up to 5 years later (Elliott 1990). MEASUREMENTS (m): Height of nest: in Eglinton Valley, 14.5 (7.4; 1.7–31.3; 166) (Elliott *et al.* 1996), and 2.4–18.3 (n=15) with most >9.1 (Soper 1963); in Hawdon R. Valley, two nests, 12 and 15 (Read 1987); in Abel Tasman NP, 14.6 (2.35; 12.2–18.3; 5) (Guthrie-Smith 1936). Height of nest-tree: in Fiordland NP, 22.8 (7.12; 9) (Elliott 1990); 24 (8; 2–42; 166) (Elliott *et al.* 1996). Diameter of nest-tree at breast height (dbh): in Fiordland NP, 83.8 cm (33.96; 95); no nests were in trees with dbh of <30 cm, or in branches or trunks <20 cm diameter (Elliott 1990).

Nest, Materials Cup-shaped; built in cavity of tree, woven from rootlets, twigs, grass, sedge *Carex*, plant-fibre, dark rhizomes of ferns, leaves, moss, lichen, spider web and a few feathers; lined with fine grass, plant-fibre, blades of sedges and feathers; rim of nest built level with lower edge of entrance hole; one pair did not build nest, but laid eggs directly onto powdered rotten wood at bottom of hollow (Guthrie-Smith 1936; Soper 1960, 1963; Elliott 1986, 1990; Read 1987; Elliott *et al.* 1996). Of two claimed nests in open, one was untidy on outside and made of twigs, rootlets, moss and wool; second nest was built from moss, grass and wool, with a few feathers (NZRD). Entrance-hole to hollow either at bottom of cavity, so that hollow in trunk extends above upper lip of entrance, or is located up to 31 cm above bottom of cavity (Soper 1963; Elliott *et al.* 1996); in Eglinton Valley, of 128 nests, ten entrances (8%) were at bottom of cavity (Elliott *et al.* 1996). Only female builds; in bursts, with female making several trips to nest with material, then foraging for several hours before resuming construction. One nest took >10 days to build. Three instances of female building two nests at same time, though only one was completed and used (Elliott 1990). MEASUREMENTS (cm): Height of entrance above bottom of cavity, 13.3 (7.7; 0–31.0; 128) (Elliott *et al.* 1996); depth of two nest-cavities, 38.1 and 25.4–27.9 (Guthrie-Smith 1936). Maximum dimension of entrance hole, 10.7 (4–50; 74); minimum dimension, 4.7 (2.5–15; 74), most (90.5%) 3–6; smallest entrance hole, 4 × 3; largest entrance hole, 15 × 16 (Elliott 1990); mean size of entrance, c. 7.7 × 7.7 (9; 128); smallest diameter, 2.5; ranged from 4 × 3 to 160 × 4 (Elliott *et al.* 1996); diameter of entrance, 7.6–12.7 (Soper 1960). Cross-sectional area (cm²) of entrance, 59 (81; 12–640; 166); in parasitized nests, 135; in unparasitized nests, 53; cross-sectional area of cavity, 245 (147; 64–900; 166) (Elliott *et al.* 1996). Cross-sectional diameter of cavity, c. 10

(Elliott 1990). Internal diameter of one nest-cup, 6.4 (Guthrie-Smith 1936).

Eggs Oval to elliptical (Oliver). Pink, with pale and dark reddish-brown spots and blotches over entire shell, sometimes forming band at large end (Oliver); pale grey with pale-brown markings (Moncrieff 1957). Also described as uniform pinkish white to reddish cream, minutely and faintly spotted pale reddish-brown; some eggs faint unmarked brown; one warm salmon (NZRD). MEASUREMENTS: 23 × 18, 23.5 × 17.5, 24 × 19 (Oliver).

Clutch-size One to four (Guthrie-Smith 1936; Soper 1963; Elliott 1990). In Fiordland NP, 3.06 (0.78; 1–4; 48): C/1 × 2, C/2 × 7, C/3 × 25, C/4 × 14; no significant difference in clutch-size between first and subsequent clutches but trend towards larger clutches earlier in season: mean size of clutches laid in Oct., 3.40 (0.89; 5); Nov., 3.04 (0.72; 26); Dec., 3.22 (0.83; 9); Jan., 2.78 (0.83; 9), though monthly difference not significant (Elliott 1990).

Laying Eggs laid at daily intervals or intervals of 2 days (Elliott 1990). Often double-brooded (Elliott 1990). During four seasons in Eglinton Valley, 37 of 48 pairs (77.1%) attempted more than one clutch in a season. When re-laying, second clutches usually laid soon after fledging of first brood but some females built nest and sometimes laid second clutch before first brood had fledged (Elliott 1990). Re-use of nest-site in same season indicates either laying of a second clutch after a success or laying of a replacement clutch after a failure (Elliott *et al.* 1996).

Incubation By female only, beginning with completion of clutch (Soper 1960; Elliott 1990). At nests attended by three birds, two, claimed to be females, incubated, with one doing most; one female relieved other by entering nest with food in bill and offering it to sitting female, who accepted it and left, while entering female settled on eggs (Soper 1960, 1963). Male feeds female during incubation (see Social Behaviour: Courtship feeding). In simple pairs, female leaves nest three or four times a day to feed; if undisturbed, stays off nest for 1 h or more, and longer if observer near nest; at nests with two females, near end of incubation period, change-overs occurred every 15–20 min (Soper 1963). Female spends c. 10 min off nest every hour, during which time she forages and is fed by mate (Elliott 1990). INCUBATION PERIOD: c. 21 days (Guthrie-Smith 1936); at least 21 days (Soper 1960); in Eglinton Valley, 20.2 days (19.04–21.75; 4) (for details of method of calculation, see Elliott 1990).

Young Altricial, nidicolous. Naked at hatching; develop down by c. 7 days (Guthrie-Smith 1936). **Parental care, Role of sexes** Both sexes and any helpers feed young (Moncrieff 1925; Guthrie-Smith 1936; Soper 1960, 1963; Elliott 1986, 1990; Read 1987); young fed by males almost as often as by females (Soper 1963), though male rarely visited nest where two females fed young (Soper 1960). In Eglinton Valley, at nests with no helper, female made 42.6% (12.6; 10) of visits, and males 57.4% (12.6; 10); at nests with a helper, primary female made 31.9% (7.8; 7) of visits, primary male 37.6% (9.8; 7) and helper 30.4% (10.6; 7); frequency of feeding visits to one nest with a secondary adult and one nest without, 13.6 and 13.2 visits/h respectively (Elliott 1986); also see Food: Young. Usually enter nest to feed young but occasionally feed young from edge of hole (Read 1987). Faecal sacs removed by parents (Elliott 1986).

Fledging to independence FLEDGING PERIOD: In Eglinton Valley, 22.5 days (21.88–22.88; 3) (for details of method of calculation, see Elliott 1990); 18 days (n=1 nest)

(Soper 1960). In first few hours after leaving nest, fledgelings stayed within 1 m of ground, either perched in undergrowth, among litter or on ground; gradually move higher as they gain strength; one family group remained in same area for 2.5 days (Read 1987). Both parents feed fledgelings (Moncrieff 1925; Read 1987); fledgelings of one pair also fed by a helper (Read 1987). Females that re-lay rarely feed fledgelings of first brood so that in pairs without a helper, fledgelings fed only by male, who also feeds female when she is off nest; at nests with a helper, male and helper feed fledgelings (Elliott 1990; for rates of feeding, see Food). In Hawdon R. Valley, fledgelings fed by parents for c. 55 days (Read 1987) and, in Eglinton Valley, for up to 9 months (Elliott 1986, 1990). Remain with parents till start of next breeding season and are fed by them and by helpers; initially totally dependent on parents for food, but dependence rapidly decreases, and during winter and early spring, rarely fed by parents (Elliott 1986, 1990).

Success Over four seasons in Eglinton Valley: from 140 eggs in 46 nests, 44 (31.4%) young fledged (annual variation 22.5–44.4%); of 107 eggs in 36 nests, 58 (54.2%) hatched (28.6–69.2%); and from 66 young in 25 nests, 42 (63.6%) fledged (38.1–80.0%); of 87 nests with eggs, 62 (71.2%) hatched at least one egg (annual variation 65.4–86.7), and 48 (55.2%) fledged at least one young (40.0–63.6%). Lowest fledging success in year of high rate of predation by Stoats. Mean number of young fledged per nest: for first nests, 1.08 (1.24; 50); for subsequent nests, 1.20 (1.38; 40). Mean number of fledgelings per pair (n=50 pairs): first clutches, 1.36 (annual variation 0.91–1.92); all clutches, 2.06 (0.91–2.62). Of 39 failures, 22 (56.4%) occurred at egg-stage and 17 (43.6%) at nestling stage; two (5.1%) failed as a result of accidents, four (10.3%) parasitism by cuckoos, six (15.4%) predation and 27 (69.2%) for unknown reasons. Of the six nests lost to predation, one was by Long-tailed Cuckoo *Eudynamys taitensis* (see below), and others probably by Stoats; all predation occurred in the same year, and accounted for 67% of nest-failures that year (Elliott *et al.* 1996). Stoats depredate nests and sometimes kill female in nest; during two seasons where there was an irruption of Stoats, successful nests were sited significantly higher than failed nests (Elliott *et al.* 1996). For more details on relationship between nest-height, cavity dimension, season, success and predation by Stoats, see Elliott *et al.* (1996). One nest with eggs was found deserted, with nest sodden and one broken egg at base of nest-tree (Guthrie-Smith 1936). **CUCKOOS:** Parasitized by Long-tailed Cuckoo (Soper 1963; Elliott 1990). Of 95 nests in Eglinton Valley, six (6.3%) were parasitized by Long-tailed Cuckoos (Elliott 1990); and of another 166 nests, ten (6%) were parasitized by Cuckoos (Elliott *et al.* 1996); Cuckoo chicks not always successful in ejecting Yellowhead nestlings from cavity; in two of the six parasitized nests, both Cuckoo and Yellowhead nestlings were raised together till Yellowheads fledged. However, Long-tailed Cuckoos do eat eggs and young (Soper 1963; Elliott *et al.* 1996). In Eglinton Valley, in 1984–85, parasitism caused c. 7.5% drop in breeding success of Yellowheads (Elliott 1986). Parasitized nests have significantly larger entrance holes than non-parasitized nests; in population 62% of nests have entrance holes smaller than those of the smallest parasitized nest (Elliott *et al.* 1996; see Nest, Materials).

PLUMAGES Prepared by A.M. Dunn. Fledge in juvenile plumage. Early plumages not well understood. Extent and timing of post-juvenile (first pre-basic) moult not known but probably begins shortly after fledging, and seems to result in

first immature plumage with similar appearance to adult female. After attaining complete post-breeding (pre-basic) moult each cycle produces successive adult plumages with little change in appearance. Sexes differ slightly in adult plumage. No subspecies. Descriptions based on examination of skins of ten adult males, five adult females and five with signs of immaturity, one was possibly juvenile and the other four were probably first immatures (AIM, NMNZ).

Adult male (Definitive basic). **HEAD AND NECK:** Mostly yellow (55), usually with olive-brown (c29) tips to feathers of nape and hindneck, and sometimes narrow olive-brown (c29) fringes to feathers of crown. Amount of olive-brown pigmentation to feathers varies with age and also with wear of feathers (see Ageing). In fresh plumage, usually have some olive-brown on nape, hindneck and often crown, but these areas become progressively more yellow with wear as the brown fringes and tips wear away. **UPPERPARTS:** Mantle, back, scapulars and rump, olive-brown (c30). Uppertail-coverts, olive (c51). All feathers have concealed dark-grey (83) bases. **UNDERPARTS:** Breast, flanks and upper belly mostly yellow (55); often have olive-brown (c29) suffusion to feathers at sides of breast, flanks and sides of belly. Lower belly and vent, off-white (ne). Thighs, light grey-brown (45). Undertail-coverts, off-white (ne) with strong yellow (c55) suffusion. All feathers have concealed dark-grey (83) bases. **UPPERTAIL:** Rectrices, dark olive (48) with strong yellowish-olive (51–52) suffusion, which is strongest at edges of feathers. Rectrices have very thick, strong and rather rigid shafts. Tips of feathers often wear away, leaving exposed shafts, giving spiny appearance. **UNDERTAIL:** Rectrices, grey-brown (c91) with off-white (ne) shafts and strong yellow-olive (c52) suffusion. **UPPERWING:** Marginal and median secondary coverts, olive (c51). Greater secondary coverts, alula and greater primary coverts, dark olive-brown (129) with olive (51) suffusion to outer webs. Most marginal and median primary coverts, light grey-brown (45); marginal coverts near alula, off-white (ne) with pale-yellow (c157) wash. Tertiaries, dark brown (121) with olive (51) suffusion to outer webs. Primaries and secondaries, dark brown (121) with narrow olive (51) edge to outer webs and concealed pale-yellow (c157) edge to inner webs; on p4–p10, edges to outer webs grade to light grey-brown (c119D) distally. **UNDERWING:** Secondary coverts, white with pale-yellow (157) suffusion and concealed dark-grey (83) bases. Marginal and median secondary coverts, grey-brown (91) with yellow (55) tips. Greater primary coverts, light grey-brown (45). Tertiaries, dark brown (121). Primaries and secondaries, dark brown (121) with pale-yellow (157) edge to inner webs.

Adult female (Definitive basic). Mostly as adult male but crown, nape and hindneck usually browner. Feathers of crown, nape and hindneck often have broader olive-brown (c29) tips to feathers. However, there is much overlap with males in this character, so caution must be used in identifying sex based solely on plumage (see Sexing).

Nestling Hatch naked; develop grey-blue down within 1 week (Guthrie-Smith 1936).

Juvenile The following based on single specimen with some juvenile-like characters (NMNZ 302). This specimen was lacking data, and it is uncertain whether it was in juvenile or rather fresh first immature plumage. This description appears to agree with that of Elliott (1990). Overall appearance similar to adult but with much browner top of head and slightly paler underparts. **HEAD AND NECK:** Forehead, crown, nape and hindneck, almost uniform olive-brown (c29) with

partly visible yellow (c55) suffusion to middle of feathers, and concealed grey (c84) bases to feathers. Feathers of crown of this specimen probably appear much browner than those described by Cunningham & Holdaway (1986); see Ageing. Lores, ear-coverts and sides of neck, yellow (c55) with weak olive-brown (c29) suffusion to tips of feathers. Chin and throat, yellow (c55), but not as bright as in adult. **UPPERPARTS:** Mostly as adult but with looser texture to feathers, and with partly visible narrow and diffuse cream (c92) shaft-streaks to basal half of feathers of mantle and back. **UNDERPARTS:** Slightly paler and browner than adult. Breast and upper belly, yellow (c55) with olive-brown (29) suffusion to tips of feathers, strongest at sides of breast and belly. Flanks, olive-brown (c29). Lower belly and vent, off-white (ne) to cream (c92). Thighs, brownish grey (c79). Undertail-coverts, yellow-brown (c123B). All feathers have softer, looser texture than those of adult. **TAIL:** As adult in colour, but shafts of rectrices not as thick or rigid as adult. **WING:** As adult.

First immature (First basic). Three specimens appeared to have some characters as described above for juvenile but had worn plumage and slightly more yellow on top of head and in underparts. If post-juvenile moult occurs shortly after fledging, as in other Pachycephalidae, then these were most likely in first immature (first basic) plumage. Their appearance was similar to that of adult female but averaged slightly browner on top of head, with brown shaft-streaks to feathers from forehead to hindneck, and some feathers of upperparts had diffuse cream (c92) shaft-streaks. Rectrices as described above for juvenile. It is uncertain whether differences from plumage described above for juvenile were result of moult or wear. Cunningham & Holdaway (1986) suggested that the amount of brown coloration in plumage sometimes decreases with wear (see Ageing). From observations in the field, Elliott (1990) found that first immatures appeared similar to juveniles but plumage lacked fluffy look.

BARE PARTS Based on photos (Moon 1992; O'Donnell 1996b; NZRD). Sexes similar. **Adult** Bill, black (89). Gape, black (89). When crop full, pinkish-grey (ne) patch of skin becomes exposed below base of lower mandible (see photos: O'Donnell 1996b). Iris, black-brown (119); described as black (Oliver). Orbital ring, black (89). Legs and feet, black (89). Soles, greyish-yellow (ne). Claws, dark grey (83) or black (89); or brown (Oliver). **Nestling** Skin, black at hatching (Guthrie-Smith 1936). No further information. **Juvenile** Legs and feet paler than adult (Elliott 1990). No further information. **First immature** Legs and feet darker than those of juvenile (Elliott 1990). No further information.

MOULTS Based on examination of skins of nine adults and two possible immatures (AIM, NMNZ), and published information as cited. **Adult post-breeding** (Pre-basic). Few data. Probably complete; primaries outward. None recorded with active moult of primaries or tail. One had active moult of body in Mar. and was moulting feathers in both upperparts and underparts. **Post-juvenile** (First pre-basic). Few data. Extent not known, and timing uncertain. Probably occurs Jan.–Mar. (Cunningham & Holdaway 1986). Neither of two possible immature skins was moulting.

MEASUREMENTS (1–2) SI, skins (AIM, NMNZ): (1) Adults; (2) Immatures. (3) Eglinton Valley, adults, live (Gill & McLean 1986). (4) Eglinton Valley, adults, live (G. Elliott); includes data in sample (3).

		MALES	FEMALES	
WING	(1)	81.4 (2.76; 77–85; 10)	80.6 (2.51; 77–83; 5)	ns
	(2)	81, 83, 85	–	
	(3)	82.5 (1.66; 13)	75.6 (2.56; 8)	**
	(4)	82.6 (1.73; 80–86; 20)	77.4 (2.71; 72–80; 14)	**
TAIL	(1)	68.4 (3.69; 60–73; 10)	67.4 (2.19; 64–70; 5)	ns
	(2)	68, 71, 76	–	
	(3)	65.7 (3.38; 12)	61.1 (3.14; 8)	**
	(4)	65.1 (3.19; 61–72; 19)	61.9 (3.11; 56–69; 14)	**
BILL S	(1)	15.1 (0.87; 15.0–16.8; 10)	15.1 (0.86; 14.1–16.0; 5)	ns
	(2)	14.7, 15.7	–	
BILL F	(4)	12.7 (0.64; 11.5–13.8; 20)	12.1 (1.00; 10.5–13.9; 15)	*
TARSUS	(1)	30.5 (0.55; 29.8–31.4; 8)	29.9 (0.62; 29.3–30.6; 4)	ns
	(2)	29.7, 30.3	–	
	(3)	33.1 (1.70; 13)	32.0 (0.98; 8)	ns
	(4)	33.0 (1.46; 31.0–37.8; 20)	31.8 (0.97; 30.3–33.8; 14)	**
TOE C	(4)	14.9 (0.81; 13.4–16.4; 20)	14.3 (0.78; 12.9–15.6; 14)	ns

Unsexed: (5) SI, skins (AIM, NMNZ).

		ADULTS	JUVENILE AND IMMATURE
WING	(5)	81.9 (2.93; 76–85; 9)	78, 82
TAIL	(5)	67.1 (2.85; 63–71; 9)	64, 71
BILL S	(5)	15.7 (0.79; 14.4–16.7; 6)	15.4, 15.9
TARSUS	(5)	30.1 (1.28; 28.0–31.2; 5)	29.0, 31.2

Unsexed: (6) SI, all ages, skins (Cunningham & Holdaway 1986).

		YELLOW-NAPED	BROWN-NAPED	
WING	(6)	79.2 (2.56; 21)	77.7 (2.94; 18)	*
BILL F	(6)	11.5 (0.63; 20)	11.0 (0.75; 22)	*
BILL W	(6)	5.2 (0.28; 19)	5.3 (0.38; 23)	ns
BILL D	(6)	5.1 (0.35; 18)	4.9 (0.36; 22)	*
TARSUS	(6)	25.2 (0.84; 22)	25.4 (0.98; 21)	ns

Elliott (1990) also provides mean measurements for adults sexed from behavioural observations but sample sizes not given.

WEIGHTS (1) Eglinton Valley, adults, live (Gill & McLean 1986). (2) Eglinton Valley, adults, live (G. Elliott); includes data in sample (1).

		MALES	FEMALES	
(1)		29.7 (1.28; 13)	25.9 (1.99; 7)	**
(2)		29.5 (1.16; 28.0–32.5; 19)	26.0 (1.91; 23.0–29.5; 13)	**

Elliott (1990) also provides mean weights for adults sexed from behavioural observations but sample sizes not given.

STRUCTURE Wing moderately long and broad. Ten primaries: p5 and p6 longest, p7 sometimes equal; p10 30–35 mm shorter, p9 13–16, p8 3–5, p7 0–1, p4 1–3, p3 5–7, p2 9–11, p1 12–15. P5–p8 slightly emarginated on outer webs; no emarginations on inner webs. Nine secondaries, including three tertials; tips of longest tertials fall short of tips of secondaries on folded wing. Tail moderately long and slightly rounded at tip, and rectrices rather stiff with downward (concave) curve; 12 rectrices. Bill rather short and straight; about half length of head. Tarsus moderately long and very thick; scales scutellate on front, fused to rear. Tibia fully feathered.

Middle toe with claw 20.4 (1.43; 17.7–21.5; 6). Outer toe 93–100% of middle, inner 67–85%, hindtoe 93–103%. Claws rather strong; rear claw very long.

AGEING Poorly understood. Information gathered from skins and presented above in main descriptions (this study) differs slightly from that presented by Cunningham & Holdaway (1986), particularly in description of juvenile. The following summarizes information from Cunningham & Holdaway (1986). Brown coloration on nape varies with wear, and in adults appears to be stronger when plumage fresh and weaker with wear. In adults, feathers of crown and nape are mostly yellow (shafts and barbs are yellow and so are most barbules) but barbules near tips of barbs are olive-brown, resulting in olive-brown tips to feathers. The brown parts of the feathers appear to wear more than the yellow parts, resulting in yellowing of the crown and nape with wear. Feathers of nape have more brown barbules than those of crown, resulting in browner appearance for longer. Feathers in crown of birds assumed to be in first year (juveniles and first immatures) have an extra band of dark-brown barbules against rachis, which appears as a central band joining the brown tip. These feathers cause an even browner appearance to crown and nape than in adults, and the brown persists for much longer. Further, Elliott (1990) found that, in adults, the amount of olive on the nape tended to diminish with successive moults.

SEXING Cunningham & Holdaway (1986) found that colour of nape was not a good indicator of sex. However, they found that when principal component analysis (PCA) was applied to measurements (wing-length, bill-length, bill-depth, bill-width and tarsus-length), a plot of the first two principal components resulted in two non-overlapping clusters. This suggests that measurements might be useful in separating the sexes (see Cunningham & Holdaway 1986).

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