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):

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.;

DICAEIDAE (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.

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 Muscicapoidea (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 Dicruridae and Corvidae (cf. Dicruridae–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, taxomony 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 widepread, 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:

Mohoua	three species, endemic to NZ;
Falcunculus	monotypic Crested Shrike-tit *F. frontatus*, endemic to Aust.;
Oreoica	monotypic Crested Bellbird *O. gutturalis*, endemic to Aust.;
Pachycephala	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;
Colluricincla	shrike-thrushes; four species in HANZAB region (two of which, *C. harmonica* and *C. megarhyncha*, 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 corvoid 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 oblately 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 rain-forests (Little *Colluricincla megarhyncha* and Bower's *C. boweri* Shrike-thrushes), and mangroves (White-breasted *Pachycephala lanioides* 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 under-storey (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 glean-ing, 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-lored *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-lored 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 novaeseelandiae **Brown Creeper**

COLOUR PLATE FACING PAGE 1025

Parus novaeseelandiae Gmelin, 1789, *Syst. Nat.* 1(2): 1013 — Dusky Sound, South Island, New Zealand.

Specific name based on Latham's (1783; *Gen. Synop. Birds*, **II**, p. 558), 'New-Zealand Titmouse'.

OTHER ENGLISH NAMES New Zealand Titmouse.

MONOTYPIC

FIELD IDENTIFICATION Length *c.* 13 cm; wingspan 14–15 cm; weight: male 13 g, female 11 g. Smallest *Mohoua*; noticeably smaller than Yellowhead *Mohoua ochrocephala*. Distinctive small NZ passerine with short, sturdy bill and slightly graduated tail. Adult mostly dark reddish-brown above with dark-greyish face, hindneck and sides of neck, indistinct narrow pale stripe behind eye, and undertail marked with narrow dusky subterminal band; and paler pinkish-brown below. Sexes alike. No seasonal variation. Juvenile very similar to adult but recently fledged birds separable by pale-yellow gape and calls (see below). Immature inseparable from adult. **Adult** Forehead and broad area through centre of crown form dark reddish-brown forecap, barely contrasting with dark brownish-grey hindneck and sides of head and neck, which are sharply demarcated from pale pinkish-brown chin, throat and underbody; very indistinct short and diffuse pale brownish-grey stripe extends behind eye. Rest of upperbody and uppertail, dark reddish-brown. Folded wing, dark brown, with slightly paler grey-brown outer edges to outer primaries. Underbody, light grey-brown grading to light pinkish-brown at sides and on flanks. Undertail, light brown with indistinct narrow dusky subterminal band. Bill, pale pinkish-grey with darker grey top of upper mandible. Gape, light brownish-grey. Iris, black or dark brown. Legs and feet, pale pinkish-grey or grey-brown. **Juvenile** Very similar to adult; best distinguished by combination of: slightly duller brownish-grey head with only barest hint of pale stripe behind eye (a feature shared with some adults); prominent yellow gape when recently fledged; and distinctive and persistent begging calls.

Similar species Unlikely to be mistaken, though singing birds could by confused with **Yellowhead** (q.v.). Ought not to be confused with superficially similar **Dunnock** *Prunella modularis*, which, in adult plumage, has mostly dark-grey head, neck and breast, but is boldly dark-streaked above and on flanks, and more finely streaked on crown, has brownish (not grey) ear-coverts, much finer bill, shorter and paler brown legs, very different calls, and is more solitary and skulking, feeding mainly on ground close to cover. Juvenile Dunnock is less strongly greyish on head, neck and breast than adult, but otherwise differs from Brown Creeper in same ways as described for adult.

Gregarious; usually seen in pairs during breeding season, but in autumn and winter usually seen in small noisy groups or larger flocks of up to 50 birds, moving quickly through trees and shrubs; often form mixed-species feeding flocks with other forest birds such as Grey Warblers *Gerygone igata*, Silvereyes *Zosterops lateralis* and Grey Fantails *Rhipidura fuliginosa*. Forage by gleaning insects from foliage, twigs, branches, trunks and under loose bark of shrubs and trees at all levels of forest, though rarely from ground. When foraging, move through canopy in series of hops and short flights; flight characteristic with drooping wings and tail; very agile and acrobatic when searching for prey: often hang upside-down from branches and twigs when gleaning for insects, or clinging to or working along trunks and underside of branches while probing under bark, moss and lichen. Calls distinctive; include loud nasal and scratchy Song of male and much shorter Song of female, often give short, raspy *chee* repeated several times as well as other harsh chattering and trilling notes (see Voice); when singing, feathers of crown and throat raised and tail flicked.

HABITAT Native forests, mainly with a simple structure, such as high-altitude beech *Nothofagus* forest and stands of *Leptospermum* (Clout & Gaze 1984; Gaze 1985); sometimes also recorded in exotic pine plantations, which also have a simple structure (Clout & Gaze 1984; Heather & Robertson 1997). Often recorded in regrowth forest (Falla *et al.* 1975; Gill *et al.* 1980; CSN 19, 22) and mature forest (McLean & Gill 1988; CSN 19). Recorded from high altitudes to sea-level (Penniket 1955; Wilkinson & Guest 1977; Oliver; CSN 19, 38).

Mainly inhabit beech forest, such as those dominated by Mountain Beech *Nothofagus solandri* or Silver Beech *N. menziesii* (Penniket 1955; Henderson 1977; Heather & Robertson 1997; CSN). In survey in L. Sumner SF, Canterbury, recorded mainly in high-altitude forest, and absent from forest from lower altitudes: (1) Mountain Beech forest, often forming tree-line, generally with simple structure and few associated species, most commonly *Coprosma pseudocuneata* and Shield Fern *Polystichum vestitum*; (2) mixed forest of Red Beech *Nothofagus fusca* and Mountain Beech with subcanopy of Silver Beech, and many other species, such as *Coprosma foetidissima*, *C. parviflora* and Shield Fern in lower layers; mostly on terraces and lower slopes, but sometimes also at higher altitudes; (3) Mountain Beech forest with scattered Silver Beech, a shrub layer containing *Olearia lacunosa* and *Pseudopanax simplex*, and diverse ground cover; usually on steep upper slopes. Not recorded on lower slopes and terraces in mixed forest of Red Beech, Mountain Beech, Broadleaf *Griselinia littoralis* and *Coprosma pseudocuneata* (Wilkinson & Guest 1977). In lowland forest in West Coast, dominated by Red Beech and Silver Beech with some emergent Rimu *Dacrydium cupressinum*, recorded only where subcanopy and upper understorey are well developed, but lower layers and ground cover are open, and there are few epiphytes (Onley 1980). Often recorded in Manuka *Leptospermum scoparium* and Kanuka *Kunzea ericoides* forest and scrub (Henderson 1977; Oliver; CSN) with either a dense or open understorey (Gill 1980; Cunningham 1985). Said to prefer mature, diverse forest such as tall dense Kanuka forest with low dense understorey of introduced broom *Cytisus* with a few other

shrubs (Hunt & Gill 1979; Gill 1980). Often occur in regrowth, e.g. of Totara *Podocarpus totara* (Falla *et al.* 1975; Gill *et al.* 1980; CSN 19, 22). Elsewhere, often occur at ecotone between forest and scrub (Turbott 1967; Child 1975; Oliver). Also often recorded among exotic conifers (see Modified habitats, below). Occasionally inhabit subalpine scrub, but usually near tree-line (Child 1975; Falla *et al.* 1975; Gill *et al.* 1980). When Silver Beech forests at high altitudes are covered in snow, birds sometimes move to coast, inhabiting low closed Kamahi *Weinmannia racemosa* forest, with emergent Rimu and Northern Rata *Metrosideros robusta*, poorly developed understorey and open ground layer (Onley 1980). Also occasionally inhabit podocarp–broadleaf forest (Onley 1980; CSN 19). MODIFIED HABITATS: Often recorded in plantations of exotic conifers, such as Monterey Pine and larch *Larix* (Falla *et al.* 1975; Gaze 1985; CSN), especially in dense, mature stands with even-aged canopy (Clout & Gaze 1984). Sometimes occur in gardens (CSN), and other exotic plants such as willows *Salix*, Gorse *Ulex europaeus* and broom (Falla *et al.* 1975; CSN 19, 26).

DISTRIBUTION AND POPULATION
Endemic to SI of NZ. Early report from Great Barrier I., NI (Hutton 1868) seems unlikely (Bell 1976).

SI Widespread, especially in W. NELSON: Widespread. MARLBOROUGH: Widespread on islands in Marlborough Sounds, and recorded at scattered sites in coastal and near-coastal areas, from Okarimo and mouth of Wairau R., S to White Bluffs and Craiglochart, but more widespread S from C. Campbell, in Inland and Seaward Kaikoura Ras. Elsewhere, occur in Richmond Ra., S to n. St Arnaud Ra. CANTERBURY: In coastal and near-coastal areas, occur S to lower reaches of Hurunui R., and, farther S, widespread on Banks Pen., and also recorded along middle reaches of Rangitata R. and round Timaru. Inland, widespread on w. slopes of S. Alps, from Hanmer Springs and Lewis Pass, S to upper reaches of Rakaia R. and L. Heron, with records at a few scattered sites on w. Canterbury Plain. OTAGO: Recorded at a few sites round lower reaches of Waianakarua R., and widespread in coastal and near-coastal areas S of Shag Pt, including Otago Pen., and inland to line joining L. Mahinerangi and mouth of Clutha R. Recorded inland at scattered sites on w. slopes of S. Alps, especially near Ls Hawea, Wanaka and w. Wakatipu. SOUTHLAND: Widespread,

though sparsely scattered or absent from a few parts, e.g. area N of Catlins Forest Park and in Longwood Ra. Widespread on Stewart I. and associated islets. WEST COAST: Widespread, but more scattered N of C. Foulwind (NZ Atlas; CSN).

Breeding Probably throughout range.

THREATS AND HUMAN INTERACTIONS
Range contracted and populations declined after clearance of native forest and introduction of mammalian predators, though there has been some expansion into exotic pine forests (Turbott 1967; Heather & Robertson 1997; Oliver). In Waitutu Forest, w. Southland, lower numbers recorded in logged forests than in unlogged areas (Elliott & Ogle 1985). Eggs and young often taken by introduced Stoats *Mustela erminea* and Black Rats *Rattus rattus* (Cunningham 1985; see Breeding: Success).

MOVEMENTS
Little known. Resident or sedentary, possibly with some local and altitudinal movements (see below).

Resident or sedentary in Kowhai Bush, Kaikoura (confirmed by observations of colour-banded birds), though least abundant or conspicuous May–June (Gill 1980; Gill *et al.* 1980; Cunningham 1985; Dean 1990). Present throughout year in Dunedin (Kikkawa 1966; CSN 2), Windbag Valley, s. Westland (O'Donnell & Dilks 1994) and Cobden, Westland (CSN 33). Form flocks that move locally in autumn and winter in Otago and Southland; juveniles occurred in most flocks (Henderson 1977).

Some altitudinal movement speculated. Said to only occur in coastal forest and scrub near Punakaiki, coastal Westland, in winter, coinciding with snow at higher altitudes in Paparoa Ra. (Dawson *et al.* 1978; D.J. Onley). In w. Paparoa Ra., Westland, said to have moved to altitudes as low as *c.* 130 m asl in spring (Penniket 1955). In Rakiahua Valley, on Stewart I., occur at high altitudes throughout year, but only present in lowlands during spring (Guthrie-Smith 1914).

In detailed study at Kowhai Bush, near Kaikoura, 1979–82, found to be sedentary and territorial throughout year. Though sedentary, at higher elevations, where resources less predictable, may move more often than populations at lower altitudes. Juveniles more mobile than adults, moving in flocks over large parts of study area in non-breeding season (Cunningham 1985).

Banding Total of 297 banded in NZ, 1950–96 (Cossee 1998); though total number of retraps not known, of 25 banded 1950–74, two recoveries (8%) (Robertson 1975).

FOOD
Invertebrates, mainly insects; and sometimes fruit. **Behaviour** Mainly arboreal; gregarious, often foraging in mixed-species feeding flocks (see below). Forage in understorey and canopy of forest; among foliage, twigs, branches and trunks of shrubs and trees; occasionally forage beneath loose bark of large branches or tree-trunks, and very occasionally forage on ground (Andersen 1926; Riney *et al.* 1959; Turbott 1967; Falla *et al.* 1975; Henderson 1977; Gill 1980; O'Donnell & Dilks 1994; Heather & Robertson 1997; Oliver; CSN 23, 31). DETAILED STUDIES: At Kowhai Bush, near Kaikoura, May 1976–Sept. 1977 (Gill 1980); and in Windbag Valley, s. Westland, Oct. 1983–Dec. 1985 (O'Donnell & Dilks 1994). SIZE OF FEEDING FLOCKS: Sometimes forage in twos, but more often in flocks of 3–12 birds, including loose family groups (Andersen 1926; Turbott 1967; Blackburn 1968; Falla *et al.* 1975; Henderson 1977; Dean 1990; CSN 23, 31). At Kowhai Bush, during breeding season, territorial birds usually foraged as pairs within all-purpose territory; outside

breeding season, continued to forage as pair, but occasionally joined other foraging adults or groups of juveniles foraging within territory; juveniles usually foraged in groups, mostly with siblings, and less often with juveniles from other nests (Cunningham 1985). Sometimes occur in mixed-species feeding flocks with species such as Yellowheads, Silvereyes, parakeets *Cyanoramphus*, Grey Warblers, New Zealand Robins *Petroica australis*, Riflemen *Acanthisitta chloris*, Bellbirds *Anthornis melanura*, New Zealand Tomtits *Petroica macrocephala*, Grey Fantails, Common Chaffinches *Fringilla coelebs* or Common Redpolls *Carduelis flammea* (Henderson 1977; Read & McClelland 1984; Read 1987; Dean 1990; Heather & Robertson 1997; Oliver; CSN); also formerly foraged with Saddlebacks *Philesturnus carunculatus* (Oliver). At Kowhai Bush, Brown Creepers mostly formed the nucleus of feeding flocks, and determined the direction of their movement; of 76 mixed-species feeding flocks (2–6 species/flock), 81.6% contained Brown Creepers, with mean of 4.6 Brown Creepers/flock (2.1; 1–12; 76); feeding flocks occurred throughout day, but were strongly seasonal; none recorded during breeding season, Sept.–Dec. (Dean 1990). **FORAGING HEIGHTS:** Usually forage in low trees, 2–7 m above ground (Andersen 1926; Gill 1980) and in canopy of forest (Henderson 1977; O'Donnell & Dilks 1994). At Kowhai Bush, of 176 observations of foraging, foraged mostly in understorey: <1% on ground, 14% in lower understorey (<2 m above ground), 82% in upper understorey (>2 m) and 4% in canopy (7–10 m). In Windbag Valley, of 2353 observations of foraging, mostly foraged in upper strata of forest (heights not specified): 4% on ground, 18% in lower understorey, 18% in upper understorey, 34% within canopy and 30% in top of canopy. **FORAGING SITES:** At Kowhai Bush, of 175 observations of foraging: 26% among foliage, 18% in twigs, 25% on branches, 29% on trunks and 2% in litter layer; not seen foraging in air. Mostly foraged in *Leptospermum* trees (70–80%), though recorded in ten other species of plants, including *Cytisus monspessulanus*, *Pittosporum tenuifolium*, *Coriaria arborea*, *Dodonaea viscosa* and *Melicytus ramiflorus*, of which *Cytisus* was most commonly used. In Kanuka forest in Otago and Southland, spent *c.* 60% of foraging time (N not given) foraging from foliage, 30% from twigs and 10% from branches or tree-trunks; observations in other habitats suggest that >60% of time is spent foraging among foliage, except in fuchsias *Fuchsia*, where forage in masses of loose papery bark hanging from trunks and branches (Henderson 1977). In Windbag Valley, of 2353 observations of foraging, foraged in 41 species of plants (summarized in Table 1), including 11 species in canopy and 30 shrubs and other plants in understorey; invertebrates were mostly captured in Silver Beech *Nothofagus menziesii*; nectar was only taken from *Pseudopanax simplex*; and fruit taken from four species, mainly Lancewood *P. crassifolius* and *P. simplex*. Historically, during harsh conditions, said to leave native forest to inhabit sheep stations, flitting round meat gallows and picking morsels of fat from bones and skins of butchered animals (Turbott 1967). **FORAGING METHODS:** Forage mainly by gleaning, and less often by hanging. At Kowhai Bush, of 176 observations of foraging, 76% by gleaning and 24% by hanging, mostly upside-down. In Windbag Valley, of 2353 observations of foraging (figures estimated from graph), 95% were gleaning from foliage and twigs, and 5% of observations were of scanning for prey. When foraging in forests in Otago and Southland, constantly on the move; rate of progress of flock depended on richness of food supply and density of vegetation; move through canopy in series of hops and short

Table 1. Plants used for foraging in Windbag Valley, s. Westland (% of total foraging observations) (O'Donnell & Dilks 1994).

PLANT SPECIES	FOOD ITEMS			
	All feeding 2353 obs.	Nectar 1 obs.	Fruit 12 obs.	Invertebrates 405 obs.
CANOPY SPECIES				
Dacrydium cupressinum	9.6	–	–	12.4
Dacrycarpus dacrydioides	3.3	–	16.7	2.0
Elaeocarpus hookerianus	0.4	–	–	–
Lagarostrobos colensoi	0.9	–	–	2.7
Metrosideros umbellata	2.6	–	–	0.5
Nothofagus menziesii	47.3	–	–	57.5
Podocarpus hallii	1.6	–	–	1.2
P. totara	0.9	–	–	0.5
Prumnopitys ferruginea	–	–	–	–
Weinmannia racemosa	19.0	–	–	13.8
Dead trees (various species)	0.2	–	–	–
SHRUB HARDWOODS				
Aristotelia serrata	0.3	–	–	0.3
Ascarina lucida	<0.1	–	–	–
Carpodetus serratus	<0.1	–	–	–
Coprosma	0.3	–	8.3	0.7
C. foetidissima	0.1	–	–	–
C. rotundifolia	0.1	–	–	–
Fuchsia excorticata	0.1	–	–	–
Griselinia littoralis	2.8	–	–	1.7
Hebe	0.2	–	–	–
Hedycarya arborea	0.2	–	–	–
Hoheria glabrata	0.1	–	–	–
Meylicytus ramiflorus	<0.1	–	–	–
Myrsine divaricata	<0.1	–	–	–
Neomyrtus penunculata	<0.1	–	–	–
Olearia	–	–	–	–
Phyllocladus aspleniifolius	0.9	–	–	0.7
Pseudopanax colensoi	0.1	–	–	0.5
P. crassifolius	2.3	–	41.7	2.2
P. edgerleyi	0.4	–	–	–
P. simplex	1.9	100.0	35.5	1.0
Pseudowintera colorata	1.4	–	–	0.7
OTHERS				
Tree-ferns	0.3	–	–	–
Other ferns	0.1	–	–	–
Freycinetia baueriana	0.3	–	–	–
Metrosideros spp.	0.8	–	–	–
Moss	0.4	–	–	–
Muehlenbeckia australis	<0.1	–	–	–
Orchids	<0.1	–	–	–
Paraxilla	0.2	–	–	–
Ripogonum scandens	0.1	–	–	–
Rubus	<0.1	–	–	–
NOT IN PLANTS				
Ground or air	0.2	–	–	–

flights (up to 10 m) with longer flights (up to 30 m) where trees scattered or in clumps. Very agile and acrobatic when foraging, inclding manoeuvres such as hanging upside-down from branches and twigs, and walking along underside of branches while probing bark for insects. Large prey usually killed by holding it in bill and bashing it repeatedly against branch, then dismembering with bill while holding it against branch with one foot (Henderson 1977).

Detailed studies In WINDBAG VALLEY (2353 feeding obs. in 41 species of plants [see Table 1]; O'Donnell & Dilks 1994): 17.2% of observations identified as feeding on invertebrates (mainly insects), 0.5% fruit, <0.1% nectar and remaining 82.2% on unidentified items, probably invertebrates.

Other records Plants (All fruit): DICOTYLEDONS: Araliaceae: *Pseudopanax crassifolius*[4,6]; Coriariaceae: *Coriaria arborea*[5]; Pittosporaceae: *Pittosporum tenuifolium*[5]; Rubiaceae: *Coprosma propinqua*[4]; *C. robusta*[5]; *C. rotundifolia*[4]. **Animals** SPIDERS[7]. INSECTS: Larv.[4,9], ads[3,8]; Coleoptera[1,2,7]; Diptera[2,7]; Hemiptera[2]; Lepidoptera[7]. **Other matter** Animal fat[2].

REFERENCES: [1] Riney *et al.* 1959; [2] Turbott 1967; [3] Falla *et al.* 1975; [4] Henderson 1977; [5] Gill *et al.* 1980; [6] O'Donnell & Dilks 1994; [7] Heather & Robertson 1997; [8] Oliver; [9] CSN 29.

Young No information on feeding of nestlings. For feeding of fledgelings, see Breeding (Fledging to independence).

SOCIAL ORGANIZATION

Known mostly from detailed study at Kowhai Bush, near Kaikoura, 1979–82 (Cunningham 1985; Sherley & Cunningham 1985). In breeding season, usually occur in pairs (Cunningham 1984; McLean & Gill 1988; Dean 1990). Outside breeding season, often in flocks of 5–8 birds (Cunningham 1985) and occasionally flocks of 12–20 (Moncrieff 1929; Dean 1990; CSN) but occur singly or in twos at any time of year (CSN). Once, in Mar., 38 birds recorded in one tree (CSN 37) and 50 birds reported (CSN 29), apparently in close proximity. Juveniles form roaming flocks outside breeding season (Cunningham 1985). Often form nucleus of mixed-species flocks in non-breeding season (see Food).

Bonds Monogamous, and usually nest as simple pairs (Cunningham 1985; Sherley & Cunningham 1985). High mate-fidelity: 64.7% of 17 pairs remained together in two successive seasons, and 29.4% for three seasons; all changes in partner followed disappearance of mate rather than mate-swapping or divorce. Of two males and two females banded as nestlings and later found breeding, three bred in first year after fledging and remaining female bred in second year (Cunningham 1985). Pairs perform duet as part of pair-bond maintenance (Cunningham 1985; see Voice). MATE-GUARD-ING: Male guards female from a few days before nest-building begins till second or third egg laid (Cunningham 1985; McLean & Gill 1988). Guarding involves male hopping about, usually within 2–3 m of mate, and adopting searching posture (see Social Behaviour). Mate-guarding may be intermittent later in breeding season, when male is feeding fledgelings of previous brood (Cunningham 1985). Possible **Co-operative breeding** reported: two adults fed chicks while parents were being banded; also, unbanded bird fed chicks in absence of two banded adults that usually fed young, but unbanded bird was later chased off twice by banded birds when it approached with food. Suggested that co-operative breeding resulted from latent parental behaviour during drought, when conditions unsuitable for widespread breeding (McLean *et al.* 1987). **Parental care** Brooding by female only, but both sexes feed young (see Breeding: Young). Young fed mainly by male if female re-nests; sometimes non-breeding birds feed young (Cunningham 1985; see above). DEPEN-DENCE OF YOUNG: At Kowhai Bush, though capable of catching own food 18–20 days after fledging, still fed by parents (see Breeding: Fledging to independence).

Breeding dispersion Pairs usually occupy and defend all-purpose territories throughout year; mean size of territory,

0.97 ha (0.21; 39). Territorial boundaries of pairs largely consistent between years, with only minor changes. Once borders defined, territorial trespassing by adults usually rare (Cunningham 1985), though more common if neighbouring males do not share song-patterns (Sherley & Cunningham 1985). In non-breeding season, juveniles less site-specific than adults, wandering through territories of several adult pairs (Cunningham 1985).

Roosting No information.

SOCIAL BEHAVIOUR

Reasonably well known, mostly from study at Kowhai Bush, near Kaikoura (Cunningham 1985). In flocks, maintain contact with almost constant Zick calls (Cunningham 1985; Dean 1990). Several displays and postures described and functions postulated (Cunningham 1985). SINGING POSTURES: When singing in centre of territory, bird assumes upright stance with tail unfanned and held below body, bill pointed forward and feathers of crown, throat and body raised. Bird pivots through arc of 45–90° while singing. In Unison Singing (see Voice), male aligns body parallel to perch, lowers head, sleeks feathers of crown, throat and body, and occasionally spreads tail and flutters wings; points bill towards neighbouring bird and sings in response to Song of rival; Song often overlaps that of rival (see Defence of Territory). SEARCHING POSTURE: Adopted when quickly hopping from branch to branch while examining surroundings; fully extend neck, raise feathers of crown and throat, and hold tail closed; tail held at 15–20° above axis of body, and often flicked. UNDULATING FLIGHT DISPLAY: Used when bird believed to be attacking or interacting with intruder. Differs from normal flight in being extremely laboured, slow and conspicuous, with feathers of crown and throat raised, and tail spread and flicked from 15–20° above to 15–20° below horizontal, showing conspicuous dark-brown band. WING-UP DISPLAY: Usually given by adults responding to Skree calls of young and, once, by female approaching nestlings. Wings partly extended and held above back in broad V, as if bird about to fly. With wings in this position, bird leans forward, hopping round observer at close range. Feathers of crown, throat and breast raised, and tail spread and often flicked, while rapidly giving Kee call. WING-FLUTTER: Performed by female soliciting food or copulation from mate, and by young begging for food from parents; also given in territorial disputes, and by young males, females or males who have been chased; and by males in Courtship Pursuit. Involves synchronous beating of half-extended and slightly raised wings, while assuming Crouching Posture. CROUCHING POSTURE: Assumed by females and fledgelings begging for food and females inviting copulation. Bird lowers body, pulls head towards body, and points bill towards target bird, while giving wing-flutter and Zheep, Buzz or Zee calls (see Voice).

Agonistic behaviour Both sexes defend territory against conspecifics in non-breeding season and early in breeding season; after laying begins, only male involved. Utter rapid Kee calls during defence (see Voice). If female discovers trespasser in territory, she sings and male immediately flies in to help in defence. Male uses loud, complex territorial Song in defence. In playback experiments, responded more vigorously to recordings of local dialects of Song than those of more distant populations. However, also reacted more strongly to Song of stranger than to that of neighbours with local dialect (Cunningham 1984, 1985). In boundary disputes, neighbouring males may engage in Unison Singing, in which birds approach and retreat from each other in co-ordinated
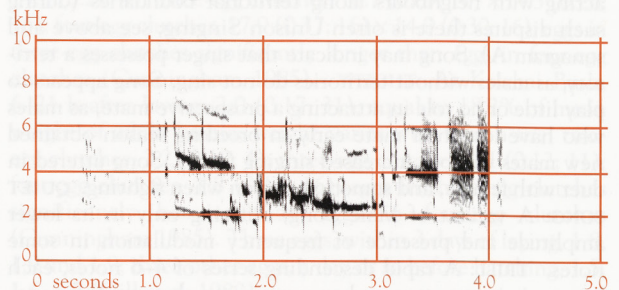
movements, facing each other from 10–20 cm apart with feathers sleeked and tail, body and head held low, repeatedly calling *chee-cup*. Unison Singing mainly occurs in breeding season and involves temporal overlap of Songs (Cunningham 1984, 1985; Sherley & Cunningham 1985; see Voice for further details). **Fighting** Occasionally occurs early in breeding season or when a pair start using a different part of their terri-tory, bringing them into contact with different neighbours (Cunningham 1985). Fights always between members of same sex, and usually begins in branches; birds may hold each other with feet and peck at one another as they fall to ground with wings fluttering; once on ground, fight resumes; both sexes Chatter throughout fights, and one or both birds may sing (Cunningham 1985; see Voice). Utter *tee-hee-hee* call when displaced by another bird, apparently as appeasement (Cunningham 1985). Sometimes aggressive towards conspecifics in mixed-species flocks, but not towards other species (Dean 1990). If juvenile setting up territory is attacked by neighbourning territorial adult male, juvenile may give quiet Song when several metres away from adult (Cunningham 1985; see Voice). INTERSPECIFIC INTERAC-TIONS: Members of breeding unit exhibit winter mobbing behaviour toward potential predators including Cats, rats, Stoats, kingfishers, Shining Bronze-Cuckoos *Chrysococcyx lucidus* and people; unrelated birds do not participate (Cunningham 1985). Twice seen chasing Grey Warbler to ground (Dean 1990).

Sexual behaviour COURTSHIP FEEDING: Female flutters wings and gives Zheep calls; male then feeds female, usually away from nest (Cunningham 1985; see Wing Flutter, above), though also at nest (Soper 1972). COURTSHIP PURSUIT: Chases lasted 2–5 min and were either long rapid flights through canopy or short flights and quick hops through dense vegetation, accompanied by chatter calls and Wing-fluttering by male (Cunningham 1985). **Copulation** Often preceded by pursuit of female by male. If ready to copulate, female crouch-es (see Crouching Posture, above) and allows male to approach; she then moves tail slightly to one side, and allows male to mount, while continuing to flutter wings. Copulation usually lasts 10 s. If female not receptive, she fans tail and hops from perch to perch, and chasing continues till copula-tion finally takes place or male distracted by rival (Cunningham 1985).

Relations within family group Young huddle together in first week after fledging, regardless of weather conditions; later, follow parents, Wing-fluttering and begging. After fledging, remain in group with siblings till following breeding season (Cunningham 1985). Respond to squeaking by chat-tering excitedly (CSN 24). Young males appear to learn Song from neighbours (see Voice). **Anti-predator responses of young** In first week after fledging, spend much time perched motionless in dense vegetation, and when in open, flee into dense vegetation in response to alarm call from parents, e.g. when Swamp Harrier *Circus approximans* flew over (Cunningham 1985). **Parental anti-predator strategies** Mob people at nest (McLean *et al.* 1987); also Mob other potential predators (see Agonistic behaviour, above).

VOICE Well known from study at Kowhai Bush, Kaikoura, and on Stewart I. (Cunningham 1985), which includes son-agrams, and from which statements taken unless stated; eight vocalizations distinguished in study of flocks in autumn and winter (Henderson (1977); and vocalizations in musical notation given by Andersen (1915, 1926). Both sexes sing;

Male Song is loud and complex (Cunningham 1984, 1985). Males do not sing continuously, and are often silent for long periods. Even when interacting vocally with neighbours, males interrupt their singing with bouts of calling and feed-ing. There is incessant calling from large flocks (>9 birds) in autumn and winter, whereas small flocks often silent for many minutes at a time (Henderson 1977). Mixed-species feeding flocks, in which members of flock widely spread, described as noisy, mostly from contact calls of Brown Creepers (Dean 1990). DEVELOPMENT OF MALE SONG: Young males appear to learn Song from neighbours with whom they interact, rather than from their fathers. Learnt in three stages: (1) Subsong, a low-volume song-like vocalization composed of slurrs of var-ied length and pitch, interspersed with harsh notes; pitch of each note has irregular frequency modulation; (2) Plastic song, with greater structure than Subsong, but each varies greatly and lacks any stereotyped pattern, as notes occasion-ally added or subtracted from sequence; and (3) Full Song, which, in a displacement experiment (but with only two males), altered little once fully developed. Analysis of Songs over time (24 and 27 months apart, but only of two individ-ual males) suggested that Songs of an individual are stable over time. Neighbouring males generally share Song-patterns but retain individually distinctive interludes (see Male Song, below), and often interact by singing in unison (see below) along common boundary; those with dissimilar Songs either do not interact, or do so infrequently. DUETS: Often performed; male and female sing their respective Songs, often during early stages of territorial disputes, as pair approaches territorial boundary (n=23). During such disputes, Zeer of female may be given in duet with Song of male (n=14). UNISON SINGING: Two interacting males temporally overlap their Songs, with one changing singing pattern to that of the other. It begins when two, sometimes three, neigh-bouring males are attracted to common territorial boundary by one of them singing or calling near the boundary. The few Songs sung at this early stage are usually given in strings, with no overlap. When males approach to within 1–2 m of each other, singing increases, and they begin to sing only single Songs (see discussion of strings of Songs and single Songs in Male Song, below), and each male responds rapidly to the other's Song, often with overlap of Songs (n>60). When two males interact closely (e.g. at 0.5 m), respond more rapidly than when farther apart (e.g. at 2.4 m). Most males show no preference to lead or to follow. Bouts last mean 14.2 min (3.1; 10–20; 20) and end abruptly when 3–4 m apart. Unison Singing from an unknown number of birds is shown in sona-gram **A**. Trill, Chatter or Chee-cup calls may occur during Unison Singing. Its apparent function is to assist in definition of territorial boundaries, and is used increasingly from late

A L.B. McPherson; Kowhai Bush, Kaikoura, SI; Oct. 1984; P106

Aug., with most interactions occurring between mid-Sept. and mid-Dec. ANNUAL PATTERN: During non-breeding season and early in breeding season, both sexes sing and defend territorial boundaries; once laying begins, males perform most territorial defence. Male Song peaks between late Aug. and late Nov., thereafter declining to very low levels from Mar. to May, then slowly increasing till late July and then sharply increasing. In non-breeding season, territorial defence is mostly made with rapid Kee calls, and Song heard only occasionally. INDIVIDUAL DIFFERENCES: Most males sing only one Song-type, which is stereotyped over time and is individually distinctive, but exhibits a measurable amount of variation between repetitions. A male recognizes Song of another male, probably from morphology and pattern of notes in interludes, which vary much between neighbouring individuals. Females sing only one Song-type, which is highly stereotyped over time; there are great differences between Songs of individual females, especially in morphology of notes within Songs. REGIONAL VARIATION: Males in different populations have different dialects, and within a population there are geographical subdialects. RESPONSE TO PLAYBACK OR IMITATION: Respond to squeaking and to playback (Soper 1976; Henderson 1977). When local and foreign dialects differed markedly, males responded more strongly to replay of local dialect, and, within that dialect, responses were greater to Songs of strangers than to those of neighbours. Recordings of same individual singing spontaneously and in response to replay appeared not to differ in sequence or morphology of notes comprising the Songs. When squeaking or replay finished, response also ceased, unusual in passerines, and suggests that singing requires presence of another singing male (Andersen 1926; Cunningham 1985; CSN 24). Males responded with Unison Singing (with overlapping Songs) for 81.2% of Songs played back near centres of territories and 71.2% on territorial boundaries, but none c. 5 m outside territorial boundaries. Female Song given by paired females in response to playback of Male Song.

Adult male MALE SONG: Loud sequence of 5–14 notes, described as slurs, whistles and harsh notes, with total duration of 1.9–4.5 s. Described as a short attractive warble, in a minor key (Soper 1976). Average rate of delivery of Song by territorial male is 6 Songs/min. Two patterns of performance: (1) a string of 2–5 Songs, the whole lasting 9.0 s (2.31; 10) with intervals between strings of 20.2 min (7.82; 10); Songs within string often, but not always, connected by an interlude, a stereotyped pattern of notes or trills or both; (2) a single Song, lasting 2.8 s (0.81; 11) with brief pause of 15.3 s (1.82; 11) before next Song. Strings of Songs given when patrolling central portions of territories or when responding to playback of Song within territory, whereas single Song given when interacting with neighbours along territorial boundaries (during such disputes there is often Unison Singing; see above and sonagram A). Song may indicate that singer possesses a territory, as males without territories do not sing; Song appears to play little or no role in attracting a prospective mate, as males who have lost their mate early in breeding season obtained new mates without increased singing (n=2). Song uttered in duet with female, and sometimes given when fighting. QUIET SONG: A variant of Male Song, differing only in its lower amplitude and presence of frequency modulation in some notes. TRILL: A rapid descending series of 4–6 notes, each harmonic in structure and appearing as a chevron in a sonagram, with most energy at 3.3 and 4.9 kHz in initial note, and 2.8 and 4.1 kHz in final note; total duration is c. 0.21 s. Given

only by males, and only in Unison Singing, just before Songs that were sung in unison.

Adult female FEMALE SONG: A rapid sequence of brief notes, with a prolonged high-pitched note at or near end. Comprising 4–9 notes, and lasting 0.8 s (0.45; 20). Apparently used to attract mate to help evict intruders (n=5) or to mob a potential predator. During non-breeding season, given by single female starting to associate with a male (n=15), and by paired females temporarily separated from mate (n=5). Occasionally given when fighting. ZHEEP: A simple buzz, descending from c. 5.6 to 4.3 kHz, with frequency modulation at c. 50 Hz. Recorded only from females, and always accompanied by Wing-flutter (see Social Behaviour). Uttered when soliciting food (n=3) or before copulation (n=2). ZEER: Usually a single descending, buzzing slur, frequency range c. 4.4–2.8 kHz, lasting c. 0.4 s (n=12). On Stewart I., one female uttered an ascending slur before the usual zeer. Given only by paired females, when with mate and involved in a boundary dispute (n=31), often when chasing a conspecific (n=20). Given both as a solo (n=17) and as duet with mate, who utters Male Song (n=14). TICK: A sharp mechanical tick, lasting c. 0.02 s, harmonic in structure. Usually uttered in series of 2–6 notes, but sometimes singly. Given only by female near nest or fledged young, in response to presence of observer (n=10) or to Swamp Harrier flying overhead (n=1).

Both sexes ZICK: A brief repeated note, lasting c. 0.05 s; harmonic in structure. When given slowly, spaced unevenly at intervals of 0.42 s (0.202; 15); when given rapidly, more evenly spaced, at intervals of 0.25 s (0.064; 20). Slow calls often changed abruptly to rapid calls when the caller flew away. The slow call may allow members of flock that have separated to rejoin each other, while rapid call may indicate that flock is moving to new location. CHATTER: A series of notes, each lasting c. 0.04 s, appearing as a chevron in sonagrams, and harmonic in structure, with most sound energy at 3.2–5.8 kHz. Given by both sexes during pre-copulatory chases (n=5) and by male during copulation (n=4); often uttered by both sexes in bouts of Unison Singing that include active chasing and physical fighting; also given when nestlings moved within nest or when they fledged. CHEE-CUP: Two notes, each appearing in sonagrams as a skewed chevron, so the descending arm is much lengthened, and with two loud and several faint harmonics, all 3.2–6.0 kHz. Usually given singly, but sometimes in series of 2–7 calls. Given by both sexes during bouts of Unison Singing, while approaching or retreating from birds with which they were interacting (n=12); also given by female forced from nest by mate (n=1). KEE: A series of kee notes, each note appearing as a chevron in sonagrams, and with a closely spaced harmonic structure. Two temporal patterns: a rapid call with notes lasting c. 0.07 s; and a slow call, with notes lasting c. 0.15 s, and greater intervals between them. Slow call probably given in response to motionless observer near nest or near foraging group (n=30), in response to small passerine near nest or fledgeling (n=17), or when parents chased persistently begging young (n=2). Rapid call given when mobbing potential predator (n=25) and during disputes when in flocks or pairs (n=10). TEE-HEE-HEE: Three notes, each harmonic in structure and appearing as a chevron in sonagrams, with most energy at c. 3.2 kHz and 4.8 kHz; first note lasts c. 0.08 s, second and third last c. 0.06 s, and intervals between notes c. 0.03 s. Given by both sexes when being attacked and displaced by another bird, either conspecific or heterospecific. CHEE: A slur, harmonic in structure, beginning at c. 3.7 kHz and descending to c. 3.3

kHz; lasts *c.* 0.15 s. Usually given in series of 2–4 notes. Given when foraging, in response to sudden appearance of observer (n=30). CHEER: Similar in structure to Chee, but with rapid frequency modulation, often more pronounced at beginning of note, giving a rough buzzing quality. Given by parents, when observer attempted to catch recently fledged young (n=12), when flock chased by a New Zealand Robin (n=1) and when a Swamp Harrier flew over (n=1). Apparently express alarm of higher intensity than Chee. **Other calls** Chatter may grade into Kee, and Chee into Cheer.

Young BUZZ: A begging call, similar to Zheep of adult female, but higher in pitch, and varying greatly in duration, depending on speed of response of parents. Given from 2–3 days after hatching till several days after fledging, always with Wing-flutter. Audible to 1–2 m in first week after hatching, and to 6–7 m just before fledging. Also described as a repeated hoarse cheep, uttered when parent nearby or approaching (Henderson 1977). ZEE: A begging call from fledgelings at least 1 week out of nest; also given by juveniles when chased by parents. Accompanied by Wing-flutter about half the time. SKREE: A harsh call given by nestlings or fledgelings when handled. CHIP: A brief call, given singly by fledgelings, probably out of visual contact with parents. SEE: A brief slur, rising then falling, given by nestlings that had fallen from nest, and which were probably out of sight of parents. SONG: Quiet Song heard from young males setting up territories who had been attacked by neighbouring males (n=10). See also Development of Male Song, above.

BREEDING Known mostly from detailed study over three breeding seasons at Kowhai Bush, Kaikoura (Cunningham 1985). Early nests defined as those in which laying began before 17 Nov. and late nests are those started after 17 Nov. Multi-brooded (Cunningham 1985); sometimes make up to four nesting attempts in a season (NZRD).

Season Sept. to Feb. At Kowhai Bush: laying, mid-Sept. to mid-Jan., but mostly late Sept. to late Dec., with peaks in late Sept., early Oct. and late Nov.; earliest second clutch started mid-Nov.; young, mid-Oct. to early Feb., but mostly late Oct. to mid-Jan.; fledge late Oct. to mid-Feb., but mostly early Nov. to mid- or late Jan. (Cunningham 1985); eggs and young, Oct.–Dec. (Gill *et al.* 1980).

Site In upright fork formed by 3–4 small branches, well concealed beneath dense canopy of vegetation (Cunningham 1985); in fork of bare twigs or in clump of dense foliage, in canopy and upper and lower understorey of forest, low scrub and 6-year-old pine plantation (Gill *et al.* 1980); usually in canopy or in vines, sometimes in a fork (Falla *et al.* 1975); between trunk and short branches growing from stunted branch of tree (Hutton & Drummond 1904; Oliver); once on horizontal branch overgrown with vine Pohuehue *Muehlenbeckia australis* (Gill *et al.* 1980); once in hole in trunk of living beech *Nothofagus* (Penniket 1955). At Kowhai Bush, of 52 nests, 48 (92.3%) built in Kanuka *Kunzea ericoides*, two (3.8%) in *Coprosma* and singles in Monterey Pine and Bush Lawyer *Rubus squarrosus* (Cunningham 1985). In same area, of 19 nests, 11 (55%) were in Kanuka, three (15%) in Akiraho *Olearia paniculata* and singles in Akeake *Dodonaea viscosa*, Kohuhu *Pittosporum tenuifolium*, Tutu *Coriaria arborea*, Gorse *Ulex europaeus* and Douglas Fir *Pseudotsuga menziesii* (Gill *et al.* 1980). In w. Paparoa Ra., West Coast, recorded in scrubby Rata *Metrosideros umbellata* and beech (Penniket 1955). MEASUREMENTS (m): Height of nest, at Kowhai Bush, 4.7 (1.52; 1.6–9.4; 52) (Cunningham 1985); in same area,

4.2 (1.2–8.0; 19), though real mean may be higher because lower nests easier to find (Gill *et al.* 1980); in w. Paparoa Ra., 2.1–3.7 (Penniket 1955). Height of nest-plant, at Kowhai Bush, 5.3 (1.65; 1.8–11.3; 52); depth of nest below top of vegetation, 7.7 cm (3.08; 3.8–15.2; 52) (Cunningham 1985).

Nest, Materials Deep, tightly woven cup; elliptical, rather than round in plan from above, and wider at base than at rim. Outer layers of strips of Kanuka bark, dry moss, lichen, leaf-skeletons and plant-fibre, bound with spider web; lined with fine grass, wool or a few feathers, usually from other species; tightly attached to branch with spider web and fine grass (Hutton & Drummond 1904; Gill *et al.* 1980; Cunningham 1985; Oliver). One nest on island off Stewart I. made of herbaceous or rush stems, rootlets and moss, lined with white feathers and feathers of Weka *Gallirallus australis* (Oliver). Only female collects material and builds nest (Cunningham 1985), though one observation of both sexes carrying material (CSN 19 Suppl.). At Kowhai Bush, most building took place before 10:00 and occurred in bouts of 10–15 min (Cunningham 1985). Estimated time taken to build nest, 11 days (7–17; 6); two nests (built after a previous nesting attempt) completed in 5 and 6 days (Cunningham 1985). MEASUREMENTS (cm): External diameter (longest axis), 9.2 (0.47; 52); external depth, 7.4 (1.16; 52); internal diameter (longest axis), 4.2 (0.76; 38) (Cunningham 1985); external diameter, 9–10 × 8–9; external depth, 6–7; internal diameter, 5 × 4–5; internal depth, *c.* 4 (Gill *et al.* 1980). Weight of nest, 11.4 (1.94; 52) (Cunningham 1985); 9–14 (Gill *et al.* 1980).

Eggs No description of shape. Ground-colour varies: mainly pale pinkish or white, and occasionally dark pink or light brown, with spots, blotches, speckles or streaks of light brown, reddish brown, dark brown or purple, varying from intense and almost confluent over entire shell to almost non-existent, though often forming zone round large end (Mathews 1930; Gill *et al.* 1980; Cunningham 1985; Oliver). At Kowhai Bush, of 57 eggs, 25 (43.9%) were white, 26 (45.6%) light pink and six (10.5%) dark pink. Pattern and colour consistent within clutches and between clutches from same female (Cunningham 1985). From same area, Gill *et al.* (1980) described three types: (1) chalky white with dark-brown speckles and blotches concentrated at large end; (2) pale brown with large dark-brown blotches and streaks, often so dense, especially at large end, that background colour difficult to determine; and (3) pale reddish-brown, with darker speckles and blotches concentrated at large end; two colour-types were present in one clutch. MEASUREMENTS: 18.6 (0.93; 17.4–19.6; 4) × 14.3 (0.38; 14.0–14.8; 4) (Oliver). At Kowhai Bush: 18.4 (0.68; 36) × 14.2 (0.32; 36); length varies with clutch-size, but not width: two-egg clutches, 19.3 (0.42; 4) × 14.3 (0.27; 4); three-egg clutches, 18.7 (0.69; 16) × 14.3 (0.26; 16); four-egg clutches, 17.9 (0.37; 16) × 14.0 (0.30; 16); eggs in three-egg clutches significantly longer than eggs in four-egg clutches (Cunningham 1985). WEIGHT: At Kowhai Bush, 6–21 h after laying: 2.0 (0.17; 31), equal to 18.2% of mean weight of adult female; weight varies with clutch-size: two-egg clutches, 2.2 (0.10; 4); three-egg clutches, 2.1 (0.12; 11); four-egg clutches, 1.8 (0.11; 16); eggs in three-egg clutches significantly heavier than eggs in four-egg clutches (Cunningham 1985). Three eggs, within 3 days of laying, 1.8, 1.9 and 1.9; three other eggs, a day or so before hatching, 1.5, 1.6, 1.7 (Gill *et al.* 1980).

Clutch-size Two to four (Oliver). At Kowhai Bush, 3.3 (0.72; 2–4; 42): C/2 × 6, C/3 × 18, C/4 × 18; early nests, 3.7

(0.47; 3–4; 22): C/3 × 7, C/4 × 15; late nests, 2.8 (0.63; 2–4; 20): C/2 × 6, C/3 × 12, C/4 × 2; clutches in early nests significantly larger than those in later nests (Cunningham 1985); 3.2 (0.56; 2–4; 15): C/2 × 1, C/3 ×10, C/4 × 4 (Gill *et al.* 1980).

Laying Eggs laid on consecutive days (Gill *et al.* 1980). For early nests, first egg laid 3.1 days (2–6; 10) after completion of nest; for two late nests, first egg laid 2 and 3 days after completion of nest (Cunningham 1985).

Incubation By female only; begins at completion of clutch in all early nests and most late nests, though in at least two late nests, incubation began before last egg laid. Females incubate for 70% of daylight hours (53–85%; n=29 bouts of 3 h obs.); attentiveness to nest usually declines during incubation period (Cunningham 1985). In mid- to late Oct., when mean monthly temperature 11.1 °C, during 12.1 h of observation at one nest, length of stints on nest, 21.9 min (9.7–35.4; 18); time spent off nest, 8.1 min (4.5–13.0; 23); in early Dec., when mean monthly temperature 15.1 °C, during 6.7 h of observation at one nest, length of stints on nest, 13.8 min (6.5–24.1; 16); time spent off nest, 7.7 min (5.1–12.3; 18) (Gill *et al.* 1980). Proportion of time spent incubating at two nests, 64% and 73%; incubating bird leaves nest in response to nearby call, or will leave nest, call and be answered from nearby (Gill *et al.* 1980). Attentiveness to nest declines through incubation period, but greater on cold or rainy days (Cunningham 1985). INCUBATION PERIOD: From laying to hatching of last egg, 19.2 days (1.10; 38) (Cunningham 1985); from laying to hatching of first egg, 19 days (n=1) (Gill *et al.* 1980).

Young Altricial, nidicolous. At hatching young have grey-brown down on top of head and along back and wings; and eyes closed (Cunningham 1985; NZRD). At 5 days, eyes begin to open; at c. 7 days, feathers on centre of breast and belly emerge from sheaths; at 9 days, feathers on back, wing and sides of breast emerge from sheaths (Gill *et al.* 1980). Only female broods (Gill *et al.* 1980; Cunningham 1984, 1985; Sherley & Cunningham 1985; Heather & Robertson 1997). Both parents feed young (Cunningham 1985; Sherley & Cunningham 1985) but very occasionally other birds also feed young (see Social Organization). **Growth** Weight and tarsus-length of young at Kowhai Bush, see Table 2. Weight at fledging, 11.7 (0.83; 10), equivalent to 96.1% mean adult weight; length of tarsus at fledging, 26.4 (0.60; 10),

equivalent to 98.9% mean adult length. Wing-length at fledging, 46.9 (1.59; 10), equivalent to 79.8% mean adult length; bill-length at fledging, 12.1 (0.93; 10), equivalent to 96.0% mean adult length. Rate of weight increase and tarsus growth independent of brood-size (Cunningham 1985).

Fledging to independence FLEDGING PERIOD: 20 days (0.60; 41) (Cunningham 1985). Young 15–20 days old liable to leave nest if disturbed by observer (Cunningham 1985). Fledgelings fed by both parents unless female re-nests. During first week out of nest, young huddle together during daylight hours, regardless of weather conditions; as wings become stronger and tail-feathers grow, young begin to follow foraging parents; at 18–20 days after fledging, young capable of catching own food but continue to beg; become independent of adults 35–65 days after fledging (Cunningham 1985), though sometimes continue to be fed till following winter (McLean & Gill 1988; Heather & Robertson 1997).

Success At Kowhai Bush, of 154 eggs in 49 nests (21 early nests and 28 late nests), 98 (63.6%) hatched and 56 (36.4%) fledged; in 21 early nests, of 70 eggs, 49 (70%) hatched and 35 (50%) fledged; in 28 late nests, of 84 eggs, 49 (58.3%) hatched and 21 (25.0%) fledged. Predation accounted for 62% of eggs lost and 66% of nestlings lost. Of 32 nests depredated, 90.6% thought to have been by mustelids and 6.3% by rodents, with rest by unknown predators (Cunningham 1985). Of 38 banded nestlings that fledged, at least 33 (87%) survived more than 20 days. In one season, 12 pairs produced 32 clutches, or 2.67 clutches/pair/ year; with a mean clutch-size of 3.3 and fledging rate per egg of 36.4%, equivalent to 1.60 fledgelings/adult/year (Cunningham 1985). CUCKOOS: Parasitized by Long-tailed Cuckoo *Eudynamys taitensis* (HANZAB 4).

PLUMAGES Prepared by A.M. Dunn. Fledge in juvenile plumage. Early plumages poorly understood. Extent and timing of post-juvenile (first pre-basic) moult not known, but probably begins shortly after fledging and seems to result in adult-like appearance. After attaining adult plumage, a complete post-breeding (pre-basic) moult each cycle produces successive adult plumages without change in appearance. Sexes similar. No subspecies. Descriptions based on examination of skins of 29 adults and one juvenile (AIM, NMNZ).

Adult (Definitive basic). HEAD AND NECK: Forehead and crown, rufous-brown (c136) to dark reddish-brown (c121A)

Table 2. Weight and length of tarsus of young Brown Creepers.

AGE (days)	WEIGHT		TARSUS	
	Cunningham (1985)	Gill et al. (1980)	Cunningham (1985)	Gill et al. (1980)
Hatching	1.5 (0.10; 1.3–1.6; 31)	1.7 (n=5)	7.6 (0.47; 6.8–8.4; 31)	7.8 (n=5)
2	2.6 (0.28; 2.2–3.0; 31)	2.9 (n=6)	9.3 (0.50; 8.5–10.2; 31)	9.8 (n=6)
4	4.2 (0.39; 3.2–4.6; 30)	4.5 (n=5)	12.5 (1.16; 10.8–14.7; 30)	12.7 (n=5)
6	6.3 (0.59; 4.9–7.1; 32)	6.6 (n=4)	15.1 (1.42; 12.4–16.6; 32)	16.1 (n=4)
8	8.7 (0.92; 6.5–10.5; 31)	8.8 (n=3)	18.2 (1.68; 15.4–20.0; 31)	20.1 (n=3)
9	–	9.6 (n=2)	–	21.4 (n=2)
10	10.3 (1.09; 8.2–11.7; 30)	–	21.2 (1.54; 17.4–22.7; 30)	–
12	11.2 (1.20; 9.0–13.0; 30)	–	23.3 (1.44; 20.8–24.7; 30)	–
14	12.3 (1.44; 10.5–14.5; 31)	–	25.4 (1.13; 23.0–26.7; 31)	–
16	12.5 (1.21; 11.2–14.0; 19)	–	26.0 (1.00; 25.1–27.2; 19)	–
18	12.0 (1.00; 11.0–14.0; 12)	–	26.4 (1.11; 25.2–27.7; 12)	–
20	11.7 (0.96; 10.2–13.8; 12)	–	26.4 (0.90; 25.4–27.7; 12)	–

with mostly concealed dark-grey (83) bases to feathers; grades to dark grey (83) with rufous-brown (c136) tinge on nape, and to dark brownish-grey (ne) on hindneck. Supercilium, sides of neck, most of lores and most of ear-coverts, dark brownish-grey (ne), contrasting only slightly with top of head. Faint narrow stripe behind eye, and faint, short, narrow stripe above front of lores, light grey-brown (119D). Chin, throat and malar region, light grey-brown (c119D), often with slight pinkish (ne) wash; malar area can appear slightly paler than chin and throat. UPPERPARTS: Mantle, back, scapulars and rump, dark reddish-brown (c121A). Uppertail-coverts, brown (c223B). UNDERPARTS: Centre of breast, centre of belly, and vent, light grey-brown (119C–119D), often with slight pinkish (ne) wash. Sides of breast, sides of belly, and flanks, light brown (c25) or pinkish brown (ne). Thighs, light grey-brown (c27). Undertail-coverts, light brown (c25). UPPERTAIL: T1, brown (223B). T2–t5, brown (c223B) with broad black-brown (119) band 5–10 mm wide across inner webs *c.* 1 cm from tip. UNDERTAIL: T1, light brown (c25) with cream (92) shaft. T2–t5, light brown (c223B) with cream (92) shafts and dark-grey (c83) band across inner webs. UPPERWING: All secondary coverts, dark brown (c121A). Marginal primary coverts beside alula, light grey-brown (119D). Rest of marginal primary coverts and median primary coverts, brownish grey (c79). Greater primary coverts and alula, dark grey (c83) with dark-brown (c121A) suffusion to edge of outer webs. Tertials mostly brown (c33) but grade to greyer brown (c28) near tips. Primaries and secondaries, dark greyish-brown (c121) with brown (c33) edge to outer webs, and concealed narrow off-white (ne) edge to inner webs; on p6–p10, edges to outer webs grade to light grey-brown (c27) distally. UNDERWING: All coverts, pink-buff (121D) with mostly concealed dark-grey (83) bases. Tertials, dark grey-brown (ne). Primaries and secondaries, dark grey-brown (ne) with narrow off-white (ne) edges to inner webs.

Nestling Based on photos (NZRD). Grey (84) down on top of head, back and upperwing. Down also described as grey-brown (Gill *et al.* 1980; NZRD).

Juvenile Very difficult to distinguish from adult. Differs by softer, looser texture to feathers of upper-parts and under-parts, and in pattern of feathers on head. Fore-head and crown duller than in adult; mostly dark brownish-grey (ne) with dark-brown (c121A) suffusion to feathers. Has only barest hint of pale stripe behind eye, and lacks pale feathers above front of lores; whole of lores, most of ear-coverts and sides of neck, dark brownish-grey (ne).

First immature (First basic). Probably not separable from adult. Not known whether juvenile wing and tail retained.

BARE PARTS Based on photos (Moon 1992; NZRD), published descriptions as cited, and information from museum labels. Sexes similar. **Adult** Bill mostly grey (84) grading to brownish grey (80) at base; also described as pale brown (Oliver); and pale pinkish-grey with darker grey top of upper mandible (D.J. Onley). Gape, brownish grey (80). Iris described as black (Oliver); dark brown or grey (AIM, NMNZ). Legs and feet, grey-brown (ne); pale brown (Oliver); brown (NMNZ); or grey with pinkish-brown over-tones (D.J. Onley). **Nestling** When newly hatched: Egg-tooth, white; gape, yellow; inside of mouth, yellow; skin, orange; claws, white (Gill *et al.* 1980). Egg-tooth lost at least 8 days after hatching (Gill *et al.* 1980). At unknown age: Gape, pale yellow (c157). Inside of mouth, orange-yellow (18). Bare skin of throat, pink (c3). **Juvenile and first immature** No

photos. Before May, juvenile said to be distinguished from adult by yellow gape, yellow inside of mouth and darker brown legs (Cunningham 1984; Heather & Robertson 1996); legs of juvenile said to be pinker than in adult, and yellow gape probably only persists for a few weeks after fledging (D.J. Onley).

MOULTS Based on examination of skins of 16 adults and one juvenile (AIM, NMNZ). **Adult post-breeding** (Second and subsequent pre-basic). Few data. Complete; primaries outward. Only one recorded with active moult of primaries, with PMS 16 in Nov. None recorded with active moult of tail. Active moult of body was recorded in Nov. (n=1), Feb. (n=4), Apr. (n=2) and July (n=1), and appeared most active in Apr. when the two examined had heavy moult to both upperparts and underparts. **Post-juvenile** (First pre-basic). Timing uncertain and extent not known. One from Feb. had slight moult to feathers of upperparts. Probably starts soon after fledging.

MEASUREMENTS (1–2) SI, skins (AIM, NMNZ): (1) Adults; (2) Juvenile. (3) Kowhai Bush, adults, live, sexed by behaviour (Cunningham 1984).

		MALES	FEMALES	
WING	(1)	62.2 (3.09; 58–67; 11)	60.1 (2.19; 57–64; 7)	ns
	(2)	62	–	
	(3)	61.0 (1.17; 59.6–63.6; 26)	56.9 (1.00; 54.7–58.5; 18)	**
TAIL	(1)	61.4 (2.84; 58–66; 11)	58.1 (3.39; 53–62; 7)	*
	(2)	61	–	
BILL S	(1)	12.0 (0.76; 10.8–13.2; 11)	12.0 (0.83; 10.3–12.8; 7)	ns
	(2)	12.7	–	
	(3)	13.0 (0.45; 12.0–14.3; 50)	12.4 (0.32; 11.6–13.2; 25)	**
BILL W	(3)	3.6 (0.25; 3.0–4.0; 50)	3.4 (0.19; 3.1–3.8; 25)	**
BILL D	(3)	4.0 (0.14; 3.8–4.3; 50)	3.6 (0.17; 3.3–3.8; 25)	**
TARSUS	(1)	23.3 (0.90; 22.3–24.9; 11)	22.5 (0.42; 22.0–23.1; 7)	*
	(2)	24.3	–	
	(3)	27.3 (0.43; 26.1–28.4; 50)	26.1 (0.62; 24.6–27.3; 25)	**

Unsexed: (4) SI, adults, skins (AIM, NMNZ). (5) Kowhai Bush, adults, live (Gill 1980); Wing U = minimum chord of flattened but unstraightened wing.

		UNSEXED
WING	(4)	62.0 (2.31; 59–65; 10)
WING U	(5)	61.8 (2.27; 58–66; 11)
TAIL	(4)	62.0 (3.08; 56–67; 9)
	(5)	64.4 (2.58; 61–68; 11)
BILL S	(5)	12.1 (0.66; 11.2–13.5; 10)
	(5)	12.2 (0.44; 11.3–12.8; 11)
BILL W	(5)	3.7 (0.27; 3.3–4.4; 11)
BILL D	(5)	3.9 (0.32; 3.4–4.3; 11)
TARSUS	(4)	23.1 (0.81; 21.8–24.2; 10)
	(5)	26.1 (0.96; 24.6–27.4; 9)
TOE	(5)	13.4 (0.57; 12.7–14.4; 9)

WEIGHTS (1) SI, adults, from museum labels (NMNZ). (2) Kowhai Bush, adults, live (Cunningham 1984).

	MALES	FEMALES	
(1)	13.5, 14.0, 14.5	11.0, 12.0	
(2)	13.4 (0.69; 12.0–15.0; 51)	11.0 (0.43; 10.5–12.0; 24)	**

One juvenile male from Hunter Mts, Otago, weighed 13 g (NMNZ). Heaviest female in study at Kaikoura and Stewart I. weighed 13.0 g, 1–2 days before laying three-egg clutch (Cunningham 1985). Unsexed live adults from Kowhai Bush weighed 13.1 g (0.88; 10.9–13.9; 10) (Gill 1980).

STRUCTURE   Wing rather short, broad and rounded. Ten primaries: p5 and p6 longest; p7 sometimes equal; p10 22–28 mm shorter, p9 10–14, p8 3–5, p7 0–2, p4 1–4, p3 4–8, p2 7–11, p1 9–13. P4–p7 slightly emarginated on outer webs; no emargination on inner webs. Nine secondaries, including three tertials; tips of longest tertials fall short of tips of secondaries on folded wing. Tail moderately long with rounded tip; 12 rectrices. Bill rather short and straight (see Keast 1976); about one-third length of head. Tarsus moderately long and slender; scaling holothecal. Tibia fully feathered. Middle toe with claw 15.4 (1.02; 14.0–16.6; 6). Outer toe 75–84% of middle, inner 69–80%, hindtoe 87–100%.

SEXING   From study of live birds at Kowhai Bush, no overlap in wing-length between sexes; males had Wing ≥59.5 mm and females had Wing ≤58.5 mm (Cunningham 1984).

GEOGRAPHICAL VARIATION   None.

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