

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 AX-Y (AX in *Dicrurus* [drongos]). Ambiens absent. Iliofemoralis externus usually absent, but present in some groups as 'developmental anomaly' (Raikow 1982). Tensor propatagialis brevis tendon present. Hypocleideum present (except Menuridae [lyrebirds]). Wings eutaxic. Usually ten primaries, but p10 often reduced or absent; 11 primaries in Menuridae (lyrebirds), most Eurylaimidae (broadbills), most Furnariidae (ovenbirds), and some Passeri (oscines [see below]). Usually nine secondaries (ten in Menuridae [lyrebirds]). Usually 12 rectrices, but from six (*Stipiturus* [Maluridae]) to 16 (Menuridae). Lesser primary and secondary coverts usually reduced or absent (Zeidler 1966; Morlion 1985; Winkler & Jenni 1996), but a few well-developed lesser primary coverts are present in Superb Lyrebird (Morlion 1985). Uropygial preen glands naked. No basipterygoid process. Nasal glands minute. Foot anisodactyl. Hallux incumbent, large and directed backwards; toes 2, 3 and 4 directed forward; digital formula 2-3-4-5. Deep plantar tendons usually of type VII (lacking vinculum), but often type I in Eurylaimidae (broadbills). Spermatozoa bundled with coiled head and large acrosome.

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

The Passeriformes divide into two main groups:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Family ACANTHISITTIDAE New Zealand wrens

Very small passerines (7.5–10 cm in total length and weighing 5–20 g) with very short tails, short wings, long tarsi and rather straight and slender bills. Six species in four genera (Millener 1988; Sibley & Alquist 1990), all limited to NZ (including Stewart I. and some offshore islands). Rifleman *Acanthisitta chloris* and Rock Wren *Xenicus gilviventris* extant; Stephens Island Wren *Traversia lyalli* extinct; and Bush Wren *Xenicus longipes* almost certainly extinct. North Island Stout-legged Wren *Pachyplichas yaldwyni* and South Island Stout-legged Wren *P. jagmi* both extinct in late Holocene and known only from subfossil remains. Taxonomic history of family reviewed by Sibley *et al.* (1982) and Sibley & Ahlquist (1990). Studies of anatomy of syrinx (Forbes 1882; Pycraft 1905; Ames 1971), myology (Pycraft 1905; Raikow 1987), osteology (Pycraft 1906; Oliver 1945; Feduccia 1974, 1975; Millener 1988) and egg-white proteins (Sibley 1970) suggest New Zealand wrens form a distinct passerine lineage, but there is no consensus on their affinities with the oscines or suboscines. DNA–DNA hybridization studies (Sibley *et al.* 1982) suggest that the acanthisittids are members of an ancient passerine lineage and place them within the suborder Tyranni (suboscines), in keeping with previous authors (Wetmore 1930; Stresemann 1934; Mayr & Amadon 1951). Sibley *et al.* (1982) suggest that the acanthisittids may belong to a third suborder with no close living relatives; this notion is supported in previous studies (Wolters 1977; Peters).

Structure fairly homogeneous. Following summary based principally on studies of osteology (Millener 1988), myology (Raikow 1987) and general anatomy (Pycraft 1905; Sibley & Ahlquist 1990). Bill slightly decurved; posterior articulation with enlarged process, internal process having large pneumatic foramen. Rostrum medium length, triangular, pointed. External nares holorrhinal (Millener 1988), considered schizorrhinal in *Acanthisitta chloris* (Pycraft 1905). Cranium wide and depressed dorsoventrally; interorbital bridge constricted; ectethmoid plate inflated; post-orbital and squamosal processes minute; interorbital septum traversed by a single bony bar; maxillo-palatine process very long and slender in *Acanthisitta*. Sternum fenestrated; carina reduced, markedly so in *Traversia*; manubrial spine enlarged and bifid except in *Traversia*; anterior processes large and sharply triangular; posterior lateral processes widely divergent. Iliac crests firmly fused along midline in *Traversia* and *Pachyplichas* but not in *Acanthisitta* or *Xenicus*. Other osteological features summarized by Millener (1988). *M. flexor hallucis brevis* absent. *M. flexor hallucis longus* vestigial. *M. flexor perforatus digiti IV* resembles oscine type. Syrinx haploophone, lacking intrinsic muscles. Wings short with rounded tip. Ear opening in *Acanthisitta* composed of narrow horizontal slit giving access to chamber extending downward to opening of auditory meatus. Ten primaries; putative p11 in *Acanthisitta*; nine secondaries; eutaxic; s9 degenerate. Tail extremely short. Ten rectrices. Tarsus fairly long; scaling pycnaspidean; planta covered with moniliform scales. Soles covered with distinct papillae. Claws long and acute, particularly hallux. Outer and middle toes joined basally. Stephens Island Wren probably the only flightless passerine (Millener 1988).

Adult plumage rather dull, somewhat brighter in *Acanthisitta*. Degree of sexual dimorphism differs from species to species. Bare parts mostly black, grey, brown or flesh-coloured; iris usually brown or black. Post-breeding (pre-basic) moult of adults apparently complete. Moult of primaries apparently centrifugal. Little information on appearance of nestlings or juveniles; juvenile Rifleman similar to adults. First immature (first basic) plumage apparently resembles adult plumage. Attain adult plumage when c. 1 year old. Can first breed within first year, e.g. as young as 9 months in Rifleman (see accounts).

For following summary, see individual species accounts for fuller details and references.

Family restricted to NZ and surrounding islands. Rifleman mostly arboreal, Rock Wren and Bush Wren partly terrestrial and partly arboreal. Rifleman and Bush Wren found mainly in native forests, such as beech *Nothofagus* forest and podocarp–broadleaf forests. Rock Wren mainly restricted to alpine and subalpine zones, occurring on rocky slopes usually vegetated with low shrubland. Nothing is known on habitat of the extinct Stephens Island Wren.

Poor dispersers, especially across water (Blackburn 1968; Heather & Robertson 1997); the extinct Stephens Island Wren was apparently flightless. Rifleman sedentary, though may move altitudinally in some areas. Movements of Rock Wren and Bush Wren virtually unknown, but no evidence of any seasonal movements. Rock Wrens appear to remain in territories year-round (Heath 1986, 1989) and apparently either enter torpor or remain active under snow during winter (Child 1978).

Feed largely on insects, also spiders and occasionally fruit. Feed arboreally and on ground, but proportion of time spent feeding above ground differs between species, e.g. Rifleman spend more time feeding above ground than both Bush Wren and Rock Wren. Mainly feed by gleaning (all species), but occasionally probing (Bush Wren) or sallying

(Rock Wren). Young fed by both parents in Rock Wrens; by parents and helpers in co-operatively breeding Rifleman, usually on insects.

Social organization studied for Rifleman and Rock Wren, but little is known of Bush Wren or Stephens Island Wren. Riflemen breed co-operatively, with helpers assisting primary pair with feeding of nestlings and fledgelings. Helpers at first brood of season usually unrelated males, while those at second brood usually juveniles of season. Sex-ratio of adults appears to favour males in some years, but over several years was not significantly different from unity. Males and females become paired at first opportunity after independence, and first breed within first year. Rock Wren does not show co-operative breeding. Both Rock Wren and Rifleman breed as monogamous pairs on all-purpose territories. Territories and pair-bonds are permanent and maintained year-round. Parents show a high level of co-operation when nesting; both build nest, incubate, feed young and defend territory and young. In Rifleman, male often accompanies female before hatching. Young of Rifleman are independent roughly 3–6 weeks after fledging. Young of Rock Wren able to provide 40% of their own food as soon as they fledge, and are independent within 2–3 weeks. Outside breeding season, Riflemen, Bush Wrens and Rock Wrens seen as pairs or small groups, probably families; single birds not often seen. Riflemen sometimes feed in flocks with other birds. When roosting, Riflemen may perch alongside one another, bodies touching; Rock Wrens roost in holes in rocks. Essentially, nothing known of Stephens Island Wren.

Displays not well known. Although territorial year-round, displays of actual territorial aggression, in Rifleman at least, weak. Bush Wrens and Rock Wrens bob when alighting from short flights. Said that bobbing by Rock Wren varies over range, being much slower and less frequent in Fiordland (Thomson 1964); confirmation needed. Bobbing, extension and vibrating of wings, and calling are features of display between male and female Rock Wrens when nest being built. In all three extant species, members of pairs call to each other to maintain contact. Courtship feeding occurs in Riflemen and Rock Wren, where male feeds female, but, in Rock Wren female sometimes also feeds male.

In Acanthisittidae, syrinx differs from that of typical passerines in having no intrinsic muscles, but the presence of a well-developed drum (formed by fusion of posterior tracheal elements) suggests that such muscles may once have existed (Ames 1971). Studies of syringeal structure reviewed in Sibley *et al.* (1982). All species usually heard before being seen. Vocal repertoire not large (Ames 1971), and calls simple in structure and very high-pitched (7–15 kHz). Antiphonal calling occurs.

Breeding of Rifleman well known, and breeding of Rock Wren reasonably well known; Bush Wren virtually unknown and Stephens Island Wren unknown. Summary below thus mainly refers to Rifleman and Rock Wren. Breeding seasonal, Aug.–Jan.; Rifleman can raise two broods in a season. Breed in simple pairs; Riflemen breed co-operatively. In Rifleman, males probably choose nest-site, which female accepts or rejects; in Rock Wren, female usually selects site. Nest-sites well hidden, usually low down; Rifleman in sheltered parts of open forest, in gullies or along watercourses beneath scrub, in hollows of tree-limbs and trunks, or among exposed tree-roots; Rock Wren in sheltered crevice or cavity, among rocks, on bluffs or rocky ledges of mountains, in earthen banks; often nest in similar sites to previous season. Nest built by both sexes. Rifleman has ovoid or dome-shaped nest with side entrance, though build cup-shaped nests in small sites; Rock Wren nests are spherical, oval or cigar-shaped, with small entrance in end or side of wall. Composed mostly of sticks, grass, rootlets and leaf skeletons, and occasionally moss, pine needles, leaves, bark and cobwebs; chamber usually lined with feathers. Eggs, 2–3 for Bush Wren; 3–5 for Rifleman; 1–5 for Rock Wren. Ovoid or oval, white or creamy white. Eggs laid at intervals of c. 24 h. Both sexes incubate, only female at night; full incubation begins only when clutch complete. Incubation period 18–22.5 days. Eggs usually hatch asynchronously, 1–3 days apart. Young altricial, nidicolous. At hatching, young naked and with eyes closed; may not develop natal down. Both sexes feed and brood young, though only female broods at night. Rock Wren fledge at c. 24 days, and independent after 2–4 weeks.

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Acanthisitta chloris Rifleman

COLOUR PLATE FACING PAGE 96

Sitta chloris Sparrman, 1787, *Mus. Carlsonianum* 2: no. 33 — Cape of Good Hope = Queen Charlotte Sound, New Zealand.

The generic term is one of those hybrids beloved of French nomenclaturists in the last century, being a combination of the genera *Acanthis*, thornbill, and *Sitta*, nuthatch. The specific name is a modern coining for green or yellowish green (from Greek *χλωρός*, green).

The English name, Rifleman, thought to have arisen from the similarity of the green plumage of the male to the khaki-like green tunics of the NZ First Infantry Regiment (P.D. Gaze; G.H. Sherley); though also suggested that it was so called because its sharp, high-pitched calls reminded listeners of rifle fire and the passage of bullets (J. Jobling).

OTHER ENGLISH NAMES North Island, South Island or Alpine Rifleman; Rifleman Wren; Chuck Connors.

POLYTYPIC Nominate *chloris*, SI of NZ, Stewart I. and outliers; *granti*, Mathews & Iredale, 1913, NI of NZ, Great and Little Barrier Is.

FIELD IDENTIFICATION Length 7–9 cm; wingspan 13.5–14.5 cm; weight: male 6 g, female 7 g. Smallest NZ wren. Tiny NZ wren with very short tail, short rounded wings, longish, slightly upturned, fine bill and slim legs and feet. Noticeably smaller and slimmer than Rock Wren *Xenicus gilviventris* and Bush Wren *X. longipes*, with finer bill, shorter thinner legs, and shorter toes than both. Females slightly bigger than males. Sexes differ in all plumages. Upperparts of adult male, bright green; of adult female, yellow-brown streaked darker. Both sexes have white underparts and supercilium, pale wing-bar and dark tail with whitish tip. Juveniles separable; varying striped and spotted brown above and below, but otherwise similar to respective sexes of adults. Slight geographical variation (see that section). Males vary in brightness, especially of greens and yellows, and the underparts of both sexes vary in degree and intensity of yellowish wash, but these variations are poorly understood and could be geographically or age-related, or both. **Adult male** Forehead and crown, olive, grading to greener on nape and hindneck. Supercilium, anterior lores, chin, throat and sides of neck, white, sometimes tinged cream. Dusky spot in front of, and dusky area immediately behind, eye merge with grey-green ear-coverts to form dark eye-stripe standing out against striking pale supercilium and face and setting off narrow white arc round bottom of eye. In field, appears dark-capped, with prominent white supercilium and dark eye in a very pale face. Upperbody, bright olive-green, becoming yellower and paler on rump and uppertail-coverts. Uppertail, blackish, with feathers edged dark green towards tip and with prominent narrow white tip. Folded wing: secondary coverts, dark brown with dark-green fringes, and usually appearing similar in colour to saddle; alula and primary coverts form prominent blackish-brown patch at bend of wing; tertials, blackish brown with broad white tips to outer webs, which show as 2–3 prominent pale spots; and rest of remiges, bright olive-green merging to blackish brown at tips, and with prominent diffuse broad pale-yellow wing-bar across bases. In flight, upperwing appears mainly blackish, with olive-green secondary coverts bordered at rear by prominent narrow pale-yellow wing-bar, and with prominent white spots on tertials. Underparts, white, sometimes washed cream or pale yellow, but with distinct yellow

tinge on flanks and undertail-coverts. Undertail, dark grey with prominent white tip. Underwing mainly pale: coverts, white or yellow, and remiges, dark brownish grey with trace of pale wing-bar (as upperwing). Bill, black or dark brown with short, paler, brownish, yellowish or orange streak along cutting edge of lower mandible at extreme base, sometimes in combination with pale-orange area at extreme base of lower mandible. Iris, dark brown or black. Legs and feet vary: often dark brown or black on front of tarsi and upperside of toes and contrastingly yellowish on rear of tarsi and on soles, but feet can be entirely orange-yellow (orange with paler yellowish soles); legs and feet also described as pinkish brown to yellowish brown or brownish black with contrasting dull-yellow to orange-yellow soles. **Adult female** Similar to male but green areas replaced by dark brown and yellow-brown, and yellow areas duller. Differences from male: Top of head, hindneck, saddle and rump, yellow-brown (tinged olive on rump) with narrow but distinct blackish-brown streaking that becomes broader and more diffuse on saddle and rump; uppertail-coverts slightly brighter, yellow-brown or yellow-olive, contrasting with darker saddle and rump and with blackish tail. Ear-coverts duller, yellow-brown, faintly and diffusely streaked darker brown. Upperwing as male except smaller secondary coverts, yellow-brown with dusky streaking (as upperbody), and greater secondary coverts have duller olive fringes; primaries and secondaries edged duller green or yellow-olive. **Juvenile male** Differences from adult male: (1) Foreparts (head and neck, mantle, scapulars and upper back, breast, upper belly and flanks, and wing-coverts) varying spotted and streaked dusky: some birds heavily spotted and streaked black-brown over entire foreparts, with almost no semblance of adult pattern and appearing very dark in field; in others, spots confined to a few pale-brown flecks on breast and upper belly, with rest of plumage appearing similar to that of adults, though upperbody often duller green than in adult, and crown, nape and wing-coverts, browner; (2) supercilium less distinct, off-white; (3) face, chin and throat, and underparts usually duller than adult; (4) feathers of lower mantle, rump, uppertail-coverts, belly, vent, undertail-coverts, tail and remiges very similar to those of adult but feathers softer and slightly duller. Bare parts poorly known; apparently similar to adult, though in

some, lower mandible, cinnamon or dark brown, and gape, orange. **Juvenile female** Very similar to adult female, but underparts like those of juvenile male.

Similar species Owing to very small size and very short stubby tail, unlikely to be confused with any other species except other NZ wrens *Xenicus*. Confusion with **Rock Wren** only likely where habitats overlap in subalpine scrub and tree-line of mountains of SI. From Rock Wren, Rifleman readily distinguished by combination of: Riflemen largely arboreal and do not bob and Rock Wrens largely terrestrial with characteristic bobbing action, but both can occur on or near the ground and both constantly flick their wings while foraging. Rifleman smaller and more slightly built than Rock Wren. Legs and feet of Rifleman slimmer and shorter, and usually dark black-brown or black with yellow on rear of tarsi and soles of feet (Rock Wrens have distinctly longer and sturdier legs, and their feet are exceptionally large, almost half the length of the body; legs and feet are also paler, uniformly flesh-brown). Bill of Rifleman looks quite long and thin and slightly upturned, whereas bill of Rock Wren looks sturdier and the upper mandible is distinctly downcurved. Female and juvenile Riflemen are spotted and streaked with dark brown whereas Rock Wrens are plain; male Riflemen is most similar to Rock Wren but face and underparts are much whiter and contrast much more strongly with greener upperparts. Riflemen have a prominent pale wing-bar visible at rest and in flight (wing of Rock Wren is uniform, with no distinct markings). Calls are a similar range of high-pitched thin *tzits* and short trills, but commonest call of Rock Wren is a distinctive trisyllabic *tzee-tzit-tzit*. For distinctions from **Bush Wren**, see that text.

Usually seen in pairs or small groups, rarely singly. Flocks get larger as breeding season progresses, as birds from earlier broods assist with rearing of later young. Most conspicuous and numerous in higher-altitude beech *Nothofagus* forest. Can be difficult to locate in thick scrub or taller forest. Best found by persistent if rather weak calls. Almost entirely insectivorous, characteristically gleaning food from lichens and mosses and from crevices on trunks and branches of trees and shrubs, from ground level upwards. Often work up one tree, fly down to base of another to work upward again. Are rarely still, constantly flicking wings while foraging and vigorously probing mosses, lichens and bark and investigating holes and hollows. Most flights are short, appearing weak, and confined to within canopy. In flight, note very short tail and small rounded wings with surprisingly obvious pale wing-bar. All calls are towards upper limit of human hearing; they are inaudible to some and difficult to hear over other noises such as running water and wind.

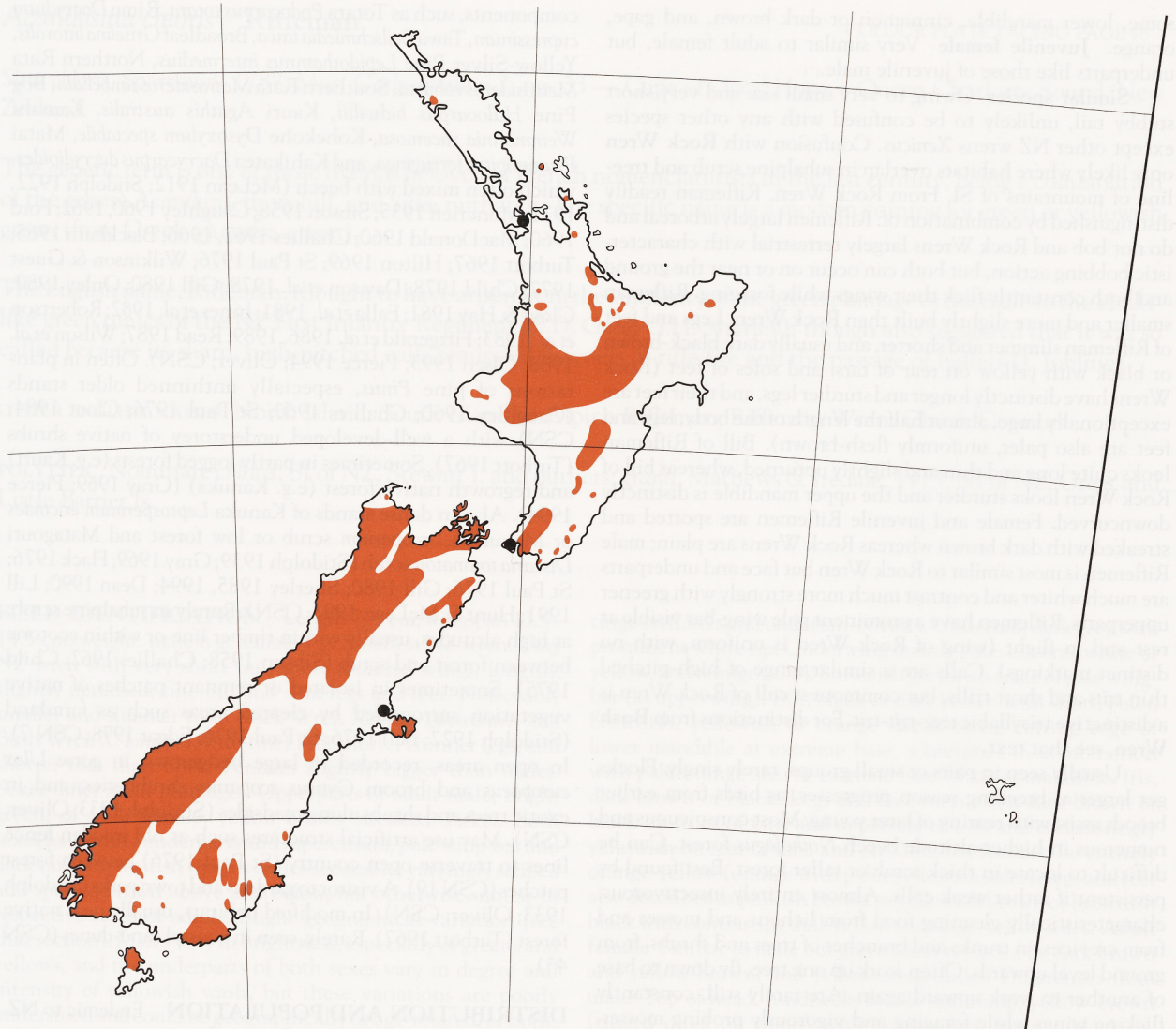
HABITAT Mostly native forests, ranging from complex structures with dense continuous canopy and a well-developed understorey, to open forests (Wilkinson & Guest 1977; Onley 1980; Clout & Hay 1981; Fitzgerald *et al.* 1989); in mountains and foothills up to c. 1550 m asl, especially in gullies, gorges, valleys and along rivers, but also on ridges and volcanic plateaux (Dove 1906; McLean 1912; Wilkinson 1924; Stidolph 1931, 1939; Moncrieff 1935; Oliver 1953; Penniket 1955; Sibson 1958; Caughley 1960, 1962; Ford 1960; Blackburn 1965; Challies 1966; Hall-Jones 1966; Scarlett 1967; Turbott 1967; Gray 1969; Reid 1970; Child 1975; Dawson *et al.* 1978; Clout & Hay 1981; Gill 1983; Fitzgerald *et al.* 1986, 1989; Wilson *et al.* 1988; O'Donnell & Dilks 1989; Olsen 1993; Oliver; CSN).

In forests of beech *Nothofagus* and other native forests, including those containing podocarp, broadleaf or hardwood

components, such as Totara *Podocarpus totara*, Rimu *Dacrydium cupressinum*, Tawa *Beilschmiedia tawa*, Broadleaf *Griselinia littoralis*, Yellow-Silver Pine *Lepidothamnus intermedius*, Northern Rata *Metrosideros robusta*, Southern Rata *Metrosideros umbellata*, Bog Pine *Halocarpus bidwillii*, Kauri *Agathis australis*, Kamahi *Weinmannia racemosa*, Kohekohe *Dysoxylum spectabile*, Matai *Prumnopitys ferruginea*, and Kahikatea *Dacrycarpus dacrydioides*, which often mixed with beech (McLean 1912; Stidolph 1922, 1931; Moncrieff 1935; Sibson 1958; Caughley 1960, 1962; Ford 1960; MacDonald 1960; Challies 1962, 1966; Blackburn 1965; Turbott 1967; Hilton 1969; St Paul 1976; Wilkinson & Guest 1977; Child 1978; Dawson *et al.* 1978; Gill 1980; Onley 1980; Clout & Hay 1981; Falla *et al.* 1981; Innes *et al.* 1982; Robertson *et al.* 1983; Fitzgerald *et al.* 1986, 1989; Read 1987; Wilson *et al.* 1988; Olsen 1993; Pierce 1994; Oliver; CSN). Often in plantations of pine *Pinus*, especially unthinned older stands (Caughley 1960; Challies 1960; St Paul 1976; Clout 1984; CSN) with a well-developed understorey of native shrubs (Turbott 1967). Sometimes in partly logged forests (e.g. Kauri) and regrowth native forest (e.g. Kanuka) (Gray 1969; Pierce 1994). Also in dense stands of Kanuka *Leptospermum ericoides* or Manuka *L. scoparium* scrub or low forest and Matagouri *Discaria toumatou* scrub (Stidolph 1939; Gray 1969; Flack 1976; St Paul 1976; Gill 1980; Sherley 1985, 1994; Dean 1990; Lill 1991; Hunt & McLean 1993; CSN). Rarely in subalpine scrub; at high altitudes, usually within timber line or within ecotone between forest and scrub (Sibson 1958; Challies 1962; Child 1975). Sometimes in isolated or remnant patches of native vegetation surrounded by cleared areas such as farmland (Stidolph 1922; Bell 1976; St Paul 1976; Edgar 1978; CSN 7). In open areas, recorded in large hedgerows, in gorse *Ulex europaeus* and broom *Cytisus scoparius* shrubberies, and in exotic trees and shrubs along roadsides (Stidolph 1933; Oliver; CSN). May use artificial structures such as old wooden fence lines to traverse open country (St Paul 1976) between forest patches (CSN 19). A visitor to gardens and town parks (Stidolph 1933; Oliver; CSN). In modified habitats, usually near native forest (Turbott 1967). Rarely, seen in coastal sand-dunes (CSN 43).

DISTRIBUTION AND POPULATION Endemic to NZ. Widespread in NI, SI and on Stewart I.

NI Isolated populations in N (Northland–Auckland–S. Auckland). Elsewhere, mostly S of 38°S, where widespread from Waikato S to Taranaki and Wanganui. Small isolated relict population Warawara Forest, N of Hokianga Harbour; also recent unconfirmed reports in Waipoua-Mataraua, Puketio-Omahuta and Raetea Forests (Pierce 1994). Resident on Little Barrier I. (McKenzie 1948; Sibson 1949; McLean *et al.* 1987; NZ Atlas); possibly also occur Great Barrier I. (Reed 1972; NZCL; cf. Bell 1976). Reported on n. Coromandel Pen. and in s. Coromandel Ra. (NZ Atlas). Recorded at a few scattered sites between Te Aroha and Tauranga, and also around Hamilton. Elsewhere in NI, mostly S of 38°S, from Waikato and Bay of Plenty, S through Volcanic Plateau to Taranaki and Wanganui: scattered records in area from line linking Kawhia in w. Waikato, Kawerau, and n. Urewera NP in w. East Coast, S to line joining s. Kaweka Forest Park and Hawera; bounded in E by line from Rakauora in East Coast, S through Ls Waikareiti and Waikaremoana, and Maungaharuru Ra., to s. Kaweka Ra. in w. Hawkes Bay; and bounded in W by line from Hawera N to Kawhia. Outside this range, scattered farther E in Raukumara Ra. in East Coast; farther W at Mt Egmont and in adjacent Pouaki Ra. in Taranaki; and widespread farther S, in w.



Wairarapa, Wellington and s. Manawatu, in Wakarara, Ruahine, Tararua and Rimutaka Ras. Also recorded at scattered sites in s. and e. Wairarapa, between Haurangi State Forest and Pahaoa R. (NZ Atlas; NZCL; CSN). **SI** Widespread throughout Nelson; and in Marlborough, except between Wairau R. and Inland Kaikoura Ra. In Canterbury, scattered in NE, round s. Seaward Kaikoura Ras; widespread throughout W; and, in E, isolated population patchily distributed on Banks Pen., and also recorded farther S from upper reaches of Orari R. S to Waimate. In Otago, recorded near Hampden, and widespread from near Waikuaitei S to Catlins State Forest Park; also recorded inland along course of Clutha R. upstream to near Roxburgh. In Southland, widespread in SE, W to Toetoes Bay and middle reaches of Mataura R., with a few records elsewhere in E; occasionally recorded near Invercargill (NZ Atlas; CSN). Many records on n. Stewart I. (NZ Atlas) and Codfish I. (Blackburn 1965, 1968; Oliver; CSN 36). In w. Southland, widespread W of line from Longwood Ra. to Eyre Mts, extending into Fiordland NP. Widespread throughout West Coast, extending W into w. Otago and w. Canterbury (NZ Atlas; CSN).

Breeding Throughout range.

Change in range, populations Have declined in a number of areas. In Northland, scarce at time of European settlement (Gill 1996); said to have been recorded at Bay of Islands in 1835 (Oliver), but thought to have gone from Northland by 1870s (Turbott 1967). However, small relict population discovered at Warawara Forest in 1993 (Pierce 1994). On Banks Pen., Canterbury, numerous till c. 1940s (Dawson & Cresswell 1949); still persist today (NZ Atlas), presumably in diminished numbers. In contrast, populations said to have increased in parts of s. Canterbury in 1940s (Graham 1948). Populations also declined in s. Otago in 1940s (Dunedin FNC 1948). Formerly plentiful around Tihoi, Minginui and Waiiau in Huiarau Ra., East Coast, but populations had declined by mid-1950s (St Paul 1976; CSN 3). May have declined in Tararua and Rimutaka Ras, Wairarapa, in early to mid-1970s (CSN 21).

Status Common (IUCN Category 7). **Populations** Near Kaikoura, 9–15 breeding pairs recorded in 6 ha; and 15–17 breeding pairs in 80 ha of Kanuka forest (Sherley 1994). At Cobb Reservoir, 12 birds recorded in 2.5 ha; and between Trilobite Hut and Cobb Valley, ten birds in 2 ha (CSN 38). Near Kowhai Bush, recorded at densities of 2.2–3.4 birds/ha (Lill 1991).

THREATS AND HUMAN INTERACTIONS Adversely affected by clearing of native forests for agriculture and by conversion of native forests to pine plantations (Turbott 1967; Clout 1984). In Fiordland NP, poisoned by 1080 baits intended for Common Brushtail Possums *Trichosurus vulpecula* (Stidolph 1979). Sometimes caught by Cats (CSN 23) and Stoats (Penniket 1955; G.H. Sherley). Sometimes involved in unprovoked attacks on people (CSN 30); sometimes become tame around camp-sites, gleaning scraps and even cleaning fat and grease from frying pans and plates (McLean 1912; CSN 22).

MOVEMENTS Sedentary (Sherley 1985, 1994; see Banding, below). Some evidence for altitudinal movements, in at least some areas (see below). Records from near Moke L., SI, suggest birds can cross areas of open, unsuitable habitat (CSN 19). During severe drought at Queenstown, SI, seen moving along fenceline, c. 1 km from bush (St Paul 1976). Most information from detailed studies at Kowhai Bush, Kaikoura, ne. SI, by Sherley (1985, 1990a, 1993, 1994); most other information also from SI.

At Kowhai Bush, pairs sedentary, staying in territories year-round (Sherley 1994), and only one adult male was observed to emigrate from study area (Sherley 1993); birds abundant here throughout year (Dean 1990). In beech forests near Reefton, nw. SI, present year-round (Dawson *et al.* 1978; but see below). Recorded all months from NI and SI (Scarlett 1967; CSN 37, 39, 41, 43). At Ohikanui, nw. SI, based on counts, Wilson *et al.* (1988) suggested that some moved to lower altitudes to breed in Sept., though they also state that numbers fairly constant throughout year at high altitudes; exact situation not known. Suggested that on Stewart I., birds bred at lower altitudes, moving to higher areas after breeding (Oliver).

Some seasonality in density of populations apparent; some such changes may, in part, be result of breeding success or local movements. In 21 ha plot at Kowhai Bush, where many birds colour-banded, density decreased a net 35% from autumn to winter, with 59% of autumn residents still present in winter (Lill 1991); indicative of some interchange of birds to and from study plot, not solely attributable to mortality. Round Reefton, recorded in higher numbers in Dec. and Feb. (Dawson *et al.* 1978). Before disappearance from Minginui, recorded in higher numbers Jan.–Apr. compared with other times of year (St Paul 1976).

Dispersal of young At Kowhai Bush, young dispersed from natal territory by onset of winter (Sherley 1994); similar numbers of each sex disperse (Sherley 1985). Four of 250 female (1.6%) and three of 214 male (1.4%) colour-banded subadults were known to emigrate to neighbouring forest areas (Sherley 1993); but this certainly an underestimate (G.H. Sherley). Five subadults that dispersed moved between study areas, a minimum distance of 300 m across pasture with small copses of remnant forest; seven immatures and one adult dispersed outside boundaries of two study areas covering 12 ha and c. 80 ha respectively (Sherley 1990a; G.H. Sherley). Except for one female, all immatures left natal territory (Sherley 1990a).

Banding Greatest distance travelled by any banded bird c. 2 km (G.H. Sherley). Of 33 banded in NI to 1974, 16 recoveries (48%); of 277 banded in SI to 1974, 55 recoveries (20%) (Robertson 1975). If member of pair died, surviving partner either moved and established territory nearby or stayed in same territory till new mate obtained. **LONGEVITY:** 14% of male chicks and 19% of female chicks leaving nest survived for at least 1 year; two banded males survived for 6 years (Sherley 1985; NZRD). At Kowhai Bush, banding study showed average

life-expectancy for adults is 2.2 years for males and 1.7 years for females (Sherley 1985).

FOOD Insectivorous; feed on large variety of insects, their larvae and spiders; rarely, fruit. **Behaviour** **DETAILED STUDIES:** On Little Barrier I. (Gravatt 1969, 1971); in nw. Fiordland, SI (Dodgshun 1976); at Kowhai Bush, Kaikoura, ne. SI (Lill 1991; Hunt & McLean 1993); and in s. Westland (O'Donnell & Dilks 1994). Mostly feed in native forests; sometimes feed in exotic trees near native forest (see Habitat). Mainly arboreal. Feed at all levels in forest, from ground to canopy, including: within canopy, subcanopy and understorey; on tree-trunks, including among epiphytic mosses and lichens on trunks (McLean 1912; St Paul 1976; O'Donnell & Dilks 1989, 1994; Lill 1991; Hunt & McLean 1993; Oliver; CSN); sometimes feed on ground, among leaf-litter or grass (Lill 1991; Oliver; CSN 23, 42). Also recorded foraging in hollow logs and roots on ground (St Paul 1976). Forage mainly by gleaning and probing, from trunks of trees and shrubs, branches, twigs and foliage. **SIZE OF FEEDING GROUPS:** Forage in pairs or small groups, usually keeping close together (McLean 1907, 1912; Dean 1990; Hunt & McLean 1993). Occasionally forage in mixed-species flocks (Dean 1990); reported to feed in mixed flocks with Yellowheads *Mohoua ochrocephala* (Read 1987) and Silvereyes *Zosterops lateralis* (Oliver). **FEEDING HEIGHTS AND SITES:** Forage at all heights, but mostly in upper strata. On **LITTLE BARRIER I.** (Gravatt 1969, 1971), in habitat ranging from *Leptospermum* forest in various transitional stages to Kauri and Hard Beech *Nothofagus truncata* communities, fed mostly in upper part of understorey (which is continuous with subcanopy); of 73 feeding observations: 76.7% in upper understorey, 2.7% in subcanopy, 12.3% in mid-storey, and 8.2% in lower understorey; not seen to forage in upper canopy or on ground; height distribution of feeding observations (n=87 obs.): 4.6% at 0–1.5 m above ground, 13.8% at 1.5–3 m, 31.0% at 3–4.5 m, 39.1% at 4.5–6 m, 9.2% at 6–7.5 m, and 2.3% at 7.5–9 m; substrate on which foraged (n=95 feeding obs.): 62.1% on tree-trunks, 24.2% on branches, 8.4% on twigs, and 5.3% on leaves. Also on **LITTLE BARRIER I.**, foraged mostly (58% of observations) on twigs and branches among foliage in understorey, and less often on trunks (30%) and on ground (12%) (CSN 23). In **nw. FIORDLAND**, fed at all levels in forest, but mostly in upper understorey (similar to Little Barrier I.); of 48 feeding observations: 13% in canopy, 10% in subcanopy, 44% in upper understorey, 29% in middle understorey and 4% in lower understorey. At **KOWHAI BUSH** (Lill 1991), foraged at all levels from ground to tree canopy; of 437 feeding records (N for autumn and winter not given separately): 47% of observations in autumn and 44% in winter on tree trunks; 35% and 36% in canopy; and 18% and 19% on ground. Females foraged significantly more on trunks than males (52±25% versus 40±25%) and significantly less in canopy (31±29% versus 39±32%) (n=225 obs. for females, 212 for males). Rate of capture of prey of males and females from various substrates similar, but overall rate in winter (17.2 prey/min) more than double that of autumn (8.3 prey/min). Also at **KOWHAI BUSH**, in patch of Kanuka forest with trees 2.5–8 m tall and forming a near continuous canopy (Hunt & McLean 1993), both breeding and non-breeding birds recorded foraging at all heights in forest, but used canopy more than lower levels (>50% of 329 feeding observations of non-breeding birds and 245 observations of breeding birds); non-breeding males and females did not differ in heights used for foraging, while breeding males foraged significantly higher than females. Substrates used for foraging included ground, trunk, large branches (>2.0 cm diameter), small branches (>0.5

cm and <2.0 cm), twigs (<0.5 cm) and leaves; birds foraging in canopy tended to use small branches, twigs and leaves, while those foraging lower in forest were likely to use large branches and bark. In s. WESTLAND (O'Donnell & Dilks 1994), mostly fed in understorey; of 2073 feeding observations, 22% of observations within canopy, 8% on top of canopy, 40% in upper understorey, 28% in lower understorey, and only 2% on ground. Foraged on 33 plant species, and known to take invertebrates from 18 species; of 2073 feeding observations, of which 381 positively identified as feeding on invertebrates: most important trees were Silver Beech *Nothofagus menziesii* (44.5% of total feeding observations and 34% of observations of feeding on invertebrates), and Kamahi *Weinmannia racemosa* (25.1%, 26%); of lesser importance were *Pseudopanax* (3.1%, 3%), Broadleaf *Griselinia littoralis* (2.6%, 3%), Horopito *Pseudowintera colorata* (2.4%, 2%) and high-altitude canopy species (Rata *Metrosideros umbellata* 5.9%, 6%, Hall's Totara *Podocarpus hallii* 2.1%, 2%); for complete list of plant species, and usage of each, see O'Donnell & Dilks (1994). FEEDING METHODS: Mostly by gleaning, including hang-gleaning, where bird hangs upside down to glean prey from lower surfaces of large branches; also by probing. Usually extract prey with bill from crevices and folds of bark, or pick prey from among lichen and mosses (McLean 1912; Soper 1963; Hunt & McLean 1993; O'Donnell & Dilks 1994; Oliver). Rarely, sally for flying insects, but never seen to do so successfully; most sallying by juveniles (G.H. Sherley). When searching for food on tree-trunks, start at base of tree, near ground, and climb to heights of 6–9 m in short jerky hops accompanied by incessant fluttering of wings; usually ascend in spiral course, before flying down to base of another tree to work their way up again (McLean 1912; Guthrie-Smith 1914; Soper 1963; Turbott 1967; Hunt & McLean 1993; Oliver). At Kowhai Bush, gleaning comprised >85% of feeding observations (Hunt & McLean 1993). SOURCES OF FOOD: In s. Westland, fed on insects throughout forest strata, and occasionally seen feeding on fruits of *Pseudopanax* in Apr.–July. Of 2073 feeding observations, 18.4% (381 obs.) positively identified as feeding on invertebrates, 0.7% (14 obs.) feeding on fruit, and 80.6% unidentified, but suspected to be mostly insects (O'Donnell & Dilks 1994). TIMES OF FEEDING: At Kowhai Bush, spent 82–83% of daylight hours in autumn and winter foraging. No significant differences in daily patterns of foraging between sexes, seasonally or overall except in winter; in winter, proportion of time spent foraging decreased from 83–90% in morning, midday and early afternoon, to 55% in late afternoon (Lill 1991). HANDLING FOOD: Said to kill and break up prey by bashing it against tree before ingesting; and that on windy days feed lower in shrub layer of forest (NZRD). COURTSHIP FEEDING: During breeding, males feed females; rate significantly increased during 6 days before laying, was highest when first egg laid (12 items/h), and continued at about same rate till day after laying of last egg. Males fed mates larger food items (c. 9 mm in length) than those usually taken during foraging by either sex (c. 3 mm). During period of courtship feeding, male collected mean 616 mg dry weight/h (248; 105 observations); female 417 mg dry weight/h (258; 88); overall, male fed 42% of food collected to females, which comprised 35% of females' total intake (Sherley 1989; also see Social Behaviour). ADAPTATIONS: Both sexes have long strong legs and hindclaw, possibly to aid climbing and support on vertical surfaces, and long and decurved bill may facilitate effective probing under loose bark. Females have significantly longer hindclaw and longer, deeper and more decurved bill than males (see Measurements, sample 8). These morphological differences are correlated with foraging patterns

when sexes had high energy requirements (when feeding young), at which time males and females foraged separately; when energy requirements were low (when not breeding), males and females fed together (Hunt & McLean 1993).

Detailed studies At KOWHAI BUSH, NE. SI (c. 330 items seen fed to females by males during courtship feeding; Sherley 1985): **Animals** SPIDERS 6% no. INSECTS: Larv. 65; Coleoptera: ads 2; Lepidoptera: ad. moths 22; Orthoptera: Stenopelmatidae 2.

Other records **Plants** Fruits and seeds⁷; Podocarpaceae: *Dacrydium* fru.⁹; Araliaceae: *Pseudopanax edgerleyi* fru.^{9,10}; *P. simplex* fru.^{9,10}. **Animals** SPIDERS¹¹: Opilioniids¹¹. INSECTS^{2,6,8,11}: Coleoptera⁴; Lepidoptera: ads, larv.^{3,5,8}; Odonata⁸. **Other matter** Food scraps^{1,2,13}. Also reported to take Diptera: Tipulidae and Orthoptera: Anastostomatidae and Rhophadophoridae: wetas¹².

REFERENCES: McLean¹ 1907, ² 1912; ³ Soper 1963; ⁴ Turbott 1967; ⁵ Gray 1969; ⁶ St Paul 1976; ⁷ Moede & Fitzgerald 1982; ⁸ Moon & Lockley 1982; O'Donnell & Dilks⁹ 1989, ¹⁰ 1994; ¹¹ Oliver; ¹² NZRD; ¹³ CSN 22.

Young Detailed study at Kowhai Bush, of food of nestlings and fledgelings, and relative contribution of sexes and helpers to feeding young (Sherley 1985, 1990a, 1994), on which account below is based. Nestlings and fledgelings fed by both parents, and any helpers present, though helpers recorded at only 8% of first broods and 4% of second broods; see Social Organization (Co-operative breeding) for full details. Overall, primary male usually contributes more to feeding of nestlings and fledgelings than breeding female, particularly to first broods, and whether helpers present or not. Also, overall contribution of breeding females to feeding of nestlings and fledgelings, of first or second broods and with or without helpers, is similar. NESTLINGS: SIZE AND TYPE OF FOOD: Size of food delivered to young summarized in Table 1; items delivered are summarized in Detailed studies below. All birds that feed nestlings generally bring similar types and size of food, for both first and second broods, and nests with and without helpers. No significant differences in size of food items delivered to nestlings by primary males, breeding females or, if present, helpers, whether first or second broods or whether helpers present or not, except for: (1) at first nests with helpers, breeding females delivered significantly larger items than helpers towards end of nestling period (Days 21–24); and (2) at second nests without helpers, primary males delivered larger items than breeding females at start of period (Days 1–4). Items brought by primary males and females to first broods without helpers tend to be larger than those brought by primary males, breeding females or helpers, at nests with helpers. FEEDING RATES OF FIRST BROODS: Summarized in Table 2. At nests WITH HELPERS, rates of feeding by primary male and breeding female similar for Days 4–12, but rates of feeding by primary male significantly higher than that of breeding female for rest of period (Days 13–24). Throughout nestling period, both parents fed nestlings significantly more often than helpers, except in last 4 days (Days 21–24), when males and helpers provided food at similar rates (which significantly higher than rate of feeding by breeding female). At nests WITHOUT HELPERS, on average, feeding rates of primary males c. 50% greater than those of breeding females. FEEDING RATES OF SECOND BROODS: Summarized in Table 2. Primary males fed nestlings at greater rate than breeding females, with or without helpers. Feeding rate by primary males significantly greater at nests without helpers than at nests with helpers; but no significant differences in feeding rates of breeding females at nests with and without helpers, except in last 4 days of nestling

period (Days 21–24), when feeding rate at nests with helpers was significantly greater than that at nests without helpers. At nests *WITH HELPERS*, rates of feeding by primary males and helpers similar, but both fed nestlings at significantly higher rates than breeding females. At nests *WITHOUT HELPERS*, primary males fed nestlings at significantly higher rates than breeding females; both parents increased rate of feeding in last days of nestling period (Days 9–24) compared with early days (Days 1–8). In Eglinton Valley, one nestling fed, on average, every 3–4 min, for periods of 20–30 min, with pauses of 30 min with no feeding before next feeding session began (Soper 1963). **FLEDGELINGS:** Size of food delivered to fledgelings and feeding rates by parents and helpers summarized in Table 3. Overall, no significant differences in size of food items delivered to fledgelings by parents between first and second broods, or with or without helpers. For *FIRST BROODS WITH HELPERS*, feeding rate of primary males and helpers similar and significantly greater than that of breeding females. For *SECOND BROODS WITH HELPERS*, feeding rates of males and females similar and significantly greater than that of helpers. For both *FIRST AND SECOND BROODS, WITHOUT HELPERS*, feeding rates of primary males significantly higher than those of breeding females.

Identified studies All at Kowhai Bush (Sherley 1990a). **NESTLINGS OF FIRST BROODS** (2946 feeds delivered by primary male, of which 503 items identified; 2065 by breeding female, 473 identified; and 649 by helpers, 128 identified): **SPIDERS:** 9% no. identified items delivered by male, 9% by female, 3.5% by helpers. **INSECTS:** Coleoptera 0.5, 1.5, –; Diptera 2, 2, 5; Lepidoptera: ad. moth 66, 64, 50, larv. 20, 20, 37; Orthoptera 0.5, 1.5, 4.5; Anastomatidae (including *Hemideina femorata*, *Hemiandrus*, *Isoplectron*) 2, 2, –. **NESTLINGS OF SECOND BROODS** (1221 feeds delivered by primary male, of which 458 items identified; 699 by breeding female, 267 identified; and 333 by helpers, 69 identified): **SPIDERS:** 20% no. of identified items delivered by male, 18% by female, 6% by helpers. **INSECTS:** Coleoptera 1, 5, 1; Diptera 9, 6, 3; Lepidoptera: ad. moth 50, 52, 68, larv. 17, 13, 19; Orthoptera 1.5, 2, 3; Anastomatidae (including *Hemideina femorata*, *Hemiandrus*, *Isoplectron*) 1.5, 4, –.

FLEDGELINGS OF FIRST BROODS (805 feeds delivered by primary male, of which 166 items identified; 309 by breeding female, 61 identified; 1155 by helpers, 12 identified): **SPIDERS** 2% no. of identified items delivered by males, 2 by female, 0 by helpers. **INSECTS:** Lepidoptera: ad. moth 59, 66, 66, larv. 39, 18, 25; Orthoptera: Anastomatidae 0, 3, 0. **FLEDGELINGS OF SECOND BROODS** (753 feeds delivered by primary male, of which 79

identified; 494 by breeding female, 66 identified; 155 by helpers, 3 identified): **SPIDERS** 4% no. of identified items delivered by males, 12 by female, 0 by helpers. **INSECTS:** Lepidoptera: ad. moth 73, 73, 100, larv. 20, 15, 0; Orthoptera: Anastomatidae 3, 0, 0.

Other records Food brought to nestlings includes moths, caterpillars, spiders and harvestmen (Opilionids), flies (Diptera), and many other insects and insect larvae (Guthrie-Smith 1914; Dawson 1950).

SOCIAL ORGANIZATION Well known from detailed studies of colour-banded population in Kowhai Bush, Kaikoura, SI: long-term (3–4 years) study of parental care and co-operative breeding, though with no DNA analyses (Sherley 1985, 1990a,b, 1994); study of behavioural energetics in autumn and winter of one year (Lill 1991); and a 6-year study of territorialism at Dunedin, SI, which included some banded birds (Gray 1974). At Kowhai Bush, the only area where breeding system studied in detail, bred both in simple pairs and co-operatively. At Kowhai Bush: in winter, forage in heterosexual pairs or in groups of up to eight birds, and, sometimes, alone (Lill 1991); when not breeding, members of pair forage together, but forage separately when feeding fledgelings (Hunt & McLean 1993). In general, birds usually seen in twos, particularly in winter and spring; occasionally in groups of 4–5 late in breeding season, or in summer and autumn, and which usually assumed to be family parties of adults and young of year (e.g. McLean 1907, 1912; Lambert 1970; Falla *et al.* 1981; Dean 1990; Oliver), though at Kowhai Bush were usually neighbouring pairs loosely grouping for a short time then splitting again (G.H. Sherley). Seen feeding in mixed-species flocks (see Food).

Bonds Long-term monogamy (Gray 1974; Sherley 1990a,b, 1994; Hunt & McLean 1993); partners stay near each other throughout year (Gray 1974; Sherley 1990a; Oliver). Pairs stable, with divorce and re-pairing very rare. At Kowhai Bush, only two divorces seen, one involving a bird emigrating (Gray 1974; Sherley 1985, 1994). If one member of pair dies, survivor either moves and establishes another territory nearby with a new mate, or stays in same territory until new mate arrives; when one breeding female disappeared during incubation, another female arrived and helped male raise chicks (Gray 1974). Suggestion of polygamy (Soper 1976) unfounded and seems unlikely as parents seen to vigorously repel conspecifics from territory before and during laying period (Sherley 1985),

Table 1. Size of food delivered to nestlings of first and second broods at Kowhai Bush, at nests with and without helpers (Sherley 1985, 1990a). N = No. of food items.

(days)	AGE OF YOUNG					
	1–4	5–8	9–12	13–16	17–20	21–24
First broods, without helpers						
Male	3.7 (1.4; 164)	3.8 (1.4; 174)	4.6 (1.3; 180)	4.2 (1.4; 217)	4.1 (1.5; 204)	3.9 (1.6; 151)
Female	3.5 (1.2; 104)	3.4 (1.4; 145)	4.5 (1.5; 170)	4.1 (1.6; 153)	3.9 (1.6; 161)	3.8 (1.7; 102)
First broods, with helpers						
Male	–	2.7 (1.4; 26)	3.1 (1.4; 118)	3.4 (1.5; 85)	3.4 (1.6; 101)	3.3 (1.5; 95)
Female	–	2.6 (1.2; 44)	3.1 (1.2; 106)	3.3 (1.6; 77)	3.2 (1.4; 65)	3.7 (1.4; 70)
Helpers	–	3.1 (1.0; 11)	2.8 (1.2; 74)	3.2 (1.3; 63)	2.9 (1.3; 62)	3.0 (1.3; 145)
Second broods, without helpers						
Male	3.4 (1.2; 121)	3.6 (1.2; 137)	3.8 (1.3; 166)	3.9 (1.4; 264)	3.9 (1.3; 248)	3.8 (1.4; 78)
Female	2.9 (1.1; 91)	3.5 (1.2; 106)	3.6 (1.2; 119)	3.8 (1.3; 170)	3.7 (1.5; 168)	3.7 (1.4; 67)
Second broods, with helpers						
Male	–	4.0 (1.2; 36)	4.0 (1.0; 52)	4.0 (1.4; 51)	3.7 (1.1; 29)	3.7 (0.7; 8)
Female	–	3.5 (0.9; 16)	3.8 (1.1; 15)	3.8 (1.2; 13)	3.6 (1.1; 15)	3.4 (1.1; 7)
Helpers	–	3.6 (1.1; 32)	3.7 (0.9; 49)	3.7 (1.2; 44)	3.9 (1.1; 26)	4.1 (1.3; 25)

Table 2. Average feeding rate (items/h) of nestlings of first and second broods, by primary males, breeding female and, if present, helpers (Sherley 1985, 1990a, 1994). Figures are means with standard deviations in brackets; N = number of 30-min periods of observation at nests.

AGIOF YOUNG (day)	NO HELPERS			WITH HELPERS			
	MALES	FEMALES	N	MALES	FEMALES	HELPERS	N
First broods							
1-4	7.3 (4.6)	5.1 (3.4)	64	-	-	-	-
5-8	12.0 (5.6)	8.4 (4.9)	45	8.8 (6.1)	10.1 (6.0)	2.9 (4.2)	14
9-12	13.5 (8.8)	10.4 (6.3)	50	9.7 (5.6)	8.7 (4.5)	5.9 (7.5)	43
13-1	16.3 (7.0)	10.2 (5.7)	44	10.8 (6.4)	7.8 (5.2)	6.1 (5.5)	37
17-2	15.2 (8.2)	9.9 (7.5)	52	12.2 (8.6)	6.9 (4.9)	8.1 (5.1)	46
21-2	17.0 (7.0)	10.8 (6.7)	37	12.0 (6.2)	7.3 (5.0)	10.5 (7.6)	57
Second broods							
1-4	7.3 (4.8)	5.2 (3.0)	58	-	-	-	-
5-8	10.6 (7.2)	6.5 (4.4)	59	15.6 (1.6)	9.2 (3.0)	10.0 (6.2)	6
9-12	15.4 (7.1)	8.4 (5.8)	49	18.8 (6.6)	8.4 (2.0)	15.0 (7.8)	8
13-1	16.9 (8.0)	9.3 (6.7)	64	18.0 (6.5)	6.4 (2.6)	13.8 (6.3)	8
17-2	16.3 (10)	11.3 (6.8)	64	13.4 (5.3)	10.8 (2.3)	13.0 (4.6)	8
21-2	13.4 (7.6)	10.8 (6.9)	26	8.2 (2.3)	5.6 (1.6)	13.4 (2.6)	13

Table 3. Average size of food (mm) delivered to fledgelings, and feeding rates (items/h) of fledgelings by parents and helpers from first and second broods at Kowhai Bush (Sherley 1985, 1990a).

	FIRST BROODS		SECOND BROODS	
	Without helpers	With helpers	Without helpers	With helpers
Size of food items				
Male	3.3 (1.3; 193)	3.8 (1.2; 24)	3.4 (1.0; 104)	3.1 (0.9; 41)
Female	3.3 (1.6; 85)	3.8 (1.2; 46)	2.9 (1.0; 104)	3.1 (0.9; 41)
Helpers	-	3.8 (1.2; 46)	-	3.1 (0.9; 29)
Rates of feeding				
Male	7.4 (2.9; 46)	3.4 (1.7; 18)	5.9 (2.7; 48)	3.4 (1.3; 32)
Female	2.6 (1.8; 46)	1.7 (1.2; 18)	3.0 (1.7; 48)	3.2 (2.0; 32)
Helpers	-	3.6 (1.9; 18)	0.7 (0.9; 48) ¹	2.3 (1.8; 32)
Total	10.0 (3.7; 46)	8.7 (2.3; 18)	9.6 (4.1; 48)	8.9 (3.0; 32)

¹ Minor contribution from a casual helper.

and helpers not allowed near nest until fifth day of nestling period (Sherley 1990a). At Kowhai Bush, an unpaired adult male once tried to mount breeding female with fledgelings (Sherley 1985); but during late Jan. or mid-Feb., no extra-pair copulations tried or occurred, with behaviour suggesting mate-guarding of laying females by males (Hunt & McLean 1993). At Kowhai Bush at start of a breeding season, virtually no unpaired females present, and unpaired adult males only able to pair with young of season once they reach independence and enter population. Nearly all extra males become helpers at nests (Sherley 1990a, 1994). At Kowhai Bush, incestual breeding observed at least twice: one father bred with his daughter over two seasons, successfully raising two broods and at least one in the second year; two siblings of different generations also bred successfully (G.H. Sherley). **AGE OF FIRST BREEDING:** Sexually mature when as young as 9 months old. However, pair at first opportunity after becoming independent, 3-6 weeks after fledging (see below): at Kowhai Bush, all juvenile females and most juvenile males paired in season they were hatched. All combinations of pairs of adults and juveniles observed; one adult male tried to mate with fledgeling female (Sherley 1985, 1990a, 1994); another adult male paired with sexually immature female and they prepared nest, but no laying occurred (Gray 1974). Fledgelings banded early in year found building nests and laying in subsequent breeding season, e.g. Aug.-Sept. of same year (G.H. Sherley). More females than males bred in first year following fledging (Sherley 1993). **SEX-RATIOS:** Ratio at

hatching and of nestlings, near unity. Ratio of males to females early in breeding season, over 4 years: 22:15, 50:35, 39:37, 20:21, but not significantly different (Sherley 1993, 1994). Over nestling period, female nestlings tend to be larger and heavier than males, though they fledge at same time; female nestlings more costly to rear (see Sherley 1993).

Co-operative breeding (Throughout: breeding female = female parent; primary male = mate of breeding female [in simple pairs or co-operatively breeding groups], assumed to be male parent; helper = bird other than parent participating in parental behaviour; first brood refers to nest, nestlings or fledgelings from first nest of season; second brood refers to nest, nestlings or fledgelings from second nest of season.) Co-operative breeding studied in detail at Kowhai Bush, on which this section based; a few anecdotal reports elsewhere. **HELPERS:** Extra birds are found at nests of both first and second broods. They are either adults other than parents or juveniles from first brood. For first broods, helpers are usually adult males (apparently sexually active) and occasionally females, apparently unrelated to birds they helped, though one adult female helped a daughter in an adjacent territory. Helpers feed nestlings, remove faecal sacs from nest and defend young, but do not brood them. For second broods, helpers usually independent juveniles from first broods, who gradually, over c. 7 days from when nestlings c. 5 days old, acquire habit of feeding their parents' second brood: first they visit nest without food, then bring food but do not offer it to nestlings, and finally, bring food,

stimulate a begging response from chicks and feed them. However, overall, juveniles contribute little to feeding of offspring (Sherley 1985, 1990a). At nest, parents not aggressive to helpers, and often make way for them when birds queue at entrance of nest to feed young; in particular, primary males display little aggression to adult helper males. Adult helpers gave no sign that they were trying to oust primary males or acquire their mates; but were not allowed near breeding female during pre-laying, incubation and early nestling periods (Sherley 1985, 1990a). Helpers can be categorized as either casual or regular helpers. A *REGULAR HELPER* makes a significant contribution to feeding young at only one nest throughout each day (but not starting to do so till 5 days after young have hatched). These are usually unpaired adult males; of 40 juveniles who helped with second broods, only six were regular helpers. A *CASUAL HELPER* makes infrequent visits to one or more nests every hour or so, not necessarily every day, and contributes little; though some are unpaired adult males, most are offspring from first broods, helping parents with second broods, and are most often seen at second broods (Sherley 1990a); casual helpers visit an average of two different nests each year (Sherley 1985). Nests with helpers have only one regular helper, but can also have casual helpers, or can have only casual helpers. The most helpers seen at a nest were four first-brood offspring and an adult female (mother of breeding female), all of which were regular helpers at a second brood. Both casual and regular helpers continue helping after young fledge (Sherley 1985, 1990a). Only once did a helper (a regular) of first brood assist again with second brood (Sherley 1990a). At Kaikoura, of 83 first broods, 28% had helpers, including 15% which had regular helpers; of 50 second broods, 52% had helpers, with 14% having regular helpers (Sherley 1990a).

FEEDING OF YOUNG: Detailed studies at Kowhai Bush, on feeding rates of young at nests of first and second broods, with and without helpers (though no comparisons with and without helpers in first 4 days of 24-day nestling period because helpers excluded for this period). All birds that feed nestlings—primary male, breeding female and helpers—bring the same size and types of food for much of the time, though items brought by primary males and females to first broods without helpers tend to be larger than those brought at nests with helpers, and possibly result in young getting more food. Overall, primary male usually contributes more to feeding of nestlings and fledgelings than breeding female, particularly to first broods, whether helpers present or not. Also, overall contribution of breeding females to nestlings and fledgelings of first or second broods, and with or without helpers, similar. For full discussion of comparative rates of feeding of nestlings and fledgelings by attendant birds, see Food (Young). Feeding of young by regular helpers occurs at only 8% of first broods and 4% of second broods (Sherley 1990a, 1994), suggesting breeding pairs cannot rely on presence of helpers (Sherley 1990a). Though regular helpers at nests contribute much food to nestlings and fledgelings, overall amount fed to young does not increase compared with nests without helpers; instead, feeding rate of primary males drops significantly. With or without helpers, there is no difference in number of offspring fledged, weight of nestlings near fledging, or post-fledging care (Sherley 1990a, 1994). Co-operative breeding in Rifleman thought to be more opportunism by helpers than kin selection. Adult helpers sexually active and unrelated to offspring they fed, and with a mean life expectancy for males of 2.2 years, it is probably very important that they quickly find a mate; some adult helpers, usually regular helpers, paired with young from nest where they help, and one paired in the same season with

breeding female when her mate died. By helping, males have access to unpaired juvenile females who are potential mates; by feeding fledgelings, the helper probably establishes social bonds with potential mates and has opportunity to select a mate (Sherley 1985, 1990a, 1994). Juveniles casually helping parents with second brood seem just to imitate behaviour of parents with little benefit for parent or siblings, but perhaps a small benefit for themselves in learning to feed young or in establishing themselves on parents' territory, in case one parent dies; juvenile helpers do not pair with offspring from nest at which they help. In co-operative breeding system, primary males are main beneficiary from regular helpers, as they then need to provide less parental care; also, more female young from nests with helpers survived into following breeding season, compared with female yearlings who had had no helpers; no difference in survival of males at each type of nest (Sherley 1990a). Additional birds at nests also noted elsewhere. On SI, helpers fed young at four of six nests: two had one male and two females; one had two males and one female; and one had two males and two females with one of each sex appearing juvenile; at one nest, females usually arrived together and male rarely came with food (Soper 1960, 1961). Also see Gray (1969) for a few further details of co-operative breeding at another site.

Parental care Highly co-operative. Both male and female take part in building nest and all parental care and territorial behaviour (Sherley 1985, 1994); both sexes defend young (Gray 1969). Overall, male makes greater contribution to feeding and caring for eggs and young and feeding partner during and before laying; both sexes contribute almost equally to territorial defence. However, for both males and females, territorial behaviour, before and during laying, and building of first nest require <1% of their time; apparently time spent in territorial behaviour for rest of breeding cycle and building of second nest is also very low (Sherley 1985, 1994). Chances of survival of each parent to the next breeding season not significantly different (Sherley 1994). If mate dies, single parent not able to raise young to fledging (Sherley 1994). (For details of roles of each parents in nest-building, incubation, feeding of young, see Breeding; for roles in territorial behaviour, see Breeding dispersion.) **AGE OF INDEPENDENCE:** 21 days after leaving nest, by which time young gather most of their own food (Sherley 1990a); 4–5 weeks after leaving nest for first and second broods, with feeding of fledgelings of first brood overlapping by c. 3 weeks with next breeding attempt, and performed mainly by primary male (Sherley 1994); 4–6 weeks after leaving nest, when no longer fed by parents (Hunt & McLean 1993); juveniles of one brood pushed from parents' territory 3–4 weeks after leaving nest (Gray 1974). Young of first brood can help rear young of second brood (see Co-operative breeding above). Young disperse from natal territory by onset of winter (Sherley 1985, 1994); families may stay together until late winter (Hunt & McLean 1993); at Dunedin, juveniles established territories <1 km from natal territories (Gray 1974).

Breeding dispersion At Kaikoura, nine of 15 pairs bred successfully in 6 ha and 15–17 pairs in 80 ha (Sherley 1994); in Orongorongo Valley, NI, 3–4 pairs found in 8 ha (Sherley 1985). At least two pairs in 4–5 ha of Kauri *Agathis australis* forest (Pierce 1994). At Dunedin, up to 25 territories recorded but size of area not known; two nests c. 20 m apart, but before both had eggs, one pair forced other farther away (Gray 1974). Sometimes build several nests before choosing one (see Breeding). **Territories** Defend all-purpose territories, in which pairs remain year-round; hold same territory for life (Gray 1974). Also said that pairs seem to stay more or less within regular

home-ranges (Oliver), and many pairs stay even if area destroyed by fire (McLean 1912). Some territories, or home-ranges, appear not to abut and there is no obvious territorial behaviour, such as fighting or displays (Hunt & McLean 1993). Territories established by young of season (either solitary males or pairs) in autumn, sometimes very quickly, and pairs then breed in next breeding season; juveniles often establish territories next to or close to parental territories, and may even annex part of parents' territories (Gray 1974). Primary male and female defend territory equally ($n=63$ territorial disputes); sometimes only male or female defends nest, but at other times both do (Sherley 1994). At Dunedin, territorial boundaries were most clearly defined in areas where population was densest; boundaries seemed to change with presence or absence of adjoining pairs and time of year; often occurred at ecotones between types of vegetation, particularly in years when population density low. Boundary disputes most common in early spring and when young had left nest in early summer, but are rare for rest of year. Twice, breeding pairs were forced to leave because neighbours were aggressive (Gray 1974). At Kowhai Bush, no seasonal trends in frequency of boundary disputes (Sherley 1985); territorial behaviour considered weak, with boundaries of territories not well defined, and conspecifics often tolerated within territories, even close to nests, late in breeding season (Sherley 1990a, 1994); this probably facilitated having helpers at nest (Sherley 1990a). However, parents seem to repel others vigorously from their territory over pre-laying and laying periods (Sherley 1985), and helpers not allowed near nest until fifth day of nestling period (Sherley 1990a). Territorial behaviour occupied $<1\%$ of time-budget of male and female during pre-laying and laying periods (Sherley 1989). **SIZE OF TERRITORIES:** Varies. At Dunedin, two territories that were occupied throughout year (one in Kanuka and other in pines) were about the same size, 1.6–2 ha, with one of these reduced to 0.8–1.2 ha in breeding season; one new breeding territory was c. 0.4 ha (Gray 1974). In Orongorongo Valley, NI, breeding territories averaged 6.25 ha/pair and non-breeding territories, 3.6 ha/pair (Sherley 1985).

Roosting At night. In sheltered sites, such as in canopy of Kanuka or in hollows in trees used for nesting (Lill 1991); in bad weather, twice seen roosting in holes in beech trees (St Paul 1976). When roosting, perch immobile, in physical contact with conspecifics, with plumage fluffed and head usually tucked into dorsal plumage (Lill 1991). During incubation, primary male roosts near nest; female, who roosts in nest, has a thermal advantage over male (Sherley 1990b). Birds seem to move all day from dawn to sunset (McLean 1912), but during daylight sometimes rest, perching or standing immobile and silent, with sleeked plumage, and may or may not appear more alert, moving heads or bodies, or calling. At Kaikoura (winter and autumn only), commonly moved to roosts in daylight for 7 weeks in winter, but rarely did so in autumn: pairs selected nocturnal roosting sites and slept 45 min (105; 13–98; 15) before dusk. In autumn, resting while alert takes up 3.2% of daylight; in winter, 1.8% of daylight (with roosting late in day taking up 5.4% of daylight); no differences between sexes. Comparing autumn and winter, roost more and fly less in winter, and estimated to expend 23–29% less energy in winter than in autumn; often opt for inactivity rather than more foraging on cold but fine winter afternoons. Little other seasonal change in daily activity between autumn and winter (Lill 1991).

SOCIAL BEHAVIOUR No detailed studies but some information from long-term studies of colour-banded populations at

Kowhai Bush, Kaikoura, SI (Sherley 1985, 1990a,b, 1994), and at Dunedin (Gray 1974); a few details in short study, late Jan. to mid-Feb. 1990, at Kaikoura (Hunt & McLean 1993). Single birds call less often than pairs and are less likely to be detected (Gray 1974). Often said to be shy, but during breeding season may be lured into the open hand by rapidly twirling a leaf (simulating fluttering of a bird) while imitating its call (Buller 1888); shy, more so in spring, and trusting but easily alarmed; not inquisitive (McLean 1907, 1912); tame (Graham 1948). Bathe in water in foliage and in grass wet with dew, seldom after 13:00 but as late as 15:00 (St Paul 1976; Lill 1991; G.H. Sherley). At Kowhai Bush, in autumn, maintenance behaviour takes up 3.0% of daylight, and flying 9.4%; in winter, maintenance, 2.6% and flying, 6.7%; no differences between sexes (Lill 1991). Sometimes sun themselves, fluffing up feathers of body and spreading wings to catch sunlight (G.H. Sherley).

Agonistic behaviour Do not advertise territories with calls but do call to advertise position (Sherley 1985). Parents show aggression towards helpers, though less towards regular helpers; aggression decreases as nestling period progresses; adult helpers are not allowed near breeding female during pre-laying, incubation and early nestling periods, and parents seem to vigorously repel conspecifics from territory before and during laying period. Despite this, territorial aggression is considered weak, with parents showing little aggression towards helpers feeding young (Sherley 1985, 1990a). In Dunedin, one young of first brood, who later fed second brood, was harried away from nest by one or both adults during incubation period (Gray 1974). Other observers have also found little obvious territorial behaviour, such as fighting or displays; neither sex seen to defend other sex from conspecifics (Hunt & McLean 1993); see mate-guarding below. During disputes at territorial boundaries, pairs can quiver outstretched wings while perched, attack by diving, snap bills or give Alarm Trill (Gray 1974). Rarely, males may display yellow of remiges in a threat or alarm display (G.H. Sherley). Also, rarely, birds are found locked together fighting, and in such circumstances an apparent submissive call can be heard. In one very aggressive interaction, 9 days after young fledged, primary male went to nest after a male helper had entered to feed young; primary male pulled helper out of nest by a leg, with much protestation from helper (Sherley 1985). Seen to be attacked or chased by New Zealand Tomtits *Petroica macrocephala* and Brown Creepers *Mohoua novaeseelandiae*; pair seen to call angrily at Tomtit perched near their nest; one fledgeling knocked off branch by a Tomtit (Gray 1969). **Alarm** May give Alarm Trill when alarmed or excited (McLean 1912; Sherley 1985), and either sex may lower wings (McLean 1912). Staccato Call given if mild threat, such as when a Swamp Harrier *Circus approximans* flies overhead; Alarm Trill given if threat intensifies (Sherley 1985). One male faced and scolded falcon that sat too close (McLean 1912).

Sexual behaviour During pre-laying and laying periods, primary male and female spend average 91.2% of time ($n=64$ h obs.) within 20 m of each other, which may help prevent extra-pair copulations; from laying to just after hatching, primary male keeps other males away from breeding female (Sherley 1989, 1994). In another study, in late Jan. to mid-Feb., mate-guarding of laying females by males appeared not to occur, and on five occasions male left mate to go elsewhere when neighbouring male within 2 m of her (Hunt & McLean 1993). (For aggression associated with mate-guarding, see above.) **BEHAVIOURS DIRECTED BY HELPER MALES TOWARDS FEMALES:** One helper male, perched with a juvenile female in front of an empty nest-box, moved slowly in and out of nest-box with wings slightly

lowered, but with no apparent reaction from juvenile female; same male, when foreign adult female present, flew up to this female chattering, then repeatedly flew back and forth from her to nearby empty nest-box, and then moved in and out of box as he did with female juvenile, alternating this with flying back to female and moving about her. One casual helper approached family it had been helping, gave Punctuated Call that elicits juvenile begging, and then tried to mount juvenile female, but was driven off by primary male. One primary male moved outside its normal range, joined family group with fledged young and tried to mount primary female (Sherley 1985). Elsewhere, unmated territorial male fed female fledgeling in adjacent territory, then bred with her in his territory next season (Gray 1974). **Greeting** When feeding, pair appears to maintain contact by constant exchange of Single-note Calls (Gray 1974), particularly round time of laying (Sherley 1989); if pair becomes separated, use Two-note Call as contact call. When changing over during incubation, before leaving nest, sitting bird usually waits for specific call from just outside nest, from mate (probably Single-note Call), who then immediately enters nest (Sherley 1985, 1990b). **Courtship feeding** At times, male feeds female, but without ceremony: male finds food-item, usually pulverises it and gives soft Chattering just before giving it to female; female briefly stops foraging, takes item straight away, and then both birds resume foraging. Sometimes female chases mate if he has particularly large item, or when he spends some time extracting a food item, but seldom succeeds in robbing him of food. Seen mainly in Sept.; begins 10–12 days before start of laying, increases markedly 6 days before laying, and peaks during laying; ends with completion of clutch or start of incubation; most food delivered c. 3.5 days after first oviposition. Occurs only with first clutches, though if first clutch fails before hatching, usually occurs with replacement clutch. Female fed larger items than usually taken by either member of pair, and, overall, male fed 42% (by weight) of food he collected to female, which was 35% of her total intake over pre-laying and laying periods (see Food). Despite male's efforts in courtship feeding, members of pair spend similar amounts of time foraging. Estimated that female catches enough food for her maintenance, and courtship feeding provides food needed for formation of eggs. Courtship feeding probably also helps keep members of pair close to each other before and during laying (Sherley 1989). Courtship feeding not seen with laying of second clutches possibly because: (1) average size of second clutch is smaller, and less energy needed than for first clutch; (2) availability of food probably greater and days are longer; and (3) primary male usually feeding still-dependent young of first brood (Sherley 1985, 1989). Once, male presented mate with feather and, another time, moss; female took them but soon resumed feeding (Sherley 1985). **Copulation** Of 13 attempts: earliest seen c. 12 days before laying began; ten occurred after laying of first egg; was not observed after start of incubation. Four occurred just after courtship feeding; nine occurred apparently without ceremony, while birds foraging together. During mounting, female adopts lowered posture and gives call similar to juvenile Begging Call (Sherley 1989).

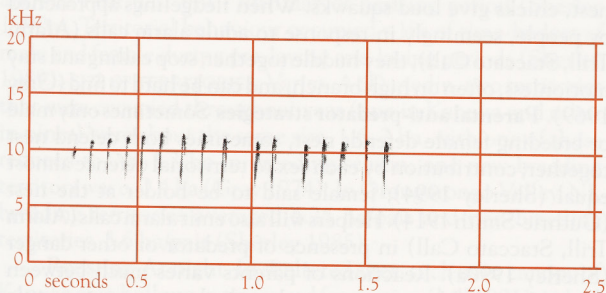
Relations within family groups For first 4 days after hatching, chicks just able to raise heads, open bills and emit soft peeping sounds to beg (Sherley 1994). Parents fed young one food item at a time (Sherley 1990a). Birds with food approach nest giving Single-note Calls and flying in short stages from shrub to shrub; perch near nest-hole before entering; young call more sharply as they are fed (Guthrie-Smith 1914). On first day out of nest, young reluctant to fly and usually stay huddled

together well above ground (Gray 1969; Sherley 1985); in first week, fledgelings continuously utter a piping Begging Call and are usually fed by parents and helpers, and rarely take any food themselves; Begging Call longer than that of nestlings, and birds will gape, showing orange-yellow of inside mouth. After 10–14 days, start to forage, usually with little success, and begin CHASE-BEGGING, in which young chase adults while calling constantly, begging for food; after 2 weeks, young still receive most food from parents, and spend about half their time Chase-begging and rest of time foraging for themselves. At 2–3 weeks, young feed themselves more but still fed often by adults, and brood often splits into individuals or into pairs, which chase adults. By 3 weeks, take most of their own food, but some more competent than others. After this, brood rarely seen together and Chase-begging rare. Helpers and parents do not feed particular individuals or sexes, either in nest or after young have fledged (Sherley 1985, 1990a). Juveniles have an adult repertoire of calls before independence (Sherley 1985). Just after fledging, adults respond well to tape-recorded calls of juveniles begging (Sherley 1994). Aggression between siblings often occurs in fledgeling groups, mostly by females towards males: females chased and pecked males or displaced them from perches. Aggression also occurs between broods: juveniles from first broods seen chasing and pecking fledgelings from second broods; possibly related to parents sometimes feeding juveniles in presence of fledgelings (Sherley 1985). For details of feeding of nestlings and fledgelings, by parents and helpers, see Food (Young). **Anti-predator responses of young** When taken from nest, chicks give loud squawks. When fledgelings approached by people, seemingly in response to adult alarm calls (Alarm Trill, Staccato Call), they huddle together, stop calling and stay motionless, often on high branch, and can be hard to find (Gray 1969). **Parental anti-predator strategies** Sometimes only male or breeding female defends nest, sometimes both defend nest together; contribution by each sex to territorial defence almost equal (Sherley 1994); female said to be bolder at the nest (Guthrie-Smith 1914). Helpers will also emit alarm calls (Alarm Trill, Staccato Call) in presence of predator or other danger (Sherley 1990a). Reactions of parents varies much between pairs: when building nest, some show little response to people nearby and just stay away from nest, though male may give Alarm Trill (McLean 1912); when with young, brooding adult may flush from nest (Sherley 1994); in response to alarm calls of chicks, both parents may arrive and call furiously, fly around, snap bills, and dive-bomb, sometimes hitting with their wings; may return to a branch between dives; may even land on observer, bird speading and quivering wings and giving Alarm Trill (Gray 1974). When one fledgeling was attacked by New Zealand Tomtits, adults called loudly and vibrated wings (Gray 1969).

VOICE Well known. Detailed study as part of broader study of social organization and breeding at Kowhai Bush, Kaikoura, SI, by Sherley (1985), on which account based unless stated. Sonagrams in Michelsen (1982). Said to be not vociferous (McLean 1912); also said to be often heard (Oliver). More easily detected by call than by sight (Gray 1974). Calls are described as short notes and occasional longer trills (Gray 1974); and as a series of clicks, squeaks and clucks (Michelsen 1982). Calls are very high-pitched: 7–13 kHz (Sherley 1985) with the Flight Trill as high as 15 kHz (Michelsen 1982). Calls also weak, and audible only at close quarters; they have been likened to the call of a nestling, to the winding of a watch, and to the striking together of two pieces of wire (Buller 1888;

McLean 1912; St Paul 1976; Oliver). Calls uttered with bill open a little (Andersen 1926). Do not call to advertise territory. Calling said to become louder and more continuous towards evening (Buller 1888). Thought to call less in spring than in winter (McLean 1912). During period of courtship feeding (see Social Behaviour), pairs spend >90% of daylight hours in continuous contact, maintained by almost constant exchange of *ssip* calls (Sherley 1989). Antiphonal calling reported (Michelsen 1982). Calls less musical and more rapidly repeated than those of Rock Wren (Williams 1963; Soper 1976; Michelsen 1982). Respond to imitation of calls (see Social Behaviour). **NON-VOCAL SOUNDS:** Vibration of wings audible (Buller 1888). Adults heard to snap bills when dive-bombing a person handling chick (Gray 1974).

Adult SINGLE-NOTE CALL (=SSIP CALL): Extremely short, truncated, single-note *ssip*. Most common call; made constantly by members of pair when foraging together. Also described as faint *zee*, being made when carrying food for young, and becoming sharper when young are being fed (Guthrie-Smith 1914); as distinctive cheep (CSN 3). A contact call (G.H. Sherley). **STACCATO CALL:** A few Single-note Calls run together in a staccato fashion. Possibly this call shown in sonagram **A**. Uttered as low-intensity alarm call, e.g. when Swamp Harrier flew overhead (Sherley 1985). **ALARM TRILL:** A decrescendo of extremely short notes run together, lasting a maximum of 3 s; starts at a high frequency and drops rapidly to a sustained note, with individual notes discernible during later stages. Described as a scolding rattle *str-r-r* (McLean 1912).



A L.B. McPherson; near Kaikoura, SI, NZ; Oct. 1983; P106

Uttered as high-intensity alarm call (Sherley 1985); uttered during confrontations between neighbouring pairs, or when chicks handled (Gray 1974). **LOCATION TRILL:** A series of notes like those of Alarm Trill, but spaced farther apart and without decrescendo. Function apparently to advertise position (Sherley 1985). **TWO-NOTE CALL:** Strong short truncated note followed by another truncated note, slightly longer and of lower frequency. Second most common call, uttered when pair become separated (Sherley 1985). Rapidly, but irregularly, repeated *tsit-tsit* (Soper 1976) probably this call (but see Punctuated Call below). **SUBMISSION CALL:** A series of monotonic *sseep, sseep* calls, with length and rapidity of repetition depending on degree of excitement. Similar to juvenile Begging Call (Sherley 1985, 1989). Rarely heard; uttered in apparent submission, e.g. by adults fighting and by female during copulation (Sherley 1985). **Other calls** During courtship feeding, male often uttered soft protracted **CHITTING** just before giving food to female (Sherley 1985, 1989). Male gave excited **CHATTERING** when apparently courting female (see Social Behaviour: Sexual behaviour). **PUNCTUATED CALL:** Described as extremely short, truncated two-syllable call *tsitt, tsitt* (G.H. Sherley); normally given by adult to elicit juvenile begging; once given by a

juvenile just before attempted copulation (see Sexual behaviour). **FLIGHT TRILL:** Heard only once: lasted 0.9 s and comprised seven brief notes slowly dropping in pitch (Michelsen 1982). Never heard during hundreds of hours of observations at Kowhai Bush (G.H. Sherley).

Young NESTLINGS: **BEGGING CALL:** For first 4 days after hatching, utter soft peeping sounds when begging; older nestlings beg with call similar to Submission Call of adult (Sherley 1985). **ALARM CALL:** Utter loud squawks when handled (Gray 1969). **FLEDGELINGS:** **BEGGING CALL:** In first week after fledging, continually utter protracted single-note piping *seeee, seeee*, given as often as needed to get food; call longer than Begging Call of nestlings. After 2 weeks, fledgelings call constantly during Chase-begging (see Social Behaviour). Free-ranging young are far more vocal than adults; often give call similar to Location Trill of adults. Young can give all adult calls before independence.

BREEDING Very well known. Detailed studies of nominate *chloris* of SI at Dunedin (Gray 1969) and at Kowhai Bush, Kaikoura, (Sherley 1985, 1989, 1990a,b, 1993), both over three seasons, using nest-boxes. Subspecies *granti* of NI not well known. On SI, breed in simple pairs and co-operatively, with helpers either being unpaired adults, or young from first brood (see Social Organization). Can raise two broods in a season (Gray 1969; Sherley 1985; Oliver), unless first clutch destroyed by predators (see Laying), though Sherley (1989) also says will re-lay if first clutch fails.

Season NOMINATE CHLORIS: Breed Aug.–Jan. At Dunedin: laying, late Sept. to late Dec.; hatching, mid-Oct. to late Jan.; fledging, mid-Nov. to mid-Feb. Second clutches laid early Nov. to early Jan. At Kowhai Bush, for first and second clutches combined: laying, early Sept. to mid-Dec.; hatching, early Oct. to early Jan.; fledging, late Oct. to late Jan.; second clutches usually laid between early Nov. and early Dec. **SUBSPECIES GRANTI:** Breed Aug. to at least Nov. (Oliver); young in nest, Nov. (Wilkinson 1924); fledgelings in family groups, Apr. (McLean 1907). Second clutches laid 3–4 weeks after first young fledge (Oliver).

Site Well hidden. Mostly nest in sheltered parts of open forest, in gullies or along watercourses (Dove 1906; McLean 1912; Wilkinson 1924; Mathews 1930; Oliver; CSN 19); sometimes in gardens in settled areas (Stidolph 1933; CSN 4, 5). Usually in hollow in living or dead limb or trunk of tree, or in log, often by a creek bank. Also in stumps, among roots under butt of felled tree at top of steep rocky face; among dead foliage of Cabbage Trees *Cordyline australis* hanging beneath crown; in Rabbit burrows; in hollow fence posts; under eave of brick shed; between slabs of a bush hut; in skull of a horse; and in nest-boxes; single records of nests in a roll of bark that hung and swung in a vine *Convolvulus*; under thatched eave of Maori hut; in stone wall; and in underground cavity under boulder (Guthrie-Smith 1914; Wilkinson 1924; Turbott 1967; Gray 1969; St Paul 1976; Gaze 1978; Sherley 1985; Oliver; CSN 38). Usually nest low down but occasionally in high positions (St Paul 1976; *contra* NZRD). At Kowhai Bush, preferred nest-boxes placed in dry sites with enough low foliage around to enable discreet entry and exit. **Wetas** (*Hemideina*: Orthoptera) will live in nest-boxes, and up to 12 have been found in a nest-box, usually just under the lid; their size and daytime activity disturb Riflemen (Wetas are bigger and heavier than the bird, and can scare them) and may have caused desertions (Sherley 1985). Males probably choose a site, which female accepts or rejects (Sherley 1985). **MEASUREMENTS:** Subspecies *granti*: One nest, c. 2.1 m

high (Oliver); another c. 25 cm high, in hollow log (Guthrie-Smith 1914).

Nest, Materials Build ovoid or dome-shaped nest with side entrance; nest in hollows; may build a cup-shaped nest in sites too small for domed nest. Composed mostly of sticks, grass, rootlets and leaf skeletons, and occasionally moss, pine needles, small dead leaves, fur, bark, wood chips and cobweb; chamber usually lined with feathers; one nest lined with fern fibres and very fine moss; one nest of subspecies *granti* lined with feathers, most of which from Goldfinch *Carduelis carduelis* (McLean 1907; Guthrie-Smith 1914; Gray 1969; St Paul 1976; Sherley 1985; Oliver). One nest in a hollow log built almost completely of pigeon feathers, with only a few leaf skeletons forming a frame round egg-chamber (Guthrie-Smith 1914). One nest in hollow in fence post, with a 23 cm high ridge in centre of hollow, was filled with material on either side of ridge until a flat mat, 24 cm thick at deepest, was formed; nest was then built on top of mat (Gray 1969); a pair that nested in a hollow log had filled in part of a fissure with nesting material and wrapped cobwebs and moss round rough edges of the knothole through which birds entered nest (Guthrie-Smith 1914). One pair that nested in a cavity under a boulder appeared to have enlarged cavity by scraping away soil with their feet (Gray 1969), though whether this intentional not known for certain. At Dunedin, a mat of sticks and fern rootlets woven on floor of nest-box and built up to level of entrance hole; mat usually slopes upward towards back of nest-box where a shallow saucer-shaped depression c. 4 cm in diameter is formed; a dome and tunnel of sticks and fern rootlets is then woven over mat; after completion of dome, a layer of leaf skeletons is woven into inside of dome; after several days' rest, a thick lining of feathers is woven into depression at end of tunnel, mostly contour-feathers of Blackbird *Turdus merula*, thrush and New Zealand Pigeon *Hemiphaga novaeselandiae*. In nest-boxes at Dunedin, length of tunnel varied, as long as 7.6 cm from entrance to back of box, and as short as a narrow but high lip projecting up across entrance. At Kowhai Bush, construct a base c. 20 mm thick, out of coarse material, including small sticks, which is built up into a bowl; gradually weave a dome out of finer and longer material, such as grass; walls of dome thickened from inside with grass and leaf skeletons; next, a tunnel is woven into dome, opening above floor of nest-bowl; orientation of tunnel usually off-centre from cavity entrance; woven sections of nest tight-knit and tidy; line dome with a layer of coarse feathers, usually remiges of other birds, then a finer layer of soft downy feathers. Materials used vary; composed of common plants growing nearby (Sherley 1985). At Dunedin, completed nests contained an average of 840 (279.3; 600–1300; 5) pieces of material, mostly leaf skeletons (40.4%), feathers (34.3%) and sticks (14.3%); length of sticks, 6.4–7.6 cm; length of leaf skeletons, 5.0–12.7 cm; length of contour-feathers, 3.8–10.1 cm. Both sexes build, but males make more trips with material than females (Gray 1969; Sherley 1985, 1994). Carry one piece of material on each trip to nest (Gray 1969). At Kowhai Bush, males made 8.6 trips/h with material (5.9; 56 observations), females 4.4 trips/h (3.9; 57 observations). At Dunedin, one nest comprising 700 pieces of material was finished in 25 days. Rate of building increases during periods of cold and wet weather; once, during 3 days of cold wet weather, two nests in nest-boxes progressed from mat stage to complete but unlined in 3 days; in another nest-box, a complete but unlined nest built within 4 days. At Kowhai Bush, feathers added to nest during incubation, mostly by male; for first clutches (number not stated), males brought a total of 80 feathers and females a total of 42; for second clutches (number

not stated), males brought a total of 105 feathers and females a total of 29. Feathers lining nest can become damp from condensation or water leaking into nest; wet feathers either taken out and dried by brushing them against a perch, or discarded and replaced with new dry feathers (Sherley 1985). Build one or more incomplete nests before completing nest for breeding (Gray 1969; G.H. Sherley). Build new nest in different site for replacement and second clutches; often finish an earlier and partly built nest; one pair that deserted shortly after laying, rebuilt in same nest-box after observer removed original nest (Gray 1969). **MEASUREMENTS:** SI: Length, 15 cm; width, 10 cm (Oliver). At Kowhai Bush: width of entrance tunnel, 11–30 mm; diameter of nest-bowl, c. 35 mm; thickness of top of dome, 15–25 mm. Weight (g) of nests from nest-boxes of same internal dimensions, first-clutch nests, 40.5 (6.7; 124); second-clutch nests, 37.6 (6.7; 46). NI: One nest (cm): length, 14.0; width, 13.0; height, 12.7; diameter of entrance, 2.2; length of tunnel, 5.6; diameter of nest-bowl, c. 6.4 (McLean 1907); for one nest in root of log: vertical diameter of entrance, 3.8 cm; horizontal diameter of entrance, 2.5 cm (Wilkinson 1924).

Eggs Oval; white; slightly glossy (Mathews 1930; Oliver). **MEASUREMENTS:** At Kowhai Bush, first-clutch eggs, 15.9 (1.44; 84) × 12.5 (0.40; 83); second-clutch eggs, 15.5 (0.70; 37) × 12.5 (0.32; 37). **WEIGHT:** At Kowhai Bush, for freshly laid eggs, 1.34 g (0.10; 35); c. 19% of mean weight of adult female.

Clutch-size Three to five (Mathews 1930). At Dunedin, 3.6 (0.73; 2–4; 16): C/2 × 2, C/3 × 3, C/4 × 11; first clutches, 3.8 (0.41; 3–4; 6): C/3 × 1, C/4 × 5; second clutches, 3.0 (0.89; 2–4; 6): C/2 × 2, C/3 × 2, C/4 × 2. At Kowhai Bush, first clutches, 4.4 (0.5; 106); second clutches, 3.8 (0.6; 41).

Laying At start of season (first clutches), laying may not begin for at least 3 weeks after completion of nest; for second clutches, laying may begin within 2 days of completion of nest (Gray 1969). At Kowhai Bush, eggs of eight first clutches laid between 06:30 and 07:30; one at 10:30; eggs of two second clutches laid between 04:00 and 04:30. Interval between laying of consecutive eggs: in first clutches, 2.1 days (0.6; 116); in second clutches, 2.1 days (0.7; 14), and sometimes >5 days. By implication, Sherley (1993) says Riflemen usually re-lay if first brood successful but not if first clutch lost, though may re-lay if first attempt at laying fails (Sherley 1989). At Dunedin, eggs laid at intervals of 48 h; in one nest, second egg laid 3 days after first; in another, a second clutch, last (third) egg laid 4 days after second. At Kowhai Bush, of 91 pairs, 39 (42.9%) were single-brooded; 52 (57.1%) laid a second clutch, including 47 (51.6%) that hatched young; percentage of pairs per season that laid second clutches ranged from 37.9% (n=29) to 72.7% (n=22). One pair successfully raised three broods in a season (G.H. Sherley). At Kowhai Bush, mean interval between fledging of first brood and laying of second clutch, 8 days (4.0; 2–16; 38) (Sherley 1985, 1994). At Kowhai Bush, two unusually large clutches probably from two females laying in same nest. In one nest, three eggs were laid in 63 h, rather than the expected 96 h, suggesting that egg-dumping may have occurred. Male feeds female during laying of first clutch but not during laying of second clutch (Sherley 1989, 1990b).

Incubation By both sexes; contribution by male greater during day; only female incubates at night, usually beginning when clutch complete (Gray 1969; Sherley 1985, 1990b, 1994); once known to start on day before last egg laid (Gray 1969). At Kowhai Bush, start of incubation sometimes delayed for up to 5 days after completion of clutch; mean length of delayed incubation: in first clutches, 2.3 days (1.0; 13); in second clutches, 2.4 days (n=5). At Kowhai Bush, males incubate more

than female during day, though contribution by male in early part of second clutch lower because he is still feeding fledgelings from first brood. Median attentiveness (% of daytime) incubating: for first clutches, males 48 (47–55); females 33 (32–35) ($n=225$ h of observation); for second clutches, males 45 (33–48); females 33 (25–39) ($n=152$ h of observation). Little variation in attentiveness during incubation of first clutches; for second clutches, males incubated 10–14% less during first 4 days than during the rest of the incubation period. For more details of parental attentiveness during first and second clutches, for five 4-day intervals during incubation, see Sherley (1985, 1990b, 1994). During change-over, incubating bird waits for specific call from relieving bird before leaving (Sherley 1985). Often block entrance to nest with downy feathers, when bird leaves nest during cold weather; sitting bird usually blocks entrance hole from inside with feathers, during day and at night (Sherley 1985). At Dunedin, eggs usually hatch within 24 h of each other; between 17:00 and 07:00 next day. At Kowhai Bush, eggs hatched within 48 h of each other. Unhatched eggs not removed, and remain in nest after young fledge (Gray 1969; Sherley 1985). Male does not feed female during incubation (Sherley 1994). **INCUBATION PERIOD:** From start of incubation to hatching, 20 or 21 days (Gray 1969); 19.7 days (0.8; 80) (Sherley 1985, 1990a).

Young Altricial, nidicolous. Blind and naked at hatching (Gray 1969; Sherley 1985). At Dunedin: at 4 or 5 days, feather-tracts become visible; at 10 days, eyes begin to open, and feathers in pin, up to 2 mm long, cover most of body; at 12 days, feathers begin to emerge from pins, on rump, flanks and sides of breast at first (Gray 1969). At Kowhai Bush: at 6 days, feather-tracts visible beneath skin, and eyes partly open; at 7 days, primaries emerge from pins; at 12 days, feathers in pin over whole body, most with feathers emerging, and eyes fully open; at 15 days, able to sex nestlings on plumage. **Growth** All following from Kowhai Bush. **WEIGHT:** At hatching, 1.0–1.4 g. Mean weight of nestlings up to 22 days old in Table 4. No significant difference in mean rate of increase between young in nests with helpers and those in nests without helpers. **CULMEN, TARSUS:** Mean length summarized in Table 4. **Parental care, Role of sexes** Both sexes brood during day; only female at night (Sherley 1985). At Kowhai Bush, young brooded for 12 days after hatching. Proportion of daytime spent brooding young by male and female summarized in Table 5. For more details on the role of each sex during brooding, see Sherley (1985). Both parents feed young, though at most stages male feeds young more (Gray 1969; Sherley 1994); male visits nest less often as young grow and is rarely seen round nest when young near

fledging (Gray 1969; Oliver). At Kowhai Bush, average feeding rate (items/h) of young in first broods with and without helpers summarized in Food (see, especially, Table 2). No significant difference between feeding rates of young of first broods with helpers and those without helpers. At Dunedin, adults remove faecal sacs (Gray 1969); at Kowhai Bush, both parents and helpers remove faecal sacs.

Table 5. Mean proportion of daytime spent brooding by parents (primary male, breeding female), for first and second broods (from Sherley 1985). (N = number of 30-min watches.)

	AGE OF YOUNG (DAYS)	MALES	FEMALES	N
FIRST BROODS	1–4	39±19	28±18	63
	5–8	14±18	12±12	37
	9–12	1±5	1±4	48
SECOND BROODS	1–4	32±18	28±17	68
	5–8	23±18	17±15	55
	9–12	9±14	6±11	45

Fledging to independence **FLEDGING PERIOD:** 24 or 25 days (Gray 1969); 24.0 days (1.2; 50 broods) (Sherley 1985, 1993). Young usually fledge in early morning, before 07:00 (Gray 1969); young all fledge within 2 h of each other (Sherley 1985). At fledging, young are poor flyers; move about with short flying hops but prefer to remain perched high up, in a group (Sherley 1985). At Kowhai Bush, during first week after fledging, young largely dependent on parents, and helpers if present, for food. For full discussion of comparative rates of feeding of nestlings and fledgelings by attendant birds, see Food (Young). Ten days after fledging, young start foraging for themselves; after 14 days, young spend about equal amounts of time foraging for themselves and soliciting food from adults; after 21 days, young obtain most of their own food. Largely independent 4–6 weeks after fledging (see Social Organization: Parental care).

Success At Dunedin, for 1966–67 and 1967–68 seasons: from 47 eggs in 14 nests, 27 (57.4%) hatched, 23 (48.9%) fledged; five nests failed at egg-stage; one brood abandoned when nestlings c. 10 days old. At Kowhai Bush, mean number of young fledged per nest: (1) **FOR FIRST CLUTCHES:** (1a) with helpers, 3.9 (1.0; 10); (1b) without helpers, 3.7 (0.9; 80); (2) **FOR SECOND CLUTCHES:** (2a) with helpers, 3.4 (1.9; 7); (2b) without helpers, 3.3 (1.0; 27). For birds banded as nestlings, 18.2% ($n=214$) of male nestlings and 22.8% ($n=250$) of female nestlings survived to their first year (Sherley 1985, 1993). A nest containing nine eggs, probably a result of more than one

Table 4. Weight (g) and length of culmen and tarsus (mm) of male and female nestlings.

AGE (days)	WEIGHT		CULMEN		TARSUS	
	MALES	FEMALES	MALES	FEMALES	MALES	FEMALES
2	1.1 (–; –)	1.3 (–; –)	4.0 (–; 1)	4.4 (–; 2)	5.7 (0.52; 10)	5.6 (–; 2)
4	2.2 (–; –)	2.5 (–; –)	4.8 (0.58; 17)	5.0 (0.57; 12)	6.9 (1.35; 14)	7.8 (0.31; 9)
6	3.5 (–; –)	3.8 (–; –)	5.9 (0.55; 22)	6.3 (0.51; 15)	9.3 (1.69; 22)	10.4 (0.94; 17)
8	4.6 (0.6; 37)	5.2 (0.7; 32)	7.0 (0.41; 33)	7.3 (0.50; 27)	12.8 (1.39; 33)	13.2 (1.17; 26)
10	5.7 (0.6; 39)	6.3 (0.9; 38)	7.6 (0.40; 39)	8.0 (0.66; 37)	15.3 (0.78; 38)	15.3 (2.85; 35)
12	6.6 (0.8; 37)	7.6 (0.7; 35)	8.4 (0.51; 36)	8.8 (0.57; 33)	17.2 (0.77; 35)	17.6 (0.98; 33)
14	7.2 (0.7; 40)	8.3 (0.6; 36)	9.0 (0.54; 36)	9.2 (1.72; 34)	17.9 (0.78; 36)	18.4 (0.87; 34)
16	7.4 (0.7; 39)	8.6 (0.6; 32)	9.2 (0.68; 41)	9.9 (0.45; 31)	18.4 (0.81; 40)	19.2 (0.78; 34)
18	7.3 (0.6; 37)	8.5 (0.6; 33)	9.6 (0.65; 40)	10.2 (0.48; 31)	18.6 (0.83; 38)	19.3 (0.75; 33)
20	7.4 (0.4; 57)	8.3 (0.6; 62)	10.1 (0.55; 54)	10.5 (0.70; 70)	18.4 (0.63; 54)	19.1 (0.59; 58)
22	6.8 (0.4; 31)	7.8 (0.6; 38)	10.6 (0.90; 11)	11.2 (0.95; 15)	19.8 (–; 4)	20.0 (0.67; 12)
24	–	–	10.4 (–; 5)	10.6 (–; 2)	18.5 (–; 3)	18.9 (–; 2)

female laying in nest, deserted by breeding pair; a brood of young, 16 days old, lost through human interference; another brood taken by Stoat.

Predators of adults Sacred Kingfisher *Todiramphus sanctus* once seen to catch and fly off with a Rifleman (*A. Lill*).

PLUMAGES Prepared by J.S. Matthew. Young naked at hatching (Gray 1969; Sherley 1985) and do not develop natal down (Sherley 1985); see breeding for development of plumage. Fledge in juvenile plumage. Then undergo post-juvenile (first pre-basic) moult, probably starting soon after fledging and finishing before onset of winter; not known if this moult partial or complete, and thus sequence of plumages to adult not certainly known. Resultant first basic plumage either adult if post-juvenile moult complete, or adult-like with some retained remiges and rectrices if partial. Then undergo a complete post-breeding (second pre-basic) moult, probably when c. 1 year old; subsequent plumage definitely adult. Thereafter, a complete post-breeding (pre-basic) moult each cycle produces successive adult plumages with no change in appearance. Juveniles and adults sexually dimorphic. Nominate *chloris* described below; based on skins of four adult males, five adult females, five juvenile females and three juvenile males.

Adult male (Second and subsequent basic). **HEAD AND NECK:** Forehead and forecrown, dark olive (c46) or olive (150); some have light-brown (c26) tinge or diffuse light-brown (c26) streaks. Hindcrown, nape and hindneck, bright olive (150) or dark green (260). Well-marked supercilium, white, extending from above lores and eye to above ear-coverts. Eye-ring, white. Lores, white anteriorly, becoming grey-black (82) posteriorly; forming distinct dark loreal spot. Feathers behind eye, dark grey (83) or grey-black (82), forming narrow grey-black (82) stripe behind eye. Ear-coverts vary from white to light tawny brown (c223D) or light greyish olive (c43) with exposed dark-grey (83) bases. Malar area, chin, throat, and sides of neck, white or pale cream (c92). **UPPERPARTS:** Mantle, scapulars, back and rump, bright olive (150) or dark green (260). Uppertail-coverts, lime-green (59) or bright yellow-olive (52), merging to white towards bases, and contrasting with rump. All feathers of upperparts have concealed dark-grey (83) bases. **UNDERPARTS:** Breast and belly, white; with pale-cream (c92) or straw-yellow (c56) suffusion in some. Flanks, pale yellow (c157) or off-white (ne) with pale-yellow (c157) tinge. Axillaries, white. Feathers of thighs, brown (28) with off-white (ne) fringes. Undertail-coverts, pale yellow (c157). All feathers of underparts have concealed dark-grey (83) bases. **UPPERTAIL:** Rectrices, blackish brown (c119), merging to dark green (260) towards tip, and with straw-yellow (56) or off-white (ne) tip, which is broadest (to 3 mm) on outer rectrices; t1 fringed dark green (260) on inner and outer web; t2–t5 fringed dark green (260) on outer web. Shafts, dark brown (121). **UNDERTAIL:** Patterned as uppertail but ground-colour, dark grey (83); shafts, white. **UPPERWING:** Marginal secondary coverts, dark brown (121) with dark-green (260) or bluish-green (c164) fringes. Median secondary coverts, dark brown (121) with dark-green (260) fringes. Greater secondary coverts, dark brown (121) on inner web, green (162B) or dark green (262) on outer web. Marginal primary coverts, dark brown (121) with white fringes. Median and greater primary coverts, dark brown (121) or blackish brown (c19). Feathers of alula, dark brown (121) or blackish brown (c19); longest feather of alula sometimes has white edge to outer web. Primaries, dark brown (121) or blackish brown (c19); outer web edged green (162B), light green (61) or bluish green (c164) depending on angle of view; outer edge grades to

off-white (ne) distally and pale yellow (157) basally; inner web narrowly edged white, edge not extending as far distally on outer primaries. Secondaries and tertiaries similar to primaries, but secondaries finely fringed off-white (ne) at tip when fresh, with basal one-third of outer web, pale yellow (157) and basal one-third of inner web, off-white (ne), and tertiaries broadly tipped white on outer web. Edges to outer webs of remiges combine to form green (162B), light-green (61) or bluish-green (c164) panel on folded wing, colour varying with angle of view; pale-yellow (157) base to outer webs of remiges combines to form diffuse pale-yellow (157) bar across centre of wing, obvious in flight and when wing folded. **UNDERWING:** All marginal coverts, and median and greater secondary coverts, white or pale yellow (c157). Median and greater primary coverts, white, with dark-brown (121) fringes or outer webs in some. Remiges, dark brownish grey (c79); markings similar to those of upperwing, but outer web duller (and usually concealed on normally spread wing).

Adult female (Second and subsequent basic). Similar to adult male, differing by: **HEAD AND NECK:** Forehead, crown, nape and hindneck, blackish brown (c119) with bold well-defined yellow-brown (123B) streaking; feathers, blackish brown (c119) with broad yellow-brown (123B) shaft-streaks and concealed dark-grey (83) bases. **UPPERPARTS:** Mantle, back, scapulars and rump, dark brown (121) with bold light-brown (26) streaking; feathers, dark brown (121) with bold light-brown (26) shaft-streaks; and rump tinged olive (c51). Uppertail-coverts, yellow-olive (c52) or yellow-brown (c24), duller than in adult male. **UPPERTAIL:** Very similar to adult male, but fringes to rectrices usually less intensely dark green (260) or concolorous with rest of feather. **UPPERWING:** Marginal and median secondary coverts, dark brown (121) with olive (50) fringes and dull yellow-brown (c24) shaft-streaks, which are broader towards tips. Greater secondary coverts, dark brown (121), becoming olive (150) or dark green (c260) at edges of outer webs. Remiges similar to adult male, but edges of outer webs, light green (c61) or yellow-olive (c52). Edges to outer webs combine to form indistinct light-green (c61) panel on folded wing. Rest of upperwing as adult male.

Nestling Covered with black papillae when c. 10 days old; feathers emerge on rump when 12–15 days old: males have greenish tips to feathers, females have dusky-ochre tips (Grey 1969).

Juvenile male Similar to adult male, differing by: **HEAD AND NECK:** Supercilium less distinct, off-white (ne). In some, chin and throat mottled brown (28) or dark brown (121). **UPPERPARTS:** Mantle, scapulars and upper back vary from greyish olive (c43) to dark brown (121) with or without indistinct yellowish-brown (c24) streaking or suffusion; feathers vary from dark brown (121) with dull yellow-brown (c24) shaft-streaks, to olive (51, 150) or dull yellowish brown (c24). Lower back and rump, bright olive (150) or dark green (260). **UNDERPARTS:** Breast, upper belly and flanks similar to adult, but with varying degree of brown (28) or dark-brown (121) mottling, some with only a few scattered brown (28) flecks, others with bold brown (28) or dark-brown (121) mottling.

Juvenile female Very similar to adult female, but underparts similar or identical in appearance to those of juvenile male.

First immature male and female (First basic). Little known. Possibly indistinguishable from respective adult sexes (Sherley 1985). Two adult-like females collected in Apr. and May (AM, NMNZ, CM) with slightly worn primaries and a few

faint brown (28) spots on breast possibly first immatures, as possibly one collected in Oct. (NMNZ) with well-worn primaries and a few faint brown (28) spots on lower breast. Two adult-like males collected in Feb. and July (NMNZ) with slightly worn primaries, a few brown (28) spots on breast and a few juvenile-like feathers on nape and hindneck, also possibly first immatures.

BARE PARTS Based on photos (Soper 1976; Moon & Lockley 1982; Moon 1988, 1992; Haddon 1990; NZRD), information from museum labels (AM, CM, NMNZ) and other information. **Adult** Bill, nasal groove and tomia, grey-black (82); also described as black (Oliver; NMNZ) or dark brown (AM). Palate described as yellow (Oliver). Gape, grey-black (82); also described as orange (Oliver). Orbital ring, dark. Iris described as dark brown (AM), black (Oliver) or brown (NMNZ). Legs and feet, pinkish brown (c221D); also described as pale brown or yellowish brown (AM, NMNZ) or brownish black (Oliver). Soles, orange-yellow (18); also described as gamboge (Oliver) or dull yellow (NMNZ). **Nestling** Bare skin described as light pink (Sherley 1985). No other information. **Juvenile** Differences from adult: Lower mandible described as cinnamon or dark brown (NMNZ). Gape described as orange (AM). Oliver mentions no difference between adults and immatures (probably referring to juvenile). **First immature** No information. Probably similar or identical in appearance to adult.

MOULTS Based on examination of skins (AM, CM, NMNZ): 20 adult and seven juvenile *chloris* and 13 adult and three juvenile *granti*; and other information as cited. **Adult post-breeding** (Possibly third and subsequent pre-basic). Apparently complete. Primaries moult outward, starting at p1. In *chloris*, starts in last 10 days of Jan. and finished by Apr.; duration 50–60 days; female started moult before male in six of 14 pairs (Sherley 1985). One *chloris* collected in Nov. with active moult of primaries (PMS=12). Of 32 adults, seven with all primaries new or very slightly worn in Mar. or Sept.; rest with all primaries worn between Mar. and Dec. (only very slightly worn between Mar. and June). Timing of moult probably similar between subspecies. Nothing known of timing or sequence of moult of tail, wing-coverts or alula. Moult of body probably starts before start of moult of primaries, and not finished till after finish of moult of primaries. **Post-juvenile** (First pre-basic). Very little known. Post-juvenile moult of body recorded from four skins collected in Feb. and Mar. Not known if remiges or rectrices replaced; four putative first immatures, collected in Feb. and July, with slightly worn primaries, and one collected in Oct. with well-worn primaries, suggest that juvenile primaries may be retained. Post-juvenile moult starts on breast, and finished before start of winter (Sherley 1985). **First immature post-breeding** (Second pre-basic). Nothing known (but see Post-juvenile moult). Timing and extent probably similar to adult post-breeding.

MEASUREMENTS **NOMINATE CHLORIS:** (1–2) SI, skins, sexed using labels and plumage (AM, CM, NMNZ): (1) Adults (possibly including some first immatures); (2) Juveniles. (3–4) Kowhai Bush, SI, live, sexed by plumage (Sherley 1993): (3) Adults; (4) Second-brood nestlings 20–21 days old, not long before fledging. **BILL WF** and **BILL DF** measured at feather-line or where rectal flange joins bill.

Additional measurements of nestlings in Breeding (see Table 4).

		MALES	FEMALES	
WING	(1)	47.8 (1.85; 46–50; 10)	51.4 (2.59; 47–55; 10)	**
	(2)	49, 50	51.5 (0.58; 51–52; 4)	
TAIL	(1)	23.3 (1.90; 21–26; 10)	22.1 (1.86; 19–24; 7)	ns
	(2)	21, 22	23.8 (0.96; 23–25; 4)	
BILL S	(1)	13.5 (0.62; 12.7–14.5; 9)	14.4 (0.50; 13.4–15.1; 10)	**
	(2)	11.6, 12.7	14.0 (0.77; 13.0–14.7; 4)	
	(3)	12.2 (0.62; 34)	13.2 (0.67; 20)	**
BILL WF	(4)	9.8 (0.60; 22)	10.5 (0.40; 17)	*
	(3)	2.9 (0.32; 34)	3.3 (0.37; 21)	**
BILL DF	(4)	2.8 (0.10; 13)	3.0 (0.20; 9)	*
	(3)	2.2 (0.17; 34)	2.4 (0.18; 21)	**
TARSUS	(4)	2.2 (0.10; 20)	2.3 (0.10; 17)	*
	(1)	19.1 (0.73; 17.9–20.1; 10)	20.4 (1.03; 18.5–21.8; 10)	**
	(2)	19.5, 19.9	20.7 (0.54; 20.0–21.3; 4)	
	(3)	19.3 (0.91; 30)	20.0 (0.75; 18)	**
	(4)	18.1 (0.60; 23)	19.0 (0.80; 17)	*

SUBSPECIES GRANTI: (5–6) NI, skins, sexed using labels and plumage (AM, CM, NMNZ): (5) Adults (possibly including some first immatures); (6) Juveniles. (7) Orongorongo Valley, NI, live, adults, sexed by plumage (Robertson *et al.* 1983).

		MALES	FEMALES	
WING	(5)	46.8 (0.75; 46–48; 6)	48.4 (1.51; 46–50; 7)	*
	(6)	47, 50, 51	–	
	(7)	46.7 (1.72; 43–49; 18)	47.8 (1.64; 45–50; 9)	ns
TAIL	(5)	22.2 (1.17; 21–24; 6)	23.3 (1.75; 21–26; 6)	ns
	(6)	21, 22, 24	–	
BILL S	(7)	21.4 (1.36; 19–24; 16)	21.7 (1.80; 18–24; 7)	ns
	(5)	13.2 (0.58; 12.6–14.2; 6)	14.4 (0.49; 13.5–15.0; 7)	**
BILL F	(6)	11.7, 13.5, 13.9	–	
	(7)	10.1 (0.89; 9–12; 16)	11.1 (0.93; 10–13; 9)	**
TARSUS	(5)	19.1 (0.26; 18.9–19.4; 6)	19.7 (1.18; 18.3–21.8; 7)	ns
	(6)	19.3, 20.1, 20.4	–	
	(7)	19.5 (0.80; 18–21; 12)	19.7 (0.45; 19–20; 5)	ns

CHLORIS AND GRANTI COMBINED: (8) NI and SI, skins, ages combined, basis for sexing not known (Hunt & McLean 1993).

		MALES	FEMALES	
WING	(8)	46.5 (1.31; 22)	49.9 (1.73; 26)	**
TARSUS	(8)	18.9 (0.76; 20)	19.8 (0.76; 26)	**
HINDCLAW	(8)	5.7 (0.42; 22)	6.9 (0.72; 27)	**
BILL N	(8)	7.2 (0.38; 22)	8.1 (0.35; 25)	**
BILL D	(8)	2.1 (0.16; 17)	2.3 (0.13; 20)	**
BILL W	(8)	2.4 (0.18; 21)	2.5 (0.18; 20)	*

WEIGHTS **NOMINATE CHLORIS:** (1–2) Kowhai Bush, SI, live, sexed by plumage (Sherley 1993): (1) Adults; (2) Second-brood nestlings, 20–21 days old. (3–4) SI, from museum labels (NMNZ): (3) Adults; (4) Juvenile. **SUBSPECIES GRANTI:** (5) Orongorongo Valley, NI, live, adults, sexed by plumage (Robertson *et al.* 1983).

		MALES	FEMALES	
(1)		5.6 (0.30; 33)	7.0 (0.70; 20)	**
(2)		7.1 (0.40; 25)	9.5 (0.50; 21)	*
(3)		5.0, 7.3	–	
(4)		5.3	–	
(5)		6.3 (0.60; 5.0–7.0; 21)	7.7 (0.52; 7.0–8.5; 6)	**

Additional weights of nestlings in Breeding (see Table 4). In nominate *chloris*, first-brood female nestlings weigh more

than first-brood male nestlings over most of the nestling period (Sherley 1993).

STRUCTURE Wing short; tip of longest primary reaches to about three-quarters length of tail when wing folded. Ten primaries: p7 longest (p8 or p5–p6 sometimes equal longest); p10 7.5–9.5 mm shorter than p7, p9 1.5–3.5, p8 0–0.5, p6 0–0.5, p5 0.5–2.5, p4 3.0–4.5, p3 4.0–6.0, p2 5.0–7.5, p1 6.0–8.5. Slight emargination to outer webs of p6–p8, sometimes also p5, and inner webs of p7–p10. Nine secondaries, including three tertials; tip of longest tertial does not reach p1 on folded wing. Tail very short, slightly rounded at tip; ten rectrices; t1–t3 longest, t4 2–6 mm shorter than t1–t3, t5 4–7. Bill rather short, about same length as head or slightly shorter; upper mandible straight with slight notch on top edge just in front of nostrils; lower mandible curved slightly upward towards tip; tip of upper mandible extends slightly over tip of lower mandible. Nares occupy less than half length of exposed culmen; external nares open directly upward in aperture with round lips (Pycraft 1905). Tibia fully feathered. Tarsus long and laterally compressed; scaling: anterior surface (podotheca) covered by single large scale with no divisions, indistinct division between anterior and posterior surface; posterior surface (planta) covered in small oblong or moniliform scales (Pycraft 1905). Middle front toe longest, 15.9 mm (1.09; 14.9–17.3; 6) including claw; outer front toe 75–85% length of middle front; inner front toe 70–80%; hindtoe 85–95% length of middle front toe. Hindclaw, very long, c. 7 mm long.

AGEING Juveniles distinguished from adults by plumage (q.v.). First immatures said to be identical in appearance to respective adult sexes (Sherley 1985). Not known if remiges or rectrices replaced in post-juvenile moult; adult-like birds with very faint brown markings on underparts, and worn primaries in autumn, possibly first immatures with retained juvenile primaries. Further work required to determine if first immature plumage exists.

SEXING Sexes differ in plumage (q.v.) and size, at all ages: adult and juvenile females average larger than males. Hunt & McLean (1993) indicate that females have deeper and more decurved bill compared with males.

GEOGRAPHICAL VARIATION Two subspecies recognized (NZCL), though differences between them not well understood (this study). Mathews & Iredale (1913) claim *granti* only slightly tinged yellow on underparts and on rump (probably referring to uppertail-coverts), whereas this colour prominent in *chloris*. Oliver states that adult *granti* has paler yellow on flanks and undertail-coverts compared with adult *chloris*. Examination of nine adult male *chloris* and four adult male *granti* (CM, NMNZ) reveals no consistent difference between subspecies; one *granti* from Ohakune, NI, slightly darker, duller olive (c46) on upperparts compared with *chloris*, but this difference not obvious in other skins of *granti*. Two adult male skins labelled *granti*, collected Sept. 1909 at Silverstream (probably on NI as collection date same as skin from Ohakune), slightly duller olive on upperparts compared with *chloris*. Of three adult female *granti*, two from Rotorua area have richer straw-yellow (c57) shaft-streaks to feathers of upperparts, and richer green (c260) rump compared with five adult female *chloris* (skins in NMNZ); one adult female *granti* from Wellington region not different from *chloris*. Adult female *granti* have shorter Wing ($P < 0.05$) compared with adult female *chloris*, but adult males of

the two subspecies do not differ in size (this study). Results of Robertson *et al.* (1983) also indicate that live adult female *granti* have shorter Wing compared with skins of adult female *chloris* (this study).

Rifleman collected from vicinity of Dusky Sound, SI, in 1773, originally recognized as distinct species, *Acanthisitta citrina* Gmelin, 1789. This form supposedly larger and brighter yellow on rump, undertail-coverts and flanks compared with *A. chloris* (Ogilvie-Grant 1905). Oliver considers this form a subspecies, *citrina*, of Rifleman, occurring on SI from Dusky Sound region, and possibly also Bourke Hut and Makaroro region. Mathews & Iredale (1913) uncertain as to status of *citrina*. Subsequent works (Heather & Robertson 1997; NZCL) consider *citrina* synonymous with nominate *chloris*. Female (NMNZ) collected in 1953 from Reischek Ra., originally designated *citrina* (Oliver), appears similar to adult females from rest of SI (this study).

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Volume 5, Plate 1

Rifleman *Acanthisitta chloris* (page 60)

NOMINATE *CHLORIS*: 1 Adult male; 2 Adult female; 3 Juvenile male, heavily streaked individual; 4 Juvenile male, lightly streaked individual; 5 Juvenile female; 6 Adult male

Bush Wren *Xenicus longipes* (page 76)

NOMINATE *LONGIPES*: 7 Adult, bright individual; 8 Adult, dull individual
 SUBSPECIES *VARIABILIS*: 9 Age uncertain

Rock Wren *Xenicus gilviventris* (page 81)

10 Adult male, typical individual; 11 Adult male, green morph; 12 Adult female