Order PASSERIFORMES

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

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

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

The Passeriformes divide into two main groups:

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

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

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

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

MENURIDAE (lyrebirds): two species in one genus; endemic to Aust.;

ATRICHORNITHIDAE (scrub-birds): two species in one genus; endemic to Aust.;

CLIMACTERIDAE (A'asian treecreepers): six species in two genera breeding in Aust.;

MALURIDAE (Australopapuan fairy-wrens, emu-wrens and grasswrens): 22 breeding species in three genera in Aust.;

MELIPHAGIDAE (honeyeaters and Aust. chats): 76 species in 26 genera in Aust. and NZ, all breeding;

PARDALOTIDAE (pardalotes, scrubwrens, thornbills and allies): 51 species (one extinct) in 15 genera in HANZAB region, all breeding;

PETROICIDAE (A'asian robins): 23 species in eight genera in HANZAB region, all breeding;

ORTHONYCHIDAE (logrunners): two breeding species in one genus in Aust.;

POMATOSTOMIDAE (A'asian babblers): four breeding species in single genus in Aust.;

CINCLOSOMATIDAE (whipbirds, wedgebills, quail-thrushes and jewel-babblers): eight breeding species in two genera in Aust.;

NEOSITTIDAE (sitellas): single species breeding in Aust.;

PACHYCEPHALIDAE (whistlers, shrike-thrushes and allies): 17 species in seven genera in HANZAB region, all breeding;

DICRURIDAE (monarchs, flycatchers, fantails and drongos): 19 species in seven genera in HANZAB region, all breeding;

CAMPEPHAGIDAE (cuckoo-shrikes, trillers and minivets): eight species (one extinct) in two genera in HANZAB region, all breeding;

ORIOLIDAE (Old World orioles and figbirds): three species in two genera in Aust., all breeding;

ARTAMIDAE (woodswallows, butcherbirds and currawongs): 14 species in four genera in HANZAB region, all breeding;

PARADISAEIDAE (birds of paradise): five breeding species in two genera in Aust.;

CORVIDAE (crows and jays): six breeding species in single genus in Aust. and NZ, including one introduced to NZ;

CORCORACIDAE (Aust. mudnesters): two species in two monospecific genera, endemic to Aust.;

CALLAEIDAE (NZ wattlebirds): three species (one extinct) in three monospecific genera, endemic to NZ;

LANIIDAE (shrikes): two species in HANZAB region, one accidental to Prince Edward Is, the other accidental to Christmas I.;

PTILONORHYNCHIDAE (bowerbirds): ten species in seven genera in Aust. (nine species) and NZ (one species), all breeding; Piopio of NZ probably extinct (Heather & Robertson 1997);

ALAUDIDAE (larks): two breeding species in HANZAB region (including one successfully introduced to Aust. and NZ);

MOTACILLIDAE (wagtails and pipits): eight species in two genera in HANZAB region, only two breeding (one on South Georgia), the rest non-breeding visitors or accidentals;

PRUNELLIDAE (accentors): one species successfully introduced to NZ;

PASSERIDAE (Old World sparrows and A'asian finches): 22 species in nine genera (including four successful introductions) in HANZAB region, all breeding;

FRINGILLIDAE (Old World finches): seven species in four genera in HANZAB region, all introduced except one naturally occurring vagrant to South Georgia;

EMBERIZIDAE (buntings, cardinals, tanagers and allies): two successfully introduced species, occurring NZ and Lord Howe I.;

NECTARINIIDAE (sunbirds and spiderhunters): single breeding species in Aust.;

DICAEIDAE (flowerpeckers): single breeding species in Aust.;

HIRUNDINIDAE (swallows and martins): eight species in four genera in HANZAB region, including four breeding species in Aust. and NZ, one non-breeding visitor and three accidentals;

PYCNONOTIDAE (bulbuls): one successfully introduced species in Aust.;

SYLVIIDAE (Old World warblers): 13 species in eight genera in HANZAB region, including ten breeding species (one extinct) in Aust. and NZ, and three accidental to region;

ZOSTEROPIDAE (white-eyes): seven species (one extinct) in single genus in HANZAB region, all breeding;

MUSCICAPIDAE (Old World flycatchers, thrushes and chats): eight species in six genera in HANZAB region, including five breeding species (two introduced), and four accidentals (including one on Prince Edward Is);

STURNIDAE (starlings and mynas): five species in four genera, four breeding in HANZAB region (including two species successfully introduced, and one species now extinct), and one accidental.

The Aust. oscines fall into two distinct clusters, each with at least three major supra-familial lineages (DAB): One cluster is the Passerida, comprising the Muscicapoidea (including true thrushes and allies), Sylvioidea (true warblers and babblers, and swallows, and others), and Passeroidea (including larks, pipits, sunbirds, flowerpeckers and all finches and their allies). The other cluster is the Corvida, which is centred on the Australo-Papuan region (though its origins are not certain) and which also comprises three main lineages: Menuroidea (lyrebirds, scrub-birds, treecreepers and bowerbirds), Meliphagoidea (A'asian wrens, pardalotes, acanthizid warblers, and honeyeaters), and Corvoidea (A'asian robins, logrunners, A'asian babblers, whipbirds and quail-thrushes, sitellas, whistlers, fantails and monarchs, birds of paradise, butcherbirds and woodswallows, cuckoo-shrikes, Old World orioles, crows and mudnesters).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Family 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 holorhinal (Millener 1988), considered schizorhinal 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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Xenicus gilviventris   Rock Wren

Xenicus gilviventris Pelzeln, 1867, *Verh. Zool. Bot. Ges. Wien* 17: 316 — New Zealand = mountains of South Island.

The specific name refers to the yellow wash on the flanks (Latin *gilvus*, pale yellow, and *venter*, *ventris*, the belly).

OTHER ENGLISH NAMES   Fiordland Rock Wren.

MONOTYPIC

FIELD IDENTIFICATION

Length 9.5 cm (see Measurements); wingspan 14–16 cm; weight: male 15.5 g, female 19.5 g. Small ground-dwelling NZ wren with short stumpy tail, short rounded wings, short fine gently decurved bill, and very long legs and toes. Noticeably bigger than Rifleman *Acanthisitta chloris*, with shorter and straighter bill and noticeably longer legs and toes; similar in size and shape to Bush Wren *Xenicus longipes*. Sexes usually differ in adult and juvenile plumages, but more study needed (see Plumages). Adult male mostly olive-green above and pale grey-brown or cream below, with: white supercilium bordered by narrow blackish coronal and eye-stripes; prominent black patch at bend of wing; and strong yellow wash on flanks. Adult female usually duller and browner than male, with less contrasting pattern of head. No seasonal variation. Juvenile very similar to adult; separable by differing bare parts. Slight geographical variation, with adult males becoming brighter green above and brighter yellow on flanks from N to S; sexual dimorphism also said to vary geographically, being more marked in birds of Fiordland NP than elsewhere. Typical, and rather dull, birds of most of range, and brighter green morph of Fiordland NP, SI, described separately below. **Adult male** TYPICAL BIRDS: Top and sides of head and neck, dull olive-brown, grading to slightly darker and browner on forehead and crown, and grading into brighter olive-green on saddle, rump and uppertail-coverts. Bold narrow white supercilium is bordered above by narrower black coronal stripe, and below by black eye-stripe that extends across lores, narrowly below and behind eye (setting off prominent thin white arc round bottom edge of eye) to bottom of rear supercilium. Uppertail, dull olive-brown. Folded wing, olive-green as saddle, with prominent black patch at bend of wing (formed by alula); and black tertials, with prominent broad cream tips to outer webs (which often much reduced with wear). In flight, upperwing appears mostly olive-green with contrasting blackish patch just outside carpal joint. Underbody varies: mostly pale grey-brown, merging to off-white on chin and throat (which in turn merges into dull olive-brown of rest of head), and with bright-yellow wash on rear-flanks; some are paler below, with grey-brown replaced with cream or off-white, giving much less or no contrast with pale chin and throat. Bill, black. Iris, blackish brown. Legs and feet, pink-brown. Green

morphs differ from typical birds by: olive-brown or olive-green areas of head, neck and upperparts distinctly brighter olive-green, and flanks richer yellow. **Adult female** Variation poorly known. Typical birds: given direct comparison, female of breeding pair usually differs from male by: (1) upperparts and sides of head duller and browner (cf. noticeably greener in male); (2) underbody duller and more yellow-brown (cf. grey-brown, cream or off-white in male) with duller and less contrasting yellow wash on flanks; and (3) dark stripes bordering supercilium, duller brown, combining with often duller forepart of supercilium (rarely as clean white as in male) and browner top and sides of head to give duller and less contrasting pattern of head. However, sufficient variation in plumage such that some females inseparable from male in field. Female of green morph poorly known; said to differ from male by having less conspicuous yellow wash on flanks, but more study needed. **Juvenile** Poorly known. At fledging, apparently very similar to adults of respective sexes; best distinguished by bare parts: bill, dark grey with black tip and ridge of culmen; gape and base of lower mandible, orange-yellow, changing to adult colour 8–10 weeks after fledging; legs and feet darker, grey-black, with paler fawn rear-edge of tarsus.

Similar species Unlikely to be mistaken, though in distant or fleeting views beware confusion with other NZ wrens: **Bush Wren** and **Rifleman**; see those texts for details.
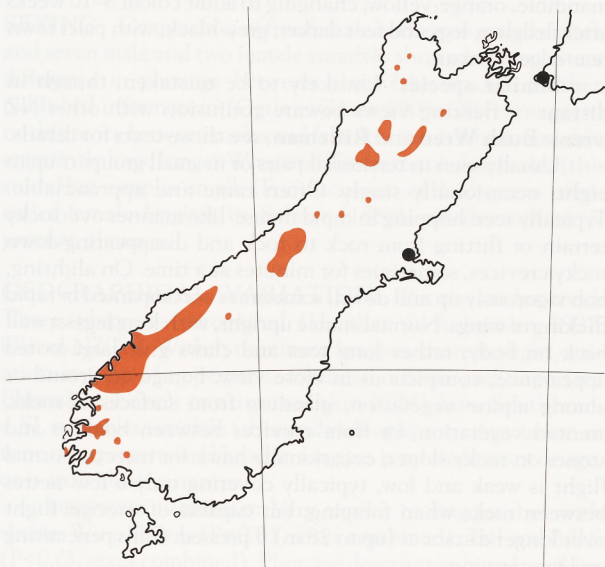
Usually seen in territorial pairs or in small groups of up to eight; occasionally singly. Often tame and approachable. Typically seen hopping in rapid mouse-like manner over rocky terrain or flitting from rock to rock and disappearing down rocky crevices, sometimes for minutes at a time. On alighting, bob vigorously up and down, sometimes accompanied by rapid flicking of wings. Normal stance upright, with long legs set well back on body; rather long toes and claws give large-footed appearance, conspicuous in close view. Forage on ground or among alpine vegetation, gleaning from surfaces of rocks, stunted vegetation, or from crevices between boulders and stones on rocky slopes; occasionally hawk for insects. Normal flight is weak and low, typically covering only a few metres between rocks when foraging; but capable of stronger flight over longer distances (up to 28 m) if pressed. Calls penetrating and far-carrying.

HABITAT Essentially restricted to alpine and subalpine zones. On mountain ranges and in valleys, and along watercourses, above timberline, between c. 920 m and 2900 m asl (mostly 1200–2400 m). Inhabit rocky slopes, including talus, open scree, glacial moraine, fellfields and rocky outcrops, usually vegetated with alpine and subalpine low shrublands. Often in areas covered with snow for much of year (Riney 1953; Jackson 1954; Soper 1961; Child 1970, 1975, 1978; Lambert 1970; Michelsen 1982; Heath 1986, 1989; Oliver; CSN). Vegetation usually consists of shrubs, such as *Olearia*, *Dracophyllum*, *Hebe* and *Hoheria*, interspersed with snow-tussock *Chinochloa*, and with a layer of herbs, such as *Celmisia* and *Ranunculus* (Riney 1953; Jackson 1954; Howard 1957; Child 1978; Heath 1989). Also recorded inhabiting beech *Nothofagus* forest on slopes on West Cape Pen. (Riney 1953). Once seen in a bouldery stream, 250 m asl; and once on driftwood and rocks on beach at Okarito (Child 1970; CSN 32).

Nest among loose rock or debris, on bluffs or rocky ledges of mountains. In detailed study in Fiordland NP, 36 nests found in zone of subalpine scrub on vegetated bluffs or on sloping fellfields, between 945 m and 1345 m asl; all nests close to large patches of vegetation (Heath 1989). See Breeding (Site), Food, and Social Organization (Roosting) for further details of use of habitat.

DISTRIBUTION AND POPULATION Endemic to SI of NZ.

SI Widespread in W, from central Nelson S to Fiordland, mainly on or W of Southern Alps. Rare in Nelson: in Anatoki Ra. and Tasman Mts, and farther S at Moss Pass and Waiau Pass; also rare in Marlborough: round Saxton Saddle and Inland Kaikoura Ra. Widespread in West Coast, and occasional records on e. slopes in Canterbury and Otago. A few scattered records in n. West Coast, with isolated record on Garibaldi Ridge, and found at scattered sites from Buller R. S to Arthurs Pass NP, including Waininihi R. and Harman Pass. Isolated record at L. Coleridge. Farther S, widespread from Mt D'Archaic and Forbes and Mathias Rs, S to near Mt Cook. Also widespread in s. West Coast and w. Southland, from Fox Glacier S to Staircase Saddle, L. Roe and L. Monowhai; farther S, scattered records from West Cape Pen. E to Takitimu Mts (Riney 1953; Child 1970, 1975; NZ Atlas; Oliver; CSN). Also at Mt Rakeahua on Stewart I. (Oliver).

Breeding Throughout range.

Status Near-threatened (Collar *et al.* 1994). **Populations** No estimates. Thought to have been formerly more common in Nelson (Oliver).

THREATS AND HUMAN INTERACTIONS Killed and eaten by introduced mammals, including House Mice and Stoats (Heath 1989). Introduced mammals main threat to species.

MOVEMENTS Virtually unknown. No evidence for any seasonal or large-scale movements. During monthly surveys in subalpine L. Harris Basin, from May 1976 to Apr. 1977, recorded only Oct. and Dec.–Mar.; not recorded in Apr. and when there was heavy snow cover, May–Sept. and Nov., despite considerable search effort, but also not reported from below tree-line (Child 1978). Lack of winter records has led to several suggestions as to behaviour of wintering birds, though no hard evidence for any of them. Suggested that might winter beneath snow, remaining within territories and active, feeding in air spaces between boulders and shrubs (Soper 1963; Child 1978; Michelsen 1982; Heath 1989), though this not proved (*contra* NZRD). Soper (1963) speculated that hibernation more likely than altitudinal movement. Also suggested that may become torpid or enter a torpid-type phase overnight (Child 1978; Michelsen 1982; Heath 1989). Claim that move to lower altitudes and into tree-line in hard weather (Moon & Lockley 1982) not supported by available evidence. In Otira Valley, Arthurs Pass NP, pair recorded in Feb. 1989, after apparent absence of 18 months (CSN 37). Weak flier (Moon 1994 *contra* Moncrieff Undated); seen to fly across gullies c. 30 m wide (Moncrieff Undated).

Banding Four banded 1971–72, none recovered (Robertson 1973).

FOOD Insectivorous; take insects and their larvae, and spiders; occasionally take fruits and seeds from alpine vegetation. **Behaviour** DETAILED STUDY: In Mt Cook NP, Fiordland (Michelsen 1982). Terrestrial and arboreal. SIZE OF FEEDING GROUPS: Usually feed in pairs, though sometimes in small groups of 4–6 (Lambert 1970); at Mt Cook NP, fed in pairs or in small groups. Also reported feeding singly, in pairs and in small flocks of 5–8 birds (Riney 1953). FORAGING SITES: Forage on bare ground and in leaf-litter on ground; from rock surfaces, including faces of rock outcrops, and among interstitial spaces between rock piles; in foliage and along branches of shrubs and stunted herbs; on foliage and, sometimes, at flower-heads of grasses, and among lichens and bryophytes on boulders and damp bluffs; also aerially (Guthrie-Smith 1936; Riney 1953; Turbott 1967; Child 1978; Michelsen 1982; Heath 1986, 1989; Oliver). At Mt Cook NP, prefer foraging on scree fields with rather coarse stone aggregates of >2 cm diameter, close to large, areas of vegetation. In autumn and winter, when soil moist, foraged more on ground than in other feeding stations. In cold windy weather, mostly foraged in sheltered places among large columnar boulders, between rock piles, and beneath subcanopy of subalpine scrub; on warmer sunny N-facing aspects (Michelsen 1982; Heath 1986). During alpine winter, may remain active under snow, possibly feeding in spaces between boulders and bases of scrub (see Movements for discussion). FORAGING METHODS: From study at Mt Cook NP, unless stated. Forage mostly by gleaning from a variety of substrates. SEARCH METHODS: In vegetation, search leaf axils, folds in foliage, seed-heads, mats of roots, bark and leaf-scales; remove loose flaky material

with bill and shake it to dislodge invertebrates. On ground, search for prey on bare ground, among mosses and in matted cushion plants, such as *Raoulia*; birds often jump up and down on mosses or matted cushion plants with feet, breaking them apart, then peck at debris to remove uncovered prey. On rocks, search bare surfaces and crevices or cling to steep faces, usually preferring damper, shadier crevices and interstitial spaces; also often disappear down holes for several minutes and can be heard calling while still out of sight. Also often search spaces between rocks for spiders and other invertebrates. When feeding, maximum horizontal distances of flight between two spots, 20 m. ATTACK METHODS: In Mt Cook NP, obtained food mainly by gleaning; of 114 h of observations of foraging, Dec. 1981 to May 1982: 41.2% of foraging time spent gleaning insects from vegetation; 28.9% gleaning from ground; 17.4% gleaning from bare rocks and from surfaces of lichens on rocks; 0.9% gleaning spiders from ground or snatching them from their webs; 1.9% sallying (including sally-strike both in air and from vegetation); 4.3% dismantling cushion vegetation of mosses and lichens in search for insects; and 5.4% eating fruits of *Coprosma*, *Gaultheria depresa* and Mountain Ribbonwood *Podocarpus nivalis*, and seeds from flower-heads of Bristle Tussock *Rytidosperma setifolium*. Gleaning was the most common method throughout the 6 months of the study, though gleaning from rocks decreased during Mar.–May; sallying was most common during Dec.–Jan., when many insects were present; and fruit-eating began in Dec., increased in Jan.–Feb. when many plants fruiting, and continued during Feb.–Mar. but almost ended in May when most plants no longer had fruit on them. HANDLING OF FOOD: Pecked at berries still attached to plants; some pecked only few times, others eaten completely before bird moved on; occasionally, berries removed with bill and taken some distance away to be eaten. Also use claws to remove berries from bill or hold down on ground while eating them. When feeding on seeds of Bristle Tussock, leant over from adjacent rocks to remove seeds from heads, or bent plant over with foot till it was on ground. When hunting jumping spiders and small insects, birds stalk prey over ground or bare rock and kill it by stabbing pecks; when collecting orb-weaving spiders, prey usually plucked from web as birds darted at them in one hop from ground. When feeding on large wingless Wetas *Pharmacus montanus*, usually take up to 5 min dismembering and handling while eating them; some uneaten portions placed between boulders or in crevices between cushion plants, bird returning between 10 min and several hours later to retrieve stored material. Short-term storage of food observed on other occasions, e.g. some moths stored in crevices between individual plants of moss mats or cushion plants. On other occasions, food taken into holes among rocks, but not known if food left for later use or eaten while in hole. Prey often battered on ground before it is swallowed (Sibson 1974). FEEDING TIMES: At Mt Cook NP, feed intensively in early morning and early afternoon hours; in winter, spend more time foraging at dusk and at dawn. DRINKING: At Mt Cook NP, drink water from small snow-melt pools on surfaces of rock; also from water dripping from rocks or trickling from snow-fields onto scree-fields. Birds not seen to drink from running streams.

Detailed studies In MT COOK NP (observations of items eaten, except insect taxa marked with asterisk which, while not observed being eaten, suggested to be part of diet; Michelsen 1982): **Plants** GYMNOSPERMS: Podocarpaceae: *Podocarpus nivalis* fru. MONOCOTYLEDONS: Poaceae: *Rytidosperma setifolium* sds. DICOTYLEDONS: Ericaceae: *Gaultheria depressa* fru.; Rubiaceae *Coprosma pumila* fru.; *C. pseudocuneata* fru. **Animals** MOLLUSCS:

Gastropods. MITES. SPIDERS: Araneae: Araneidae; Lycosidae; Salticidae. DIPLOPODS. CHILOPODS. INSECTS: Coleoptera: Unident.; Carabidae: *Neocicindella feredayi**; Cerambycidae: *Somatidia**; Coccinellidae: *Coccinella**; Curculionidae; Tenebrionidae; Diptera: Unident.; Syrphidae*; Tipulidae; Hemiptera: *Horouta inconstans**; Cicadellidae: *Arawa salubris**; Cicadidae: *Kikihia angusta**; Lygaeidae: *Hudsona anceps**; Pseudococcidae: *Pseudodantonina**; Lepidoptera: *Orocrambus aethonellus**; Neuroptera: Hemerobiidae: *Micromus tasmaniae**. Orthoptera: Gryllidae; Stenopelmatidae: *Hemideina maori*; *Pharmacus montanus*; Tettigoniidae: *Gonocephalus semivittatum*.

In FIORDLAND NP (contents of seven regurgitated pellets; Heath 1989): **Animals** SPIDERS. CHILOPODS. INSECTS: Coleoptera: Unident.; Curculionidae; Lepidoptera: larv.; Tricoptera: larv.

Other records Plants Fruit[5]. **Animals** SPIDERS: Araneae[6]. INSECTS[1,2,4,6]: Coleoptera: Unident. beetles[2]; Lepidoptera: larv.[7], ads[1]; Arctiidae: *Phaos huttoni*[2]; Orthoptera: Acrididae: *Sigaus australis*[3]. **Other matter** Food scraps[2].

REFERENCES: [1] Riney 1953; [2] Turbott 1967; [3] Sibson 1974; [4] Child 1978; [5] Falla *et al.* 1981; [6] Oliver; [7] CSN 1.

Young Fed mainly on insects; large items are broken into smaller pieces before being fed to young (Turbott 1967); parents sometimes leave nests with indigestible parts of insects, such as wings or legs, in bill (Soper 1963). In Fiordland NP, parents shared feeding of nestlings equally; brought 3–25 items/h (n=133.9 h obs. at 19 nests); more food delivered between dawn and mid-morning (mean of 16 visits/h) and during early afternoon (12 visit/h) than during other periods of day (Heath 1989). In Fiordland NP, stomach contents of younger nestlings contained significantly more small flies and soft caterpillars than those of older nestlings (see below).

In FIORDLAND NP (stomach contents of eight nestlings, direct observations of items fed to nestlings, and items from artificial gapes placed in two nests [simulated open mouths placed among nestlings]; Heath 1989): **Plants** DICOTYLEDONS: Ericaceae: *Gaultheria depressa* fru.; Rubiaceae *Coprosma* fru. **Animals** ANNELIDS. SPIDERS: Araneidae; Salticidae. AMPHIPODS. CHILOPODS. INSECTS: Coleoptera: ads, larv.; Diptera: Syrphidae; Tipulidae; Hemiptera; Lepidoptera: ads, larv.; *Metacrias erichrysa* larv. (some nests received as many as 50 of these caterpillars in 1 h brought by two adults); Geometridae: *Pseudocoremia*.

Other food offered to young: **Animals** ANNELIDS: Worm (Guthrie-Smith 1936). SPIDERS (Guthrie-Smith 1936). INSECTS: Ads (Turbott 1967), larv. (Soper 1963); Coleoptera: beetles (Soper 1963); Lepidoptera: ads, larv. (Soper 1963); Odonata (Turbott 1967); Orthoptera: grasshoppers (Guthrie-Smith 1936; Soper 1963).

SOCIAL ORGANIZATION Well known from studies of biology in Fiordland: of feeding and habitat use over 6 months (Michelsen 1982), and of breeding biology over two breeding seasons using banded birds (Heath 1986, 1989 [the latter used when there were discrepancies between these two publications]). Usually found in territorial pairs, but at times in small groups of up to eight, probably family groups; less often singly (Riney 1953; Soper 1963; Lambert 1970; Heath 1989). Unusually large concentration of 32 within *c*. 100 m in Mar. (Soper 1963); 4–5 groups within *c*. 50 m of each other in Apr. (Riney 1953). Usually, members of a pair stay fairly close together (Child 1978; Michelsen 1982; Heath 1989). Feed as pairs or groups or, less often, as individuals; tend to be more solitary when feeding as autumn approaches (Michelsen 1982), see below.

Bonds Monogamous; usually stay paired throughout year (Heath 1989). Juveniles establish territories and find mates by end of summer in which they fledge; usually pair with others that fledged in same season; one adult male left his mate at end of breeding season and paired with his female offspring, staying with her in next breeding season, by which time abandoned female had found a new mate. Courtship completed (or largely so) by autumn, and most of population ready to breed as soon as climatic conditions allow at start of next season (Heath 1989); any further courtship occurs in late winter, so that as soon as winter snows start thawing, birds begin to build nests (Heath 1986). There seems to be as little ritualized courtship activities as possible in older birds (Heath 1989). High degree of parental co-operation makes full use of short breeding season: female selects nest-site but both sexes take equal share of nest-building, incubation, brooding and feeding of young. Do not show any co-operative breeding, cf. Rifleman (Heath 1989). Heath (1989) states most young have dispersed 2–4 weeks after fledging: of 75 banded juveniles, 68% were resighted 50–500 m from nests and 7% stayed <50 m from nest. However, Heath (1986) states young stay within or close to family groups till time of post-juvenile moult, c. 3 months after hatching; by this time 60% of young have found mates and have moved away from territory of their parents.

Breeding dispersion Nest solitarily; a pair can begin a few nests within 5–10 m of each other before choosing one (Heath 1989). **Territories** Territories maintained year-round, even in winter, and alter little between seasons; maintained by pairs (Heath 1986, 1989); rarely, solitary birds hold territories (Michelsen 1982). When nests being built, territorial males and females appear equally aggressive to intruders, but after nest built and before laying, female appears to spend no time in disputes (Heath 1989). After fledging, juveniles establish territories by end of summer, and much agonistic behaviour at this time, with disputes between juveniles, or between juveniles and adults (including own parents). Tendency for adults to defend territories successfully. By end of autumn, there can be a few further changes to territorial boundaries (Heath 1989). Adult territories 1.4 ha (0.6; 0.6–4.2) in size, with most having 20–30% of area covered with bush, scrub or dense prostrate vegetation for feeding, and with varying areas of scree or rock-fall (Heath 1989); often seem to contain a source of water (Michelsen 1982). Smaller territories, of 1–2 ha, can have up to 80% vegetative cover; in large territories, up to 10 ha, vegetation sparser. Territories of first-year birds often comprise sub-optimal habitat, and can be comparatively large, with birds required to cover greater distances to feed (Heath 1986). Claim that one pair in Crow Valley, Arthurs Pass, maintained territory with radius of c. 23 m in Feb.–Mar. 1957 (CSN 7), seems too small.

Roosting At night; in deep holes under rocks, mostly in elevated sites in territory. Roosts often have very narrow entrance to chamber hidden deep under rocks; appear to be dry and free of draughts; often have platform covered with grass, such as *Rytidosperma* or *Poa*, which is carried to roost in bills and platform constructed. Food sometimes taken into holes. Pair often appears to have up to three sites within territory that are used as roosts or as short-term sheltering for up to 3 h in daytime. In strong winds, birds may go to roosts, sit on sheltered ledges, or squat closely against rock-faces, with feathers ruffled; also shelter in roosts in driving rain. Deep narrow roosting holes may help birds to avoid predators (Michelsen 1982; Heath 1986). Also reported to roost on limb of shrub in thick undergrowth (Riney 1953). During incubation and when young being brooded, only female roosts in nest at night. For 10 days

or so after fledging, young often return to nest to roost at night (Heath 1989). Birds often active at first light and at twilight (Heath 1989), particularly as winter approaches (Michelsen 1982). For daily time-budgets, see Heath (1989).

SOCIAL BEHAVIOUR Well known from studies of biology in Fiordland: of feeding and habitat use over 6 months (Michelsen 1982), and of breeding biology over two breeding seasons using banded birds (Heath 1986, 1989 [the latter used when there were discrepancies between these two publications]). Usually detected by call (Child 1978; Michelsen 1982); can be difficult to see (Child 1978), particularly during bad weather (Riney 1953). Easily followed as often noisy and conspicuous when feeding, and flight is weak (Michelsen 1982); can be curious and bold, approaching to 5–6 m (Oliver); attracted to any noise or disturbance within territory, including imitations of whistles; become used to observers and can be watched from very close quarters (Riney 1953; Michelsen 1982). Birds perform variety of bobbing and bowing movements in different circumstances (see below), including on landing and when perched (Guthrie-Smith 1925; Riney 1953; Soper 1961, 1963; Oliver). BOBBING: Up-and-down movement, with body kept more or less at same angle to ground; seen on landing but also when perched. BOWING: Lean forward, pause and then straighten up to almost vertical position, with legs set so far back on body that they appear very delicately balanced when leaning forward (Soper 1961). **Flock behaviour** All birds give simple call as they feed (which call not stated) with pairs or members of groups calling more than solitary birds; less vocal when preening or bathing. When a foraging bird is out of sight of mate or rest of group, it usually stops calling, looks up and then calls; then hops and calls again; when it hears a response, it resumes foraging. In autumn, when birds start to feed more often on their own, they call less, and social behaviour seems less important (Michelsen 1982). **Comfort behaviour** Preen often during daytime: draw feathers between mandibles, starting with plumage on back and wings; preening seldom done in groups (Michelsen 1982). For 3 days after laying, male preens much; between fourth and sixth days, female also preens much, for 3.3h/day (1.8–4.1; 22 females); female also bathes often: inundates herself with water under tiny falls of water in streams, or immerses herself in puddles of water on large rocks (Heath 1989). Dust-bathing not seen (Michelsen 1982; Heath 1989).

Agonistic behaviour Much agonistic behaviour occurs while territories being established. Disputes involving adults are ritualized, with much calling and Bobbing from a distance, with little physical contact; those involving juveniles often included vigorous physical interactions (Heath 1989). **Alarm** (Some of these behaviours could be to protect nests or eggs; also see Parental anti-predator strategies). When approached by people, adults often Bob and give single Long Squeaks, either in unison with Bob or alternating calls with Bobs; often call and hop towards person (Michelsen 1982). When frightened or alarmed, also hide among rocks (Buller 1888); one bird flushed from a tussock, flew c. 1 m or more into air towards nearby scrub but landed short and immediately sprang into air again and into scrub (Riney 1953). Once handled, some adults remain nervous in presence of people (Heath 1989).

Sexual behaviour After female has selected nest-site, she initiates building of nest by bringing a token piece of material to male; she does this with much Bobbing and wing-flicking, and often inclines head to side as she moves and makes soliciting calls; female either places token on ground in front of

male or flies away with it and pushes it into a crevice or the like, at nest-site; after this, she calls much and extends and vibrates wings; may keep material in bill and squat beside nest-site with wings spread and vibrating; after squatting, one female rubbed abdomen from side to side. Extension and vibration of wings repeated many times, more rapidly if male approaches; if male not attracted to site by these activities, female often leaves token projecting conspicuously from site and returns to male to perform further wing-flicking, Bobbing and calling; female repeats activities till male brings material to nest-site. Both birds then build nest with few further displays, though approaching bird may call to mate to accept material. Five times, nest-site was not altered after this preparatory phase, while six times birds chose another site at least once (Heath 1989). Courtship feeding occurs during nest-choosing phase (see below). **Greeting** Members of pair call to each other as they feed, sometimes antiphonally (Michelsen 1982). During incubation, when birds change over, incoming bird gives soft single call as it approaches nest, and outgoing bird usually leaves nest before incoming bird arrives. However, call often ignored and incoming bird joins incubating bird in nest; both birds then give short chittering calls for a short time before one, not necessarily the incubating bird, leaves nest; incubating bird particularly reluctant to leave nest during cold, snowy or windy weather. When moving to and from nest, each sex has its own flight-paths, with incoming and outgoing paths usually different (Heath 1989). **Courtship feeding** Occurs throughout breeding season, and probably strengthens bond; male feeds female, making a significant contribution to her diet at all stages of breeding; female will also feed male. During nest-choosing phase, both sexes feed each other, with each bird receiving 6.7 items/h (29 h observation of 11 pairs). During nest-building, both birds continue to courtship-feed; male often calls as he approaches with food for female working inside nest; male fed female 7.8 items/h (4.08 h of observations/pair, for 11 pairs); when wall of nest was being built, in three of 11 pairs, males brought all food eaten by females, and only after walls built did females leave nests to forage for themselves, often feeding males upon their return. Period between completion of nest and laying characterized by slowing in activities of female, who spends increasingly longer times preening and resting; at this time, male brought 5.2 items/h to female; female forages in a more restricted area near nest. During laying, male brought 9.2 items/h (84.5 h of observation of 13 pairs) to female, whether she was incubating or foraging for herself. After laying, for first 3 days, male spends most of his time foraging; male fed 5.1 items/h (n=*c.* 90 h of 13 pairs) to incubating female. During incubation, food often brought to whichever parent sitting, and both males and females accept food at entrance to nest (Heath 1989). **Copulation** Eight of ten attempted copulations occurred after nest was finished and before laying, with male feeding female before and after copulation; seven of these occurred 1–3 days after nest built; seen only once during nest-building phase. Male balances on female's back by fluttering wings and gripping extended wings of female with his long claws; female lowers body, stretches out head and neck, and gives *chut-chut-chut* call as male pushes her tail to one side to make cloacal contact. Mounting lasts <15 s and usually repeated 3–4 times over several minutes; between mountings, male flutters on ground beside female, vibrating extended wings and giving *chut-chut-chut* call (Heath 1989). **Relations within family groups** Both sexes take equal share of nest-building, incubation, brooding and feeding of young. Near hatching, Piping from within eggs causes change in behaviour of adults: both adults leave nest but stay nearby,
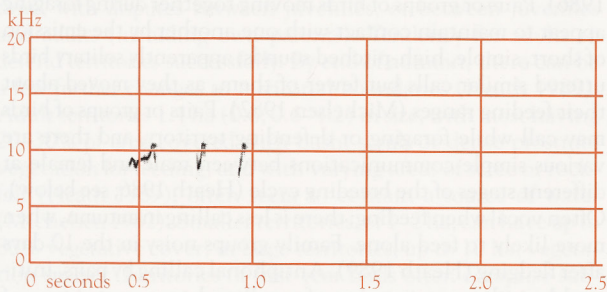
making brief visits to nest; they stop feeding, utter a twittering call among themselves, and Bob and wing-flick much (Heath 1989). Nestlings beg with weak rasping cry (Guthrie-Smith 1936) or high-pitched peeping (Heath 1989). One or two days before fledging, young extend heads through entrance of nest, jostling each other and calling often. Young usually fledge in morning; fledging takes *c.* 1 h and is noisy and conspicuous; young enticed from nest by adults, who stay some distance from nest giving soliciting calls and offering food; throughout process, parents feed each other and their young. Young stay in noisy family groups for 10 days, and then start to move away from group for increasing periods when foraging, preening and other activities. Young can provide *c.* 40% of their own food as soon as they fledge; and independent within 14–21 days of fledging (Heath 1989). For further details of dispersion of fledgelings, see Social Organization (Bonds). **Anti-predator responses of young** When handled, young near fledging extend and vibrate wings, and try to fly (Heath 1989). **Parental anti-predator strategies** In response to people: both male and female may flit about and appear distressed (Howard 1957); when eggs or young handled, some adults continue to bring food to nest, and others stay within 1 m or so and immediately resume incubation or feeding when person leaves (Heath 1989); also see Alarm above.

VOICE Quite well known. Study, including sonagrams, in Fiordland by Michelsen (1982); some additional information in later publications by same author (Heath 1986, 1989). Usually heard before seen (Child 1978; Michelsen 1982). Often heard from rock piles (Soper 1976; Michelsen 1982). Calls are penetrating and may carry for some distance (Falla *et al.* 1981; Michelsen 1982), the very high pitch (8–12 kHz) carrying well in the alpine environment (Michelsen 1982; Heath 1986). Repertoire is a small series of simple calls (Heath 1986). Pairs or groups of birds moving together during foraging appear to maintain contact with one another by the emission of short, simple, high-pitched sounds; apparently solitary birds uttered similar calls but fewer of them, as they moved about their feeding ranges (Michelsen 1982). Pairs or groups of birds may call while foraging or defending territory, and there are various simple communications between male and female at different stages of the breeding cycle (Heath 1986; see below). Often vocal when feeding; there is less calling in autumn, when more likely to feed alone. Family groups noisy in the 10 days after fledging (Heath 1989). Antiphonal calling by pairs, initiated by either sex, consists of a call-and-answer sequence of Three-note Calls repeated 10–12 times, with gaps of 0.75–1.0 s between end of call of one bird and beginning of reply; males and females do not always call in the same way, but sexes cannot be differentiated by their calls, even after analysis of sonagrams; the full repertoire of calls appears to be given by both sexes (Michelsen 1982). SIMILAR SPECIES: Calls more musical and not so rapidly repeated as those of Rifleman (Williams 1963; Soper 1976; Michelsen 1982). Said that calls might be confused with those of Richard's Pipit *Anthus novaeseelandiae* but *zit* call of Rock Wren much softer than superficially similar *scree* call of Pipit.

Adult Circumstances of use of most calls not described. THREE-NOTE CALL: Three thin high-pitched notes, the first accentuated (Falla *et al.* 1981; Michelsen 1982); described as *tzee-tzit-tzit*. A typical call comprises two initial squeaks, followed by a long note and two final squeaks, the initial squeaks occurring so close to each other and to the long note (*c.* 0.25 s from the start of the first squeak to the end of the long

note) that the gaps are inaudible, so that, to human ears, the initial squeaks and long note sound like one note, and the whole call like three notes; call varies, and one or both initial squeaks may be omitted, as may one final squeak (Michelsen 1982). Sonagram A shows a long note followed by two squeaks. ZIPT CALL: Characteristic short single-note *zipt* (Soper 1976; Michelsen 1982). Zit Creek and Zit Saddle in Kaniere, Westland, NZ, named after this call (Michelsen 1982). LONG SQUEAK: Single long squeak given when a person first seen (Michelsen 1982). PIPE: Thin pipe (Falla *et al.* 1981; Michelsen 1982). Heard only occasionally, particularly in evening (Michelsen 1982). **Other calls** All from Heath (1989). High-pitched calls, not further described, made by female, apparently attempting to initiate construction of nest, while bringing nest-building material to male. Three different calls, not further described, said to be given during construction of nest: one from approaching bird to call mate from nest to accept material; another to call mate out to join the search for material; and third used to call mate from nest when food being brought. High-pitched staccato *chut-chut-chut*, given by both sexes during copulation. Soft high-pitched single call given by incoming bird at change-over during incubation; when incubating bird failed to leave nest after this call was uttered, incoming bird entered nest where both birds gave chittering calls. Twittering call given by both adults when an egg was pipping. Calls, not described, given by adults to entice young from nest when fledging.

Young From Heath (1989) unless stated. Chick still chipping its way out of egg utters weak high-pitched single piping note. Nestling utters weak high-pitched peeping, with bill open wide, assumed to be a begging call. Begging nestlings also described as giving faint, almost inaudible, rasp, 'like faint winding of a lady's wrist-watch' (Guthrie-Smith 1936). Nestling calls loudly if handled. Very vocal in 48 h or so before and after fledging, particularly at the actual time of fledging.

A E. Samuelson; Homer Tunnel, Fiordland NP, SI, NZ; Dec. 1984; P106

BREEDING Detailed study of breeding biology in 1983–84 and 1984–85 in Fiordland NP, SI (Heath 1989), on which account based unless otherwise stated. Breed in simple pairs.

Season In Fiordland NP: building, mid-Sept. to early Nov.; laying, mid-Oct. to late Nov.; hatching, mid-Nov. to late Dec.; fledging, early Dec. to early Jan. In one season, 1-year-old females laid significantly later than older females: mean date 2 Nov. (9.82 days; 16 Oct.–16 Nov.; n=7 nests) and 23 Oct. (8.84 days; 11 Oct.–6 Nov.; n=13 nests) respectively. For one pair that re-laid after failure of first nest: laying, late Dec.; fledging, mid-Feb. Elsewhere: eggs, late Sept. (n=1); young, mid-Nov. to Dec. (n=3); fledged young, mid-Dec. and early Jan. (n=2) (Howard 1957; Soper 1961; Oliver; CSN 21, 29).

Site In sheltered crevice or cavity, among rocks, on bluffs or rocky ledges of mountains; often in sheltered crevice high on bluff. Mostly concealed beneath scrub, but also beneath large exposed roots or deep in soft moss or in soil (mud) of earthen banks (Hutton & Drummond 1904; Mathews 1930; Howard 1957; Soper 1961; Heath 1986, 1989; Oliver). Once nested in artificial rock wall (Soper 1961). In Fiordland NP, nest in holes in ground with slope >20°; usually in elevated bluff or bank; 36 nests found in zone of subalpine scrub on vegetated bluffs or on sloping fellfields, between 945 m and 1345 m asl; all nests close to large patches of vegetation; most nests (19, 52.8%) in soft clay or mud bank, 11 (30.6%) in soil of vegetated ledge of bluff or rock-face, four (11.1%) beneath large exposed roots, and two (5.6%) in soil-filled crevice between rocks; nest may be lodged in excavation in soil or woven directly into crevice or vegetation. Most (91%; n=33) nests built in sites that faced away from prevailing wind. Female usually selects site. Pairs monitored over two consecutive seasons at Fiordland NP built nests in sites very similar to those they had built in previously and within 50 m of previous nests, e.g. if a hole in the bank had been used the season before, another was used in the second year; similarly, nests beneath roots were chosen for two years in successsion. Do not re-use same site as previous year, or excavation from previous year. In two nests with young, House Mice had built a nest in woven grass wall.

Nest, Materials Build nest in a chamber at end of a short excavated tunnel. Build well-insulated spherical or cigar-shaped nests, with a tiny circular entrance hole in end or in side wall of nest. Of 36 nests, 13 (36%) broadly cigar-shaped, with entrance at one end; 6 (17%) more or less spherical; remaining 17 (47%) oval, with entrance in side and towards one end. Entrance to tunnel usually faces away from prevailing winds. Excavation begins with female removing soil or mud by flying against slope or bank in short fluttering assults from a few metres away and pecking at ground with partly open bill; aim at different spot with each peck till enough material removed to give a foothold. After this, both sexes work together, stabbing and pecking flights continuing, but pair usually take turns at digging by chiselling away with bill and scratching and raking out material with claws; male gradually takes over, especially after excavation of nest-chamber has begun. Pairs work non-stop till a hole 10–15 cm deep is dug. Excavation often finished in 1–2 h, though some pairs take nearly all day, alternating excavation with other activities. When excavation complete, pair start bringing nesting material to site, either on same day or on following day. Material of nest-wall mostly woven pieces of grass and occasionally sedge, but also fine soft sticks, leaves, leaf skeletons, bark, fern scales and fibre, spider web and animal hair; no cementing material used. Material of wall of nest laid down in a parallel or concentric arrangement, and seldom interwoven. Some nests may be waterproofed with claddings of dense moss. Inner layer of nest-wall shaped into a cup-like depression which is lined with feathers and sometimes small amounts of soft filamentous lichen and moss; lining usually contains 10–100 feathers, but up to 800 feathers (Howard 1957; Soper 1961; Heath 1986, 1989; Oliver). Both birds often work inside hole at once; later, one bird, usually female, works inside while other collects material. Male often brings food to female in nest (see Courtship feeding). In three instances, during initial construction, male supplied all food eaten by female; later, during lining of nest, female left nest to forage, often bringing food back for male. Both sexes build; proportion of time spent building divided approximately equally between sexes, though varies between pairs. Female initiates construction by selecting a token piece of material and bringing it to male (see Social Behaviour: Sexual behaviour). During con-

struction of nest-wall, each bird makes up to 50 trips/h with material, mostly collected within 50 m of nest; material usually collected from ground but sometimes plucked from banks or from branches or roots of shrubs or tussocks; up to three pieces of grass may be carried in bill in one trip. Search farther afield for lining material. Do not dismantle old nests or use material from partly finished nests. Mean time taken to build nest, 6.5 days (2.22; 3.0–9.5; 11); for 11 pairs observed for 12 h each, proportion of time spent building at different times of day varied from 4.8% in early morning to 44.7% in middle of day, and <1% near dusk. Lining of feathers constantly renewed; soiled or damaged feathers discarded, though occasionally feathers are removed from nest, teased out and air-dried, then returned to nest. Add material to nest during incubation; one pair added up to 50 items in a 12-h period during early incubation. Often build two or three incomplete nests before finishing nest for laying; one pair began seven nests. Temperature inside nests may be maintained to up to 15 °C above ambient air temperature (Heath 1986). MEASUREMENTS (cm): Horizontal and vertical circumference of one nest, 38.1 and 35.6 respectively (Howard 1957); thickness of nest-wall, 6–10 (Heath 1989). At Fiordland NP, diameter of spherical nests, 15–25; for oval or cigar-shaped nests: long axis, 20–28, width, 12–20. Diameter of entrance hole, c. 2.5 (n=2) (Howard 1957; Oliver); usually 3–4 cm, but adults tend to adjust aperture as they go in and out (Heath 1989). Mean dry weight of nest, 40.6 g (8.51; 20.1–83.9; 25).

Eggs Oval; smooth; white or creamy white; very pale pink when freshly laid, becoming opaque and chalky white and shiny when 5–6 days old (Heath 1989; Oliver). MEASUREMENTS: In Fiordland NP, 20.3 (0.74; 18.8–21.8; 83) × 15.5 (0.25; 15.0–16.1); 20.5 × 15; 19.4 × 15.4 (Oliver). WEIGHT: 2.55 (0.59; 1.99–2.87; 83); equivalent to c. 13% of weight of adult female. Mean weight on day before hatching, 1.88 (0.07; 1.63–1.97; 24); mean loss of weight during incubation, 0.67 g, or 26.1% fresh weight.

Clutch-size Mean 3.1 (0.79; 1–5; 36). Mean clutch-size for first-year females (2.8 [0.88; 7]), significantly smaller than older females (3.2 [0.76; 13]).

Laying Single-brooded but will re-lay if nests fail early in season (Heath 1986, 1989). Eggs laid at intervals of 48 h. For 42 eggs in 13 nests, 54% laid at night, and 31% between dawn and mid-morning. Interval between completion of nest and day before first egg laid, 5.4 days (2.24; 2–10; 11); interval significantly shorter for pairs building after 4 Nov. One pair that re-nested laid 8 days after start of building. Male brings food to female during laying (Heath 1986, 1989).

Incubation Both sexes incubate. Females with incomplete clutches incubated for 12–23% of daytime, and almost constantly between dusk and dawn; male does not incubate till clutch complete. Full incubation begins when clutch complete; overall, clutch incubated for 77.2% of daytime (75–80; n=134.2 h observation); in first 3 days, female attended nest for c. 75% of total incubation time; from 4–6 days, female spends only c. 20% of daylight time incubating; after 5–6 days, both sexes share incubation approximately equally; mean length of bout of incubation, 36.5 min (6.0–54.3; 134.2 h of observation). At change-over, approaching bird emits a high-pitched call; sitting bird usually leaves nest before approaching bird takes over; during cold or windy weather, incubating bird may be reluctant to leave, and occasionally both birds in nest together. At two nests checked between 23:00 and 01:00, female was incubating (Heath 1986); see Social Behaviour for more details. Sitting bird will often pull lining material across entrance to block hole (Heath 1989).

INCUBATION PERIOD: 19.6 days (0.35; 18.0–22.3; 22 nests). Eggs usually hatch asynchronously, and tend to hatch in laying order; clutch hatches on average 1.6 days apart (1–3; no N). Adults remove eggshells from nest immediately after nestling emerged; female sometimes breaks up eggshells and swallows them.

Young Altricial, nidicolous. Naked at hatching, and eyes are closed; do not develop natal down (Heath 1989), though Howard (1957) and Soper (1961) mention a few tufts of dark down at hatching, and Soper (1961) describes young at least 8 days old as covered in creamy-buff down. At 2–3 days, eyes opened to narrow slits; at 4–6 days, feathers in pin appear; at 8 days, feather-tracts well defined, with pin-feathers 2–5 mm long over most parts of body, and eyes partly or sometimes fully open; at 10–12 days, eyes fully open, and feathers have emerged from pins on sterno-abdominal area and dorsum; at 13–14 days, feathers emerged from pins over most of body, including remiges; at 14–16 days, humeral, femoral, pectoral and pelvic feathers 4–7 mm long. **Growth** Approximate weight increase for males and females respectively (estimated from growth-curve in Heath 1989): at 5 days, 2.6 and 3.0; at 10 days, 8.6 and 9.6; at 15 days, 17.5 and 21.0; at 20 days, 20.6 and 22.8; at fledging, 20.2 and 22.0. **Parental care, Role of sexes** Both sexes feed young, about equally. In Fiordland NP, young fed at rate of 3–25 items/h; rate varies with time of day and between days (see Food: Young) (Heath 1989). Interval between feeding visits also given as 1.5–90 min (Soper 1961; Heath 1986). For 2 days, observation at a nest with naked young: interval between visits to nest, 30–210 min, though not all visits were with food; young regurgitated undigested material; soft downy feathers taken into nest every third or fourth visit; no faecal sacs seen to be removed during this time (but see below) (Soper 1961). Both sexes brood young; only female broods at night. During first third of nestling period, young brooded for an average 63% of observed time (n=19.2 h observations) with female brooding for 74% of total time spent brooding. During second third, young brooded for 40–45% of observed time (n=21.6 h) and female did 61% of brooding. During final third, young brooded for an average 37.9% (4.3; 30–49; 20 h) of observed time, and difference in time invested between sexes not significant (Heath 1989). Nestlings often covered with the feathers that line nest (Heath 1989). One small young found at entrance of a nest, covered by a feather (Howard 1957). Adults remove faecal sacs; fly off and either drop them from the air, or fly to a site some distance from nest and deposit them, usually on a rock (Heath 1989); also said to be carried away and eaten (Soper 1961). Nests can become damp and mouldy during nestling period; soiled material and rotting vegetable detritus usually removed from nest by adults, who continue to add fresh feathers and dry lichen filaments to lining material.

Fledging to independence FLEDGING PERIOD: 24 days (1.11; 21–26; 33 broods). Young usually fledge in morning. One brood fledged synchronously; young enticed from nest by soliciting calls and food offerings from both adults; fledging took no more than 1 h and young were fed throughout by adults. Within a few hours of leaving nest, fledgelings move round, feed themselves and make their first tentative flights. Fledgelings receive c. 60% of food from parents during first 1–4 days after leaving nest; remain in noisy family groups for 10 days and often return to nest at night; after 10 days, spend more time away from family group; by 2–4 weeks, have left family groups and dispersed (but see Social Organization: Bonds).

Success Of 106 eggs, 91 (85.8%) hatched; 71 (67.0%) fledged; of the eggs that failed to hatch, four were infertile, two

were addled, two taken by Stoats, and seven taken by House Mice; 14 nestlings from five nests taken by Stoats. A nest containing three young, 4–5 days old, was empty 3 days later (Howard 1957). No other information.

PLUMAGES   Prepared by J.S. Matthew. Naked at hatching; see Breeding for development of plumage. Fledge in juvenile plumage, then undergo fairly rapid post-juvenile (first pre-basic) moult, 10–16 weeks after fledging; not known if post-juvenile moult partial or complete. Resultant first basic plumage either adult if post-juvenile moult complete, or adult-like 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; Heath (1989) notes seasonal variation in adult plumage but gives no details. Adults shed skin on legs during post-breeding moult (Heath 1989). Sexes differ slightly. Plumage description based on skins of three adult males from Nelson region and Arthurs Pass (e. West Coast, w. Canterbury), two adult females from Nelson, two adult females from unknown localities, and one from Arthurs Pass labelled as juvenile male (CM, NMNZ). As not known if a first immature plumage exists, possible that the adult descriptions below also apply to first immatures.

Adult male   (Second and subsequent basic, possibly also first basic). HEAD AND NECK: Forehead, brownish (c28), grading to greyish olive (43) posteriorly. Crown, nape and hindneck, olive-brown (c30) or grey-olive (43). Sides of neck, olive (c50) or dull straw-yellow (c56). Narrow coronal stripes, black (89), bordering supercilium. Supercilium, white, grading to pale yellow (157) posteriorly; broader behind than in front of eye and well demarcated from coronal stripe and eye-stripe below. Lores and feathers extending narrowly below and behind eye, black-brown (119), combining to form narrow eye-stripe. Eye-ring, white below and above eye, forming distinct white arc below eye, black-brown (119) in front of and behind eye. Malar area, chin and throat, off-white (ne) or dull straw-yellow (c56). Short black (89) pinnate rictal bristles protrude from lower lores, each with at least bifid tips. UPPERPARTS: Mantle, back and scapulars, grey-olive (c43) or dark olive (c46). Rump and uppertail-coverts, olive (c51), dark olive (46) or dark green (c260). All feathers of upperparts have concealed dark-grey (83) bases. UNDERPARTS: Breast, belly and undertail-coverts vary from light greyish brown (119D) to cream (c92) or off-white (ne), contrasting with paler throat. Flanks, off-white (ne) or cream (c92) anteriorly, grading to yellow (c55) posteriorly. Feathers of thighs, light brown (223D) or dull olive (c51). Axillaries, pale yellow (c157). All feathers of underparts have concealed dark-grey (83) bases. UPPERTAIL: Grey-olive (43) with yellow-olive (52) fringe to rectrices. Shafts of rectrices, dark brown (121). UNDERTAIL: Brownish grey (c79) with dull yellow-olive (c52) fringe to rectrices. Shafts, off-white (ne). UPPERWING: Marginal and median secondary coverts, light grey-brown (119C) with broad olive (51, 150) or yellow-brown (c123B) fringes. Greater secondary coverts, brownish grey (79) with olive (51) fringes. Marginal and median primary coverts, dark brown (121) or black-brown (119) with narrow olive (51) fringes. Greater primary coverts, black-brown (119) or dark brown (121). Feathers of alula, black-brown (119), forming distinct patch near carpal joint. Primaries, dark brown (121) with olive (51, 150) outer edge, which, on outer primaries grades to off-white (ne) distally; inner edge cream (54). Secondaries and tertials similar to primaries but with narrow cream (c54) fringe at tips when fresh; tertials and innermost second-

ary broadly tipped cream (c54), buff (124) or pale yellow (157) on outer web, and with dark-green (260) rest of outer web. Shaft of remiges, light brown (239). Outer webs of remiges combine to form olive (51, 150) panel on folded wing. UNDERWING: All marginal and median coverts, pale yellow (157), merging to brown (28) at bases; marginal coverts at carpal joint show as pale-yellow (157) patch. Greater secondary coverts, white with pale-yellow (157) fringes. Greater primary coverts, light grey-brown (119D) with narrow pale-yellow (157) fringes. Remiges patterned as upper surface, but ground-colour, brownish grey (c79); shafts, off-white (ne). Outer web of remiges concealed on normally spread wing.

Adult female   (Second and subsequent basic, possibly also first basic).   Extent of differences between sexes may vary geographically. Ogilvie-Grant (1905) suggested no difference between adult females and adult males. Heath (1989) states that adult females in Fiordland NP (Southland) have less conspicuous yellow on flanks compared with adult males. In Mt Cook NP (central West Coast), adult females have browner upperparts and more distinct cream tips to secondaries (probably referring to tertials) compared with adult males from same area (Michelsen 1982). Soper (1961) states females from Homer Tunnel, n. Fiordland NP, have olive-brown upperparts, pale-buff lower eye-ring, dark-brown alula and fawn eye-stripe. Of four skins labelled as female (CM, NMNZ: two from Nelson and two from unknown location), two do not differ from four males collected from Nelson and Arthurs Pass (w. Canterbury, e. West Coast); two females have dark-brown (121) lores and feathers below and behind eye, combining to form dark-brown (121) eye-stripe that contrasts less with white supercilium compared with adult males. One of the female skins (CM) from unknown location has yellow (55) supercilium that grades to buff (124) above lores, and buff (124) underparts, malar area, chin and throat.

Nestling   Data on development of young equivocal; see Breeding: Young for some details of development of young. Male nestlings at least 13 days old have olive-green feathers emerging on underparts; female nestlings at least 13 days old have dull-brown feathers emerging on underparts (Heath 1989).

Juvenile   Little information. One (AV 241) from Arthurs Pass and labelled as juvenile male (CM) not different from adult males above. Heath (1989) states that 10–15 days after fledging, juveniles virtually indistinguishable from adults, but have vinous colour on head, neck and breast. Juvenile males from Fiordland NP apparently greener on upperparts compared with juvenile females from same area (Heath 1989). Juvenile female said to be more 'chestnut' than adult female (Heath 1989) but no further details given. Ogilvie-Grant (1905) states that immatures (probably referring to juveniles) of both sexes have dull yellowish-brown upperparts, grading to umber on crown.

First immature   (First basic).   No information. If this plumage exists, probably very similar to adult.

BARE PARTS   Based on photos (Soper 1961; Brathwaite 1974; Moon & Lockley 1982; Chambers 1989; Haddon 1990; Moon 1992; NZRD) and published information. **Adult** Bill, nares and tomia, black (89); base of lower mandible described as light fawn (Heath 1989). Orbital ring appears blackish (NZRD). Iris described as brown (Sclater 1888; Falla 1953). Legs and feet, pinkish brown (c221D); also described as pale brown (Sclater 1888) or flesh-coloured (Soper 1961); toes also described as olive (Falla 1953). Claws, dark grey (c83). **Nestling** At hatching, skin light salmon-pink or very pale blue-grey

(Heath 1989). At 10–12 days old: gape, base to lower mandible, palate and tongue, yellow-orange; iris, brown; legs and feet, light grey with fawn-yellow or mauve posterior surface to tarsus (Heath 1989). **Juvenile** From Heath (1989). At fledging, differs from adult by: Bill, dark grey with black tip and dorsal surface of upper mandible. Gape and base of lower mandible, yellow-orange (becoming similar to adult 8–10 weeks after fledging). Legs, grey-black with paler fawn posterior surface. Soles, fawn-cream. **First immature** Apparently similar to adult (Heath 1989).

MOULTS Based on eight skins, one labelled as juvenile, rest either adult or first immature (CM, NMNZ), and published information. **Adult post-breeding** (Probably third and subsequent pre-basic). Little known. Probably complete; in adults with no active moult, different tracts show similar extent of wear. Takes place after young fledge; duration 5–8 weeks (Heath 1989). Moult of body and all marginal coverts recorded from one collected in Mar.; this bird had all new primaries. Five collected in Apr. and May had slightly worn primaries. Skin of legs also shed during post-breeding moult (Heath 1989). **Post-juvenile** (First pre-basic). Very poorly known. Occurs 10–16 weeks after fledging, and finished in 2–4 weeks (Heath 1989); short duration suggests remiges and rectrices not replaced. **First immature post-breeding** (Second pre-basic). Nothing known.

MEASUREMENTS (1–2) SI, skins, sexed using labels (CM, NMNZ): (1) Adults, possibly including first immatures; (2) Juvenile. (3) Fiordland NP, live, basis of sexing not known (R.S. Gray); methods of measurement (including Culmen) not known.

		MALES	FEMALES	
WING	(1)	51.8 (1.92; 50–52; 5)	52.8 (2.22; 50–54; 4)	ns
	(2)	51	–	
	(3)	50, 51.5	53	
TAIL	(1)	20.0 (0.00; 5)	19, 20, 21	
	(2)	20	–	
BILL S	(1)	14.6 (0.96; 13.5–16.3; 5)	15.3 (0.71; 14.7–16.3; 4)	ns
	(2)	13.5	–	
CULMEN	(1)	10.0, 10.8	11.0	
TARSUS	(1)	23.2 (0.77; 22.9–25.7; 5)	23.7, 24.3, 25.2	
	(2)	23.0	–	
	(3)	22.5, 24.0	23.5	

Heath (1989) gives total length of adults as 95 (3.10; 37).

(4–5) Unsexed, from museum labels (CM, NMNZ), method of measurement not given (Falla 1953): (4) SI; (5) Fiordland NP, s. SI.

		UNSEXED
WING	(4)	51.5 (50.0–53.2; 9)
	(5)	47.5, 49.0, 49.5
CULMEN	(4)	10.8 (10.0–11.5; 9)
	(5)	11.0, 11.0, 12.0
TARSUS	(4)	26.5 (23.0–28.5; 9)
	(5)	24.0, 24.5, 26.0
HINDTOE C	(4)	21.6 (20.0–24.0; 9)
	(5)	18.0, 20.5, 21.0

WEIGHTS (1) Fiordland NP, live adults, sexed by plumage and breeding behaviour (Heath 1989). (2) Fiordland NP, live adults, basis of sexing not known (R.S. Gray).

	MALES	FEMALES	
(1)	15.8 (1.10; 18)	19.6 (1.60; 19)	**
(2)	14.1, 14.2	16.7	

Weight of adults in Fiordland NP ranges from 14 to 23 g (Heath 1989). Single nestling, tentatively sexed as female, from Fiordland NP, 18.2 g (R.S. Gray).

STRUCTURE Innerwing short, outerwing moderately long and rounded at tip on folded wing; tip of longest primary reaches to about half length of tail. Ten primaries: p5 or p6 shortest (though p7 or p4 can be equal longest); p10 8.0–13.0 mm shorter, p9 2.0–4.5, p8 0–2.0, p7 0–1.0, p6 0–0.5, p5 0–1.5, p4 0–2.5, p3 1.0–4.0, p2 1.5–5.0, p1 2.5–5.0. Slight emargination to inner webs of p6–p10, and outer webs of p5–p7, sometimes also p8. Nine secondaries, including three tertials; tip of longest tertial does not reach tip of p1 on folded wing. Tail very short, slightly rounded at tip; ten rectrices; t1 longest, t2–t5 1–2 mm shorter than t1. Bill fairly short, about same length as head or slightly shorter; upper mandible slightly downcurved; lower mandible straight but gonys slightly inclined upward; tip of upper mandible slightly overhangs tip of lower mandible. Tarsus long, compressed laterally; scaling, non-bilaminate, single large scale with indistinct notches on anterior surface and very indistinct division between anterior and posterior surface. Tibia fully feathered. Hindtoe usually longest, length (including claw) 21.8 mm (1.77; 18.8–23.6; 6); middle front toe 90–105% length of hindtoe; inner and outer front toes 80–90%. Hindclaw, c. 10 mm long, almost as long as hindtoe.

AGEING Juvenile probably very similar to adult but with slight differences in colour of plumage (Heath 1989; see Plumages); juveniles also have conspicuous 'yellow-orange flush' to base of lower mandible and gape (Heath 1989) which is lost after finish of post-juvenile moult. Not known if first immature distinguishable from adult.

SEXING Adults probably sexually dimorphic in plumage (q.v.) and weight, with females significantly heavier than males (P<0.01); no significant differences in measurements but few data. Adult females appear to have rounder body shape compared with males (Heath 1989). Juveniles, at least those in Fiordland NP, also appear sexually dimorphic (Soper 1961; Heath 1989); too few skins to evaluate such differences elsewhere in range (see Plumages: Juvenile). It is possible that extent of sexual dimorphism varies geographically; see below.

GEOGRAPHICAL VARIATION Not fully understood and too few skins to evaluate geographical variation. It is suggested that plumage becomes increasingly green from N to S (Falla 1953; Soper 1961; Michelsen 1982; Heath 1989; Heather & Robertson 1997). Populations from Lewis NP (s. Nelson, w. Marlborough) and farther S in Arthurs Pass NP (n. Canterbury, ne. West Coast) and Mt Cook NP (West Coast) are browner on upperparts compared with greener population from Fiordland NP, far s. SI (Child 1981; Heath 1989). Population from s. Fiordland NP originally described as a separate subspecies *rineyi* (Falla 1953) but this now considered a distinct, bright-green, morph (Heather & Robertson 1997; NZCL); this morph (described below) originally discovered in Dusky Sound region, far sw. SI (Oliver). Populations NW of Nelson, far n. SI, supposedly have green plumage similar to those in Fiordland NP; these two regions environmentally similar, which may explain similarity in plumage (Heath 1989). However, comparison of skins

of two females and two males from Nelson region with two adult males and one unsexed adult from L. McArthur (s. Fiordland NP), indicates L. McArthur birds have greener upperparts (this study). DNA sequencing of a 202 base-pair region of the mitochondrial 12S gene (a slowly evolving gene) reveals a 0.5% sequence difference between the green morph from Fiordland NP and the population from Nelson, n. SI; this is compatible with a period of genetic separation between populations in s. SI and n. SI (Cooper 1994). For the 202 base-pair fragment, sequence differences between Bush Wren and Rock Wren are 6.4% (Fiordland populations of Rock Wren) and 6.0% (n. SI populations of Rock Wren); Riflemen differ by 5.4% and 6.0% from Fiordland and n. SI populations of Rock Wrens (Cooper 1994).

GREEN MORPH (Fiordland NP, s. SI). Very similar to populations farther N but wing possibly shorter and culmen possibly longer in green morph, but only three skins of green morph available (Falla 1953; Oliver). Description based on two adult male skins and one unsexed adult skin (NMNZ) collected at L. McArthur, Fiordland NP; differ from adult males collected from Arthurs Pass (w. Canterbury, e. West Coast) and Nelson by: HEAD AND NECK: Forehead, crown and nape, olive (c51). Sides of neck, bright olive (c50). UPPERPARTS: Mantle, back, scapulars, rump and uppertail-coverts, bright olive (150). UNDERPARTS: Flanks, rich yellow (c55). UPPERWING: Marginal and median secondary coverts, olive (50) with greenish-blue (164) tinge when viewed from certain angles. Greater secondary coverts, brown (28) on most of inner web, olive (51) on outer web and at tip. Marginal and median primary coverts, black-brown (119) with olive (51) fringe. Outer webs of remiges, dark green (260) at edges, combining to form dark-green (260) panel on folded wing.

Degree of sexual dimorphism apparently varies geographically (Soper 1961; Heath 1989), with populations in Fiordland NP more sexually dimorphic than at other locations. Females from Homer Tunnel, n. Fiordland NP, are similar in appearance to females from Nelson, n. SI, and slightly browner than females from L. McArthur (s. Fiordland NP), and richer green than females from farther N, in Arthurs Pass (Soper 1961). Males from Homer Tunnel are very similar to males from L. McArthur (s. Fiordland NP) but much greener than males from the Nelson region and Arthurs Pass (Soper 1961). Further research needed to assess the relationship between age, sex, locality and plumage.

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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