

## Order PASSERIFORMES

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

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

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

The Passeriformes divide into two main groups:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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## Family PARDALOTIDAE pardalotes, scrubwrens, thornbills and allies

A highly diverse family of very small to medium-sized and largely drab-plumaged insectivorous passerines. The family comprises 67–71 species in 15–16 genera, with distribution centred in Aust. and New Guinea (48 and 19–21 species respectively, with six occurring both Aust. and New Guinea); only *Gerygone* occurs beyond Aust.–New Guinea, extending W to Wallacea (three species, two endemic) and se. Asia (one species, Goldenbellied *Gerygone* *G. sulphurea*), and E to NZ (two species) and sw. Pacific Ocean (one species, Fan-tailed *Gerygone* *G. flavolateralis*), on Solomon Is, New Caledonia, Loyalty Is and Vanuatu (Wolters 1975–82; Sibley & Ahlquist 1990; Sibley & Monroe 1990; Beehler & Finch 1985; Christidis & Boles 1994; Coates *et al.* 1997; NZCL; Peters; DAB). Fifty-one species in HANZAB region (49 in Aust. and its territories, and two in NZ), one of which extinct. The second-largest family of birds in Aust. (after the Meliphagidae). Combining various sources (Sibley & Ahlquist 1990; Christidis & Boles 1994; DAB) the Pardalotidae includes the following subfamilies and genera:

**PARDALOTINAE:** *Pardalotus* (pardalotes), endemic to Aust. (4 species in genus, 4 in HANZAB region);

**DASYORNITHINAE:** *Dasyornis* (bristlebirds) (2, 2), *Pycnoptilus* (Pilotbird *P. floccosus*) (1, 1), both endemic to Aust.;

**ACANTHIZINAE:** Consists of two tribes: **SERICORNITHINI**, which includes *Acanthornis* (Scrubtit *A. magnus*), endemic to Aust. (1, 1); *Origma* (Rockwarbler *O. solitaria*), endemic to Aust. (1, 1); *Hylacola* (heathwrens), endemic to Aust. (2, 2); *Calamanthus* (fieldwrens), endemic to Aust. (2, 2); *Chthonicola* (Speckled Warbler *C. sagittata*), endemic to Aust. (1, 1); *Pyrrholaemus* (Redthroat *P. brunneus*), endemic to Aust. (1, 1); *Crateroscelis* (mouse-warblers), endemic to New Guinea (3, 0); *Oreoscopus* (Fernwren *O. gutturalis*), endemic to Aust. (1, 1); and *Sericornis* (scrubwrens) (12, 6); and **ACANTHIZINI**, which includes *Smicromis* (Weebill *S. brevirostris*), endemic to Aust. (1, 1); *Gerygone* (gerygones, fairy-warblers or flyeaters) (19–20, 12 [see above]); *Acanthiza* (thornbills) (13, 12); and *Aphelocephala* (whitefaces), endemic to Aust. (3, 3).

The taxonomy of the group is complex and has been the subject of various reviews. Studies of DNA–DNA hybridization (Sibley & Ahlquist 1985, 1990) and protein allozymes (Christidis 1991; Christidis & Schodde 1991) show that the Pardalotidae are part of the Australo-papuan corvoid lineage. These studies also indicate they belong to the superfamily Meliphagoidea, which includes the honeyeaters and fairy-wrens. Early works include the species in a number of families, including the Old World sylviid warblers (Sylviidae), Old World babblers (Timaliidae) or with the Australo-papuan fairy-wrens in a subfamily Malurinae of the Old World flycatchers (Muscicapidae) (Sharpe 1883; Mayr & Amadon 1951; Beecher 1953; Wetmore 1960; Keast 1961). Further, *Pardalotus* has formerly been placed in the Dicaeidae (Sharpe 1885; Mayr & Amadon 1947), which it resembles only by convergence; it has also been placed in a separate family, the Pardalotidae (RAOU 1926; Schodde 1975; DAB). Here we follow most works (Sibley *et al.* 1988; Sibley & Ahlquist 1990; Sibley & Monroe 1990; Christidis & Boles 1994) by including *Pardalotus* with the Dasyornithinae and Acanthizinae in the Pardalotidae. However, DNA–DNA hybridization (Sibley & Ahlquist 1990) and mitochondrial-DNA sequence analysis (Cracraft *et al.* in DAB) suggest that *Pardalotus* is a divergent genus and support recognition as a separate family (in which case the remaining genera are placed in the Acanthizidae; DAB). The New Guinea genus *Amalocichla* may also be closely related to the Pardalotidae (Olson 1987; Sibley & Ahlquist 1990; DAB). Evolutionary relationships between genera discussed more fully in Christidis (1990, 1991), Christidis & Schodde (1991), and Sibley & Ahlquist (1985, 1990).

Species range in size from very small (Weebill *Smicromis brevirostris*: length c. 8.5 cm; weight c. 6 g) to medium-sized (e.g. Rufous Bristlebird *Dasyornis broadbenti*: length c. 26 cm; weight c. 75 g); most are small. Wings rather rounded in sedentary species, more pointed in species that undertake longer movements (e.g. Western *Gerygone fuscica*); ten primaries, the outermost (p10) vestigial in *Pardalotus*; nine secondaries, most with vestigial inner (tenth) secondary (I.J. Mason). Tail varies from very short (*Pardalotus*) to very long (*Dasyornis*); 12 rectrices. Bill rather short, fairly slender in most species, more robust and finch-like in others (e.g. *Pardalotus*, *Aphelocephala*), with terminal maxillary notch and semi-operculate nares. Tarsal scaling varies with genus, either laminiplantar or holothecal. Osteological features vary considerably and a full discussion is outside the scope of this work, though some features are discussed here (after DAB). All species have twin furrows on either side of decurrent ventral tubercle at the head of the humerus. Cranial features, especially internal structure of palate, vary considerably between genera and best summarized in two main groupings: (1) Pardalotinae, with: well-ossified narial apertures; constricted

palates with attenuately subulate transpalatine processes; ossified and thickened hinges of the pterygoids with the medio-palatine processes; deeply bifid vomers with developed, round-tipped horns; temporal fossae nearly occluded by thickened zygomatic processes; nearly vestigial postorbital processes; undeveloped alae tympanicae; and two very deep twin furrows at head of humerus; and (2) Dasyornithinae and Acanthizinae, which differ from Pardalotinae in above characteristics, especially by: shallower furrows at head of humerus; club-shaped maxillo-palatines, overlying a truncated, flat and tongue-shaped vomer; and vomerine horns vestigial, except in *Acanthornis*. A detailed analysis of osteological characters for all genera is given in DAB.

Plumage of most species rather drab browns, greys or olives, except for some *Gerygone* and most *Pardalotus*, which have bright-red or bright-yellow pigmentation to parts of plumage. Markings vary considerably; some have distinct spotting or streaking on crown (most *Pardalotus*), ventral scalloping (*Dasyornis*) or streaking (e.g. *Calamanthus*, *Hylacola*, some *Sericornis* and *Acanthiza*) or distinct throat-patches (e.g. *Pyrrholaemus*, *Oreoscopus*). Many species have rather richly coloured uppertail-coverts contrasting with rather sombre rest of upperparts. Juveniles of most species similar to adults but typically duller and lacking distinct markings. Patterns of sexual dimorphism vary, with many species not plumage dimorphic, but others either obviously so (e.g. Spotted Pardalote *Pardalotus punctatus* and Fairy Gerygone *Gerygone palpebrosa*) or more subtly so (e.g. Speckled Warbler *Chthonicola sagittatus*, some *Sericornis*, *Hylacola* and *Calamanthus*). Naked at hatching or with sparse down. Post-juvenile (first pre-basic) moult usually partial, but complete or nearly so in some (e.g. *Gerygone*). In species undergoing partial post-juvenile moult, first immature (second basic) plumage resembles adult plumage. Adults undergo a complete post-breeding (pre-basic) moult each year, with no change in appearance. Primaries moult outward.

The following summary of biology and ecology based largely on HANZAB species accounts (q.v.), Rand & Gilliard (1967), Coates (1990), Bregulla (1992), Coates *et al.* (1997) and other references as cited. As could be expected in such a large and diverse family, there are few common features, with considerable variation even within genera.

Over range, found in most vegetated habitats, with representatives throughout temperate, subtropical and tropical zones, semi-arid and arid zones, and from coasts to uplands, including alpine and subalpine regions. Use of strata within habitats varies greatly, even within genera, e.g. many scrubwrens *Sericornis* primarily terrestrial or inhabit dense understorey vegetation while others primarily arboreal in mid-storey or canopy. In Aust., pardalotes *Pardalotus* and thornbills *Acanthiza* predominantly inhabit sclerophyll forests, woodlands and shrublands, usually those dominated by eucalypts, but considerable variation, e.g. Yellow-rumped Thornbills *Acanthiza chrysoorrhoa* often recorded in open habitats such as lightly wooded grasslands, Brown Thornbills *A. pusilla* mostly occur in dense shrubby vegetation, often in understorey of forests and woodlands, and Striated Thornbills *A. lineata* usually inhabit canopy of forests and woodlands. Over range, gerygones *Gerygone* occupy wide variety of habitats, from arid and semi-arid eucalypt woodlands (e.g. Western Gerygone) to rainforests (e.g. Brown Gerygone *G. mouki*) or mangroves (e.g. Mangrove Gerygone *G. levigaster*). Many species occupy dense understorey or dense low vegetation such as heathland, shrubland or grassland (including bristlebirds *Dasyornis*, scrubwrens *Sericornis*, heathwrens *Hylacola*, fieldwrens *Calamanthus*, mouse-warblers *Crateroscelis* and Fernwren *Oreoscopus guttaralis*). Whitefaces *Aphelocephala* usually occur in open habitats with low sparse vegetation, such as open chenopod or acacia shrublands. Many species commonly use modified habitats, including clearings, agricultural and pastoral land, parks and gardens; some species also use plantations of introduced pines or regrowth forests (e.g. White-browed Scrubwren).

Most species sedentary or resident, though many show some local or dispersive movements; most dispersive movements possibly by subadults. A few Aust. species partly migratory, with some populations making seasonal long-distance movements, e.g. s. populations of White-throated Gerygone *Gerygone olivacea* breed in se. Aust. in spring–summer and migrate to winter in N; and s. populations of Striated Pardalote *Pardalotus striatus* breed Tas. and se. Aust. and migrate N and inland for winter. Some altitudinal movements also recorded, e.g. Spotted Pardalote *Pardalotus punctatus* in se. Aust. (see Chan 2001; Griffioen & Clarke 2002; and species accounts). Little information on nature of passage in migratory species; White-throated Gerygone probably migrates in a succession of small parties, and, round Sydney at least, sexes appear to move separately; Tas. populations of Striated Pardalote cross Bass Str. on migration, and may migrate at night.

Mostly insectivorous; many also occasionally eat seeds, and whitefaces have short finch-like bills and hard-muscled stomachs that are adapted for collecting and digesting seeds, though also take insects. Pardalotes specialize in gleaning lerp—the protective carbohydrate coat of Aust. psyllids (Psyllidae)—using short, deep and blunt bill to glean lerp from foliage in crowns of trees. Occupy a wide range of foraging niches, varying from wholly or primarily arboreal (e.g. pardalotes, Weebill) to largely terrestrial (e.g. bristlebirds, whitefaces), with much

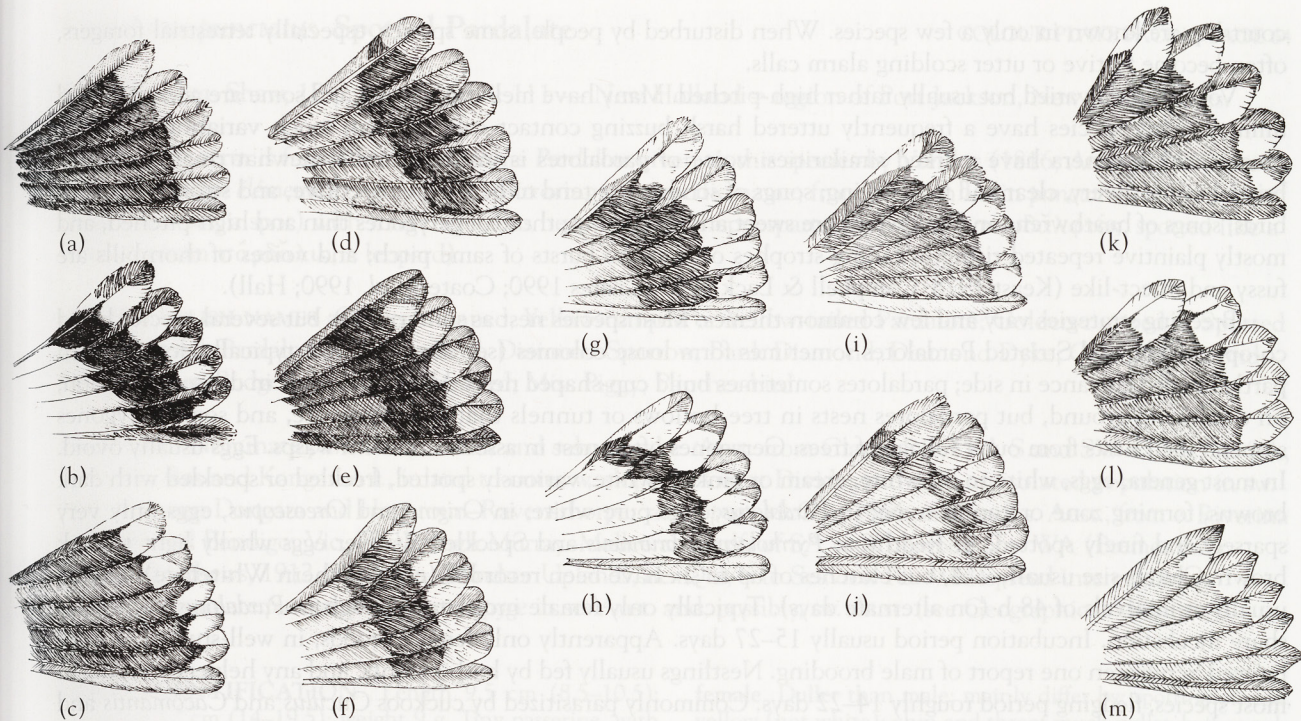


Figure 1. Undertail-patterns of *Gerygone*

- |   |   |
|---|---|
| (a) Fairy Gerygone <i>G. palpebrosa</i>                       | (g) Mangrove Gerygone <i>G. laevigaster laevigaster</i> |
| (b) White-throated Gerygone <i>G. olivaceous olivaceous</i>   | (h) Western Gerygone <i>G. fusca fusca</i>              |
| (c) White-throated Gerygone <i>G. olivaceous rogersi</i>      | (i) Western Gerygone <i>G. fusca mungi</i>              |
| (d) Green-backed Gerygone <i>G. chloronotus</i>               | (j) Dusky Gerygone <i>G. tenebrosa</i>                  |
| (e) Large-billed Gerygone <i>G. magnirostris magnirostris</i> | (k) Brown Gerygone <i>G. mouki richmondii</i>           |
| (f) Large-billed Gerygone <i>G. magnirostris cairnsensis</i>  | (l) Grey Gerygone <i>G. igata</i>                       |
|   | (m) Norfolk Island Gerygone <i>G. modesta</i>           |

variation in heights and strata used for foraging, e.g. from low dense vegetation, such as heathland, or dense understorey vegetation (e.g. heathwrens, fieldwrens, many scrubwrens) to canopy (e.g. pardalotes, gerygones); much variation within larger genera, e.g. most thornbills primarily arboreal (e.g. Striated Thornbill) but a few largely terrestrial (e.g. Slender-billed Thornbill *Acanthiza iredalei* and Yellow-rumped Thornbill). All forage by gleaning; also, but less often, by sallying, probing or hanging.

Social organization diverse, and varies even within genera. Most species typically occur singly or in pairs; some species occasionally form small flocks and most thornbills and whitefaces do so regularly; pardalotes may form flocks in non-breeding season. Many species join, or form nucleus, of mixed-species feeding flocks with variety of other small to medium-sized insectivorous birds. Most species monogamous, at least socially; in well-studied White-browed Scrubwren, subordinate males have sired young despite mate-guarding by primary male. Most species apparently breed in simple pairs. However, co-operative breeding usual for some species of thornbills and whitefaces (e.g. Striated, Yellow-rumped and Buff-rumped Thornbills *Acanthiza reguloides*) and has been reported occasionally in other species (e.g. Striated Pardalote, some scrubwrens, Speckled Warbler, Weebill). Usually nest solitarily; territorial at least in breeding season, with many species proclaiming territory with loud or distinctive songs. Striated Pardalote sometimes nests semi-colonially, defending only area immediately round nest. In at least one species, Striated Thornbill, larger area defended in non-breeding season by several pairs or groups, which form a clan; in others, such as Eastern Bristlebird *Dasyornis brachypterus*, home-ranges overlap but core-areas defended. Some species stop defending territory outside breeding season (e.g. Grey Warbler *Gerygone igata*). Social behaviour less well known than social organization in most species. There is a paucity of information on displays of most species. Distraction displays recorded in several genera (e.g. *Hylacola*, *Calamanthus*, *Sericornis*) and mobbing behaviour recorded in some well-studied species (e.g. White-browed Scrubwren). Agonistic displays, fighting and chases known for some species, many from anecdotal reports. Sexual behaviour is generally poorly known, and aspects of



courtship are known in only a few species. When disturbed by people, some species, especially terrestrial foragers, often become furtive or utter scolding alarm calls.

Vocalizations varied but usually rather high-pitched. Many have melodious songs and some are accomplished mimics; many species have a frequently uttered harsh buzzing contact call. Though much variation, voice of species within genera have marked similarities: voice of pardalotes is insistent and somewhat ringing; that of bristlebirds is silvery, clear and far-carrying; songs of scrubwrens tend to be highly repetitive, and strong for size of birds; songs of heathwrens and fieldwrens are sweet and melodious; those of gerygones thin and high-pitched, and mostly plaintive repeated rising or falling strophes or staccato bursts of same pitch; and voices of thornbills are fussy and insect-like (Keast 1978; Campbell & Lack 1985; Coates 1990; Coates *et al.* 1990; Hall).

Breeding strategies vary and few common themes. Most species nest as solitary pairs but several species breed co-operatively, and Striated Pardalotes sometimes form loose colonies (see above). Nests typically domed, with partly hooded entrance in side; pardalotes sometimes build cup-shaped nests. Most nests built in dense vegetation, on or close to ground, but pardalotes nests in tree-hollows or tunnels that they excavate, and some gerygones suspend their nests from outer foliage of trees. Gerygones often nest in association with wasps. Eggs usually ovoid. In most genera, eggs, white to off-white, cream or pinkish white, variously spotted, freckled or speckled with dark browns, forming zone or cap in some; in *Pardalotus*, eggs pure white; in *Origma* and *Oreoscopus*, eggs only very sparsely and finely spotted; in Redthroat *Pyrrholaemus brunneus* and Speckled Warbler eggs wholly light to dark brown. Clutch-size usually 2–4, but clutches of up to six have been recorded (e.g. Southern Whiteface). Laying usually at intervals of 48 h (on alternate days). Typically only female incubates, though in *Pardalotus* both sexes share incubation. Incubation period usually 15–27 days. Apparently only female broods; in well-studied White-browed Scrubwren one report of male brooding. Nestlings usually fed by both parents, and any helpers present. In most species, fledging period roughly 14–22 days. Commonly parasitized by cuckoos *Cuculus* and *Cacomantis* and bronze-cuckoos *Chrysococcyx*, with bronze-cuckoos particularly associated with gerygones *Gerygone* and thornbills *Acanthiza* (HANZAB 4).

One species, Lord Howe Gerygone *G. insularis*, and w. subspecies of Rufous Bristlebird *Dasyornis broadbenti litoralis* extinct. In HANZAB region, another 24 taxa, of 16 species, considered threatened, with three species critically endangered (n. subspecies of Eastern Bristlebird *Dasyornis brachypterus monoides*, King I. subspecies of Scrubtit *Acanthornis magnus greenianus*, and King I. subspecies of Brown Thornbill *Acanthiza pusilla archibaldi*), three endangered (Forty-spotted Pardalote *Pardalotus quardagintus*, s. subspecies of Eastern Bristlebird *D.b. brachypterus*, and Mt Lofty Ras subspecies of Chestnut-rumped Heathwren *Hylacola pyrrhopygia parkeri*), seven vulnerable, seven near threatened, and four of least concern. Extraliminally, Biak Gerygone *Gerygone hypoxantha* also endangered. In Aust., many species have been or continue to be adversely affected by clearance and fragmentation of natural vegetation; continued degradation of habitat through overgrazing is a threat to some species (e.g. Redthroat). Changes to fire regimes and wildfires also considered to be major threat to survival of some species, notably bristlebirds *Dasyornis* (Collar *et al.* 1994; Garnett & Crowley 2000).

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## *Gerygone igata* Grey Warbler

COLOUR PLATE FACING PAGE 288

*Curruca igata* Quoy & Gaimard, 1830, In Dumont d'Urville, J.S.C., *Voy. de l'Astrolabe*, Zool. 1: 201 — la baie Tasman, dans le détroit de Cook, à la Nouvelle-Zélande = Tasman Bay, Cook Strait, New Zealand.

According to Quoy and Gaimard (1830) *igata* was the name given to this bird by the Maori of the Tasman Bay area of South Island: '*igata*, par les indigènes de la baie Tasman'.

OTHER ENGLISH NAMES Grey Gerygone.

### MONOTYPIC

**FIELD IDENTIFICATION** Length 10 cm; wingspan not known; weight 6.5 g. Small and active gerygone. Adult greyish olive above and grey on face, chin, throat and breast, and otherwise white below; with: dark-red iris, contrasting blackish lores, and tail marked with broad blackish subterminal band and large white spots near tips of rectrices. Sexes alike. No seasonal variation. Juvenile similar to adult but separable by paler face and breast, and pale eye-ring. Immature inseparable. **Adult** Top of head, hindneck and sides of neck, dark greyish-olive, merging to slightly paler, dark grey, on sides of head and breast, and to pale grey or off-white on chin and throat. Lores and small patch behind eye, blackish, forming distinct but narrow eye-stripe and contrasting with diffuse narrow grey supercilium from bill to just behind eye. Some show an indistinct thin broken white eye-ring, visible only in close view. Rest of upperbody, dark greyish-olive. Uppertail, greyish olive basally grading to blackish distally, with white spots near tips of all but central pair of rectrices; white spots normally concealed when bird perched with tail closed, but visible in flight when tail partly spread, and obvious when tail fanned while bird hover-gleaning. Folded wing, dark greyish-olive with darker blackish alula and centres of tertials, and indistinct pale-olive wing-panel formed by edges of remiges. Underbody below grey breast, white, with varying pale-greyish or pale-yellowish wash along flanks. Undertail, grey-black, with prominent white spots near tips of all except central pair of rectrices. Bill, legs and feet, black. Iris, dark red. **Juvenile** Similar to adult, differing by: feathers of upperparts have softer and looser texture; face plainer and paler,

with indistinct greyish lores; supercilium, sides of throat and sides of breast varyingly washed pale yellow; eye-ring more distinct, off-white or pale yellow; iris, brown; bill paler, grey-black, merging to paler greyish or brownish flesh at base of lower mandible; and prominent pale (yellow or cream) gape in recently fledged birds.

**Similar species** The only gerygone of mainland NZ and its smaller offshore islands, and unlikely to be mistaken; combination of small size, plumage coloration, characteristic hover-gleaning behaviour and distinctive song all diagnostic and quite unlike any other NZ passerine.

Usually seen singly or in pairs, or, in non-breeding season, in small flocks of up to six or so and occasionally in larger flocks of up to 12 birds; often join mixed-species feeding flocks of other small insectivorous passerines, such as Silvereyes *Zosterops lateralis*, Whiteheads *Mohoua albicilla* and Brown Creepers *Mohoua novaeseelandiae*. General behaviour and actions similar to those of other gerygones. Often seen flitting or hovering within or outside foliage, when tail spread to reveal conspicuous white spots at tips. Forage mainly in middle and upper levels of canopy, chiefly by gleaning and hover-gleaning for insects from foliage and twigs. Song uttered by male a distinctive long musical and sweet waver-ing trill (see Voice).

**HABITAT** Inhabit all types of native vegetation, including forests, woodlands, secondary growth, forest margins, shrublands and mangroves (Creswell 1958; Challies 1966; Gill 1982a; Oliver); also recorded in modified habitats (St

Paul 1975; Gill 1982a); usually only absent from treeless areas, such as grassland, extensive pasture or alpine areas above treeline (D.J. Onley). Occur from coastal plains to ranges and subalpine regions up to 1500 m asl; usually present in smaller numbers with increasing altitude (Chambers *et al.* 1955; Sibson 1958; Guest 1975; Onley 1980; Gill 1983b; Owen & Sell 1985; Wilson *et al.* 1988; Fitzgerald *et al.* 1989; Gibb 1996; Oliver; CSN 3). Often occur in sheltered gullies, but also on slopes and ridges (McKenzie 1948; Creswell 1958; Gravett 1971; Cooper *et al.* 1986).

Occur in all types of native forests, including various associations of podocarps, hardwoods and beech, usually with a well-developed understorey and open ground cover (Guest 1975; Dawson *et al.* 1978; Onley 1980; Gill 1983b; Wilson *et al.* 1988), e.g. in beech *Nothofagus* forests (Dawson *et al.* 1978) or various mixed rata-podocarp-hardwood forests (Fitzgerald *et al.* 1989). Within mixed rata-podocarp-hardwood forest near Wellington, recorded at all levels: mist-netted in similar numbers at various heights from 1.5 m to 13.5 m above ground ( $n=70$  birds) (Fitzgerald *et al.* 1989). Often recorded at edge of forest (Oliver). Also inhabit secondary growth (Creswell 1958), e.g. at Kowhai Bush, Kaikoura, inhabit tall dense Kanuka *Kunzea ericoides* forest, up to 15 m tall, with understorey varying from patchy to dense and shrubby, dominated by either native species, such as Akiraho *Olearia paniculata* and Fivefinger *Pseudopanax arboreus*, or introduced Montpellier Broom *Cytisus monspessilanus* (Gill 1982a). Also occur in dense shrubland or thickets, such as those dominated by Manuka *Leptospermum scoparium*, Kanuka, *Hebe*, Leatherwood *Olearia colensoi* or *Senecio*, including in subalpine areas (Weeks 1949; Creswell 1958; Sibson 1958; Challies 1966; Cooper *et al.* 1986; Gibb 1996; Oliver; CSN 3). Occasionally recorded among mangroves (CSN 29, 31). Often occur in modified habitats, such as farmland, parks and gardens, often dominated by exotic plants (Stidolph 1974; Onley 1980; Gill 1989; Oliver; CSN 34, 38, 45), though most abundant in gardens with high proportion of native vegetation (Day 1995). Also occur in exotic pine plantations (Clout & Gaze 1984; Owen & Sell 1985; Oliver; CSN 34).

**DISTRIBUTION AND POPULATION** Endemic to NZ, where ubiquitous throughout NI and SI; also occur on most offshore islands, from Three Kings Is (at least historically; see below), S to Stewart I. and associated islets (NZ Atlas; NZCL; CSN).

**Snares Is** Vagrant; fewer than 15 birds, 9 July to early Oct. 1972 (Horning & Horning 1974).

**Breeding** Throughout range.

**Populations** On Green I., Mercury Grp, recorded at density of 1.65 pairs/ha (Skegg 1963; Thoresen 1967). At Waiioeka R., 10 birds recorded along c. 36.5 m of track (CSN 24). On e. shore of L. McKerrow, SI, recorded at density 0.55 birds/km along transect of 12.8 km; from n. end of L. McKerrow to Martins Bay, SI, 0.88 birds/km along 8 km; in Hollyford Valley, SI, 0.28 birds/km along 7.2 km; from Spey R. to Wilmot Pass Hut, SI, 0.83 birds/km along 9.6 km; at head of L. Monk, SI, 2.50 birds/km along 2.5 km; at Jeanie Burn, SI, 0.23 birds/km along 8.8 km (Kikkawa 1966). Total population of Whataroa Valley (area c. 388 km<sup>2</sup>) estimated at 25,000 birds in 1954 (Jackson 1954).

**Change in range, populations** Formerly recorded, but scarce, on Three Kings Is (Cheeseman 1887, 1891), and apparently extinct there by 1940s (Turbott & Buddle 1948).

**MOVEMENTS** Largely sedentary, but widely described in literature as resident or present throughout year (see below). Some movements or seasonal patterns of occurrence reported, but no information on extent of such patterns and probably local (see below). No long-distance movements known.



In garden at Masterton (daily records during two 12-month periods): recorded on 257 days in 1942–43, but on only 37 (or 39) days in 1971–72 (Stidolph 1974, 1977). Populations have declined after conversion of forest to pasture (see Threats). Round Gisborne, increases in populations recorded round Ngatapa and Aniwanuiwa in mid-1950s (CSN 7).

**THREATS AND HUMAN INTERACTIONS** Often occur in modified habitats or in exotic flora, e.g. often recorded in parks and gardens, farmland and pine plantations, and have probably benefited from modification of habitats (e.g. St Paul 1975; Gill 1982a; see Habitat). However, also said that numbers have been much reduced by clearance of forest for pasture (Oliver). Present in both unlogged and logged forests, though abundance lower in logged forests (Onley 1983).

Eggs and young eaten by introduced mustelids and rodents (Gill 1982b, 1983a). Adults sometimes attacked by Cats (Oliver; CSN 23).

At Kowhai Bush (study of banded population of 77 adults and 96 nestlings), territorial adults sedentary, and restricted to confined area throughout year. In winter, territories expanded, with birds moving up to 100 m beyond summer territorial boundary (Gill 1982a). Resident on Noises Is (Cunningham & Moors 1985), in central Auckland (Moncrieff 1928), round Maungahaumia (McLean 1907), on Wairarapa Plains (Stidolph 1923), Wellington (Moncrieff 1928) and Green I., Mercury Grp (Thoresen 1967). Present throughout year on NI, in Auckland Domain (Gill 1989), Te Kuiti (Guest & Guest 1987), Minginui (St Paul 1975; CSN 9), Tihoi (St Paul 1975), Palmerston N. (Guest & Guest 1993), Masterton (Cunningham 1943), Waikanae (Wodzicki 1946) and Orongorongo Valley, Wellington (Gibb 1996); and on SI, in Kowhai Bush, Kaikoura (Gill 1982a; Dean 1990), Hilderthorpe (Anon. 1942; CSN 2), Dunedin (Moncrieff 1928; Marples 1944), round Nelson (Wilson *et al.* 1988) and Reefton (Dawson *et al.* 1978).

As with other NZ passerines, do not move to lower latitudes in winter (Gill 1982a). Some movement reported, but extent of such movement not known and probably local (Hodgkins 1949). At Lower Ohikanui and Buller, where recorded throughout year, numbers increase significantly between Mar. and June, possibly because to birds move down valley (Wilson *et al.* 1988). Round Reefton, numbers significantly higher in low-terrace and hill-country forests Feb.–Aug., and at high altitudes Oct.–Dec.; suggested that some may move to higher altitudes by Oct. to avoid parasitism by Shining Bronze-Cuckoos *Chrysococcyx lucidus* (Dawson *et al.* 1978). Said to move seasonally to and from 'bush' (Moncrieff 1928); and many records in settled areas in winter (e.g. Moncrieff 1928; Anon. 1942; Hodgkins 1949; CSN 1, 45).

Sing throughout year (Wilkinson & Wilkinson 1952) but less vocal during winter, and apparent changes in numbers possibly result from different levels of conspicuousness (McLean 1907; Falla *et al.* 1981; Wilson *et al.* 1988; Gibb 1996; CSN 9). At Kowhai Bush, Kaikoura, SI, counts reflected vocal conspicuousness rather than abundance (Gill 1980b).

**Dispersal of young** At Kowhai Bush, of 44 banded juveniles, ten (23%) were seen when independent; the remaining 77% had either dispersed from natal territories or died.

**Banding** Of 280 banded in NZ, 1950–74, 34 recoveries (12.1%) (Robertson 1975). Of 1189 banded 1950–96, six recoveries, 1988–93 (Cossee 1989, 1991, 1993, 1995, 1997, 1998a,b; Cossee & Wakelin 1991). At Kowhai Bush, average annual survival of banded warblers at least 81.5% and annual mortality at most 18.5% (Gill 1982a). **LONGEVITY:** Adult male banded in June 1976 at Kowhai Bush was recaptured at same site in Nov. 1981, giving a minimum lifespan of 5 years 5 months; at Kowhai Bush, predicted life-expectancy was 4.9 years (Gill 1982a).

**FOOD** Almost entirely insects and their larvae, and spiders; occasionally small fruits and seeds. **Behaviour** Primarily arboreal in wide variety of native vegetation, and in some modified habitats; most food collected from foliage, by gleaning or sally-hovering at outer foliage (Stidolph 1939; Soper 1963; Atkinson 1966; Turbott 1967; Horning & Horning 1974; St Paul 1975; Falla *et al.* 1981; Moon 1992; Heather & Robertson 1997; Oliver; see Habitat). **DETAILED STUDIES:** In plantations of conifers (pines *Pinus* and firs *Pseudotsuga*) at

Kaingaroa Forest, NI, 1958–59 (Gibb 1961); in Christchurch Botanic Gardens, SI (East 1967); at Kowhai Bush, Kaikoura, SI (Gill 1980b, 1983a); on Little Barrier I. (Gravatt 1969, 1971); Windbag Valley, S. Westland, SI (O'Donnell & Dilks 1994); and from NI and Fiordland, SI (Keast & Recher 1997). **SIZE OF FEEDING FLOCKS:** Mostly forage singly, in pairs or very occasionally in small flocks of up to 5–8 birds (Ryder 1948; Stenhouse 1957; Wagener 1966; Dean 1990; Moon 1992; CSN 5; D.J. Onley). At Kowhai Bush, Mar.–July (non-breeding season), foraged in groups of 3–6 birds (Gill 1982a). Often occur in mixed-species feeding flocks of other small insectivorous passerines, such as Silvereyes, Brown Creepers, Grey Fantails *Rhipidura fuliginosa*, Whiteheads, Chaffinches *Fringilla coelebs*, Common Redpolls *Carduelis flammea*, Yellowheads *Mohoua ochrocephala* and Yellow-crowned Parakeets *Cyanoramphus auriceps* (Gill 1982a; Read & McClelland 1984; McLean *et al.* 1987; Heather & Robertson 1997). At Kowhai Bush, often feed in mixed-species feeding-flocks; recorded in 87% of 76 mixed-species feeding flocks containing 2–6 species, with mean of 2.6 Warblers/feeding-flock (2.1; 1–12; 76) (Dean 1990). Mixed-species feeding flocks strongly seasonal and not observed during breeding season, Sept.–Dec.; in non-breeding season, flocks noted throughout day (Dean 1990). **FORAGING HEIGHTS:** Forage mainly in middle levels of forests, mostly in top of understorey; occasionally forage on ground or aerially (Stidolph 1939; Gibb 1961; Gravatt 1971; Gill 1980b; O'Donnell & Dilks 1994). In Kaingaroa Forest, foraged mainly in middle levels of forest; of 180 foraging observations, divided into five different levels (data estimated from graph): none foraging on ground; c. 18% foraging in first level above ground; c. 38% in second level; c. 30% in middle level; c. 10% in second highest level; and c. 4% in highest level. In Christchurch Botanic Gardens, mostly foraged in middle level of trees and not on ground; of 91 foraging observations (data estimated from graph): c. 5% 0–0.6 m above ground; c. 45% 0.6–3.6 m; and c. 40% >3.6 m, in canopy (comprising c. 30% in lower canopy) and c. 10% in upper canopy. On Little Barrier I., where forest divided into canopy (exposed foliage), subcanopy (foliage and twigs directly below canopy), upper understorey (layer between subcanopy and tops of smaller trees that form secondary layer; typically trunks and branches), middle storey (canopy and subcanopy of secondary layer of vegetation), lower understorey (layer between middle storey and ground storey; typically trunks and small shrubs), ground storey (ground, litter, logs, herbs and grass), mainly foraged in mid-storey of forest, c. 3 m above ground; of 96 foraging observations: 8.3% on ground or in lower understorey; 54.2% in middle storey; 4.2% in upper understorey; 12.5% in subcanopy; and 20.8% in canopy; actual heights of foraging (at 1.5 m intervals from ground to canopy) were: 1.1% on ground; 9.5% 0.1–1.5 m above ground; 36.8% 1.6–3.0 m; 28.4% 3.1–4.5 m; 6.3% 4.6–6.0 m; 6.3% 6.1–7.5 m; 1.1% 7.6–9.0 m; 7.4% 9.1–11.5 m; and 3.3% >11.6 m. At Kowhai Bush, foraged mostly in understorey; of 143 foraging observations: 16% in lower understorey, 77% in upper understorey, and rest on ground or in canopy; heights of these observations (proportions estimated from graph): c. 5% up to 1.5 m above ground; c. 15% 1.6–3.0 m; c. 22% 3.1–4.5 m; c. 28% 4.6–6.0 m; c. 20% 6.1–7.5 m; and c. 10% 7.6–9.0 m (Gill 1980b). In Windbag Valley, most foraging in understorey of forest; of 6997 foraging observations: 2% on ground; 30% in lower understorey; 35% in upper understorey; 18% in shaded canopy (within canopy); 12% in unshaded canopy (on top of

canopy); and 3% in emergent foliage above canopy. **FORAGING SITES AND SOURCES:** Mostly forage among foliage of trees and shrubs. In pine plantation in Kaingaroa Forest, mainly foraged in outer foliage of pines; of 180 foraging observations (data estimated from graph): c. 75% from live needles; c. 5% from dead needles; c. 10% from branches and cones; c. 2% from trunks of trees; c. 2% in understorey; and c. 6% in air. In Christchurch Botanic Gardens, foraged mostly in foliage; of 91 foraging observations (proportions estimated from graph): c. 54% from foliage; c. 34% from twigs; c. 8% from small branches; and c. 4% from large branches. On Little Barrier I., most food collected from foliage of trees and shrubs; of 176 feeding observations: 63.1% among foliage; 25.6% among terminal shoots; 5.7% among twigs; 2.3% from branches; and 2.8% in air. At Kowhai Bush, of 157 foraging observations: 82% among foliage; 12% among twigs; 4% on branches and trunks of trees; 1% in litter layer; and 1% in air. At Kowhai Bush, mainly foraged in *Leptospermum* trees (70–80%) with rest of foraging observations in the legume *Cytisus monspessulans* (9%) or about ten other species of plants (Gill 1980b). In Windbag Valley, foraged in at least 49 species of plants, including 13 canopy species and 36 shrubs and other understorey plants (summarized in Table 1). In NI and Fiordland, SI, mostly forage among foliage of trees (c. 70–80% of obs.) with rest among foliage of shrubs, on branches and trunks of trees, in air and on ground (see Fig. 2 in Keast & Recher 1997). **FORAGING METHODS:** Forage mainly by gleaning from foliage and branches of trees and shrubs; also often sally-hover at foliage or terminal shoots; occasionally sally-strike in air to catch insects, or hang sideways or upside-down (Stidolph 1939; Gibb 1961; East 1967; Gravatt 1971; Gill 1980b). On Little Barrier I., most food taken by gleaning (percentage not given), but large proportion also taken while hovering (38.1%); most hovering was at periphery of mid-storey plants such as Mapou *Myrsine australis*, Mamangi *Coprosma arborea* or round canopy of *Leptospermum*, Hard Beech *Nothofagus truncata* and Kauri *Agathis australis*. At Kowhai Bush, most foraging by gleaning, and also often by sally-hovering; of 161 foraging observations: 54.7% gleaning; 43.4% sallying, including sally-hovering (41.0%), sally-striking on hard substrates (1.2%) and sally-striking in air (1.2%); and 1.9% hanging, mainly upside-down. In Windbag Valley, of 6997 foraging observations, foraged mostly by gleaning (c. 87%); also by sally-hovering (15%); and very occasionally by sally-striking in air (2%). In NI and Fiordland, SI, mostly foraged by gleaning (52% of 126 attempted prey-attacks in NI; and 42% of 118 in SI were gleaning from foliage, but birds also gleaned from branches and trunks) with most of rest by sallying, including sally-striking on hard substrates and sally-striking in air; rarely foraged by hanging (Keast & Recher 1997). Bash caterpillars and large beetles before eating them (Stidolph 1939; CSN 4). Once seen capturing spider from web by hovering in front of centre of web (Abraham 1951). On Snares Is, seen foraging mainly at tips of branches of *Hebe elliptica* (Horning & Horning 1974). Seen sallying for insects over open water of river (CSN 22). Once seen entering house to feed on insects (CSN 33). **SEARCH, ATTACK RATES:** In NI, foraging birds made c. 11 hops/min, c. 18 flights/min and c. 5.5 prey-attacks/min (data estimated from graph); mean distance flown during prey-attacks 1.03 m (0.81; 116). In Fiordland, SI, foraging birds made c. 13 hops/min, c. 16 flights/min and c. 4.5 prey-attacks/min (data estimated from graph); mean distance flown during prey-attacks was 1.11 m (0.86; 94) (Keast & Recher 1997).

**Table 1.** Plant species used for foraging in Windbag Valley (% of total feeding obs.) (O'Donnell & Dilks 1994).

PLANT SPECIES	FOOD ITEMS		
	All feeding (6997 obs.)	Fruit <sup>1</sup> (17 obs.)	Invertebrates (846 obs.)
<b>CANOPY SPECIES</b>			
<i>Dacrydium cupressinum</i>	9.1	5.9	7.6
<i>Dacrycarpus dacrydioides</i>	2.7	–	2.5
<i>Elaeocarpus hookerianus</i>	0.2	–	0.1
<i>Lagarostrobos colensoi</i>	0.2	–	0.5
<i>Libocedrus bidwillii</i>	<0.1	–	–
<i>Metrosideros umbellata</i>	1.8	–	2.0
<i>Nothofagus menziesii</i>	21.4	–	22.3
<i>Podocarpus hallii</i>	0.9	–	0.2
<i>P. totara</i>	0.1	–	–
<i>Prumnopitys ferruginea</i>	4.6	–	3.0
<i>P. taxifolia</i>	<0.1	–	–
<i>Weinmannia racemosa</i>	35.2	–	36.5
Dead trees (various species)	0.3	–	–
<b>SHRUB HARDWOODS</b>			
<i>Aristotelia serrata</i>	0.4	–	0.2
<i>Ascarina lucida</i>	0.6	–	0.4
<i>Carpodetus serratus</i>	0.3	–	0.6
<i>Coprosma</i>	1.0	–	1.2
<i>C. foetidissima</i>	0.3	–	0.4
<i>C. lucida</i>	<0.1	–	–
<i>C. rotundifolia</i>	0.2	–	0.1
<i>Coriaria arborea</i>	<0.1	–	–
<i>Fuchsia excorticata</i>	0.6	–	1.4
<i>Griselinia littoralis</i>	1.2	5.9	1.0
<i>Hedycarya arborea</i>	0.7	–	0.7
<i>Leptospermum scoparium</i>	<0.1	–	–
<i>Meliccytus ramiflorus</i>	0.1	–	–
<i>Myrsine australis</i>	0.3	–	0.4
<i>M. divaricata</i>	0.1	–	0.1
<i>Neomyrtus penunculata</i>	0.8	–	0.4
<i>Olearia</i>	<0.1	–	–
<i>Pennantia corymbosa</i>	0.1	–	0.5
<i>Phyllocladus aspleniifolius</i>	1.0	–	0.8
<i>Pseudopanax colensoi</i>	0.1	–	–
<i>P. crassifolius</i>	1.0	47.1	1.8
<i>P. edgerleyi</i>	0.3	–	–
<i>P. simplex</i>	0.7	35.3	0.2
<i>Pseudowintera colorata</i>	1.7	–	2.0
<i>Shefflera digitata</i>	0.2	–	0.2
<b>OTHERS</b>			
Tree-ferns	4.2	–	4.9
Ferns	0.8	–	0.5
<i>Freycinetia baueriana</i>	0.2	–	0.4
<i>Metrosideros</i>	3.4	–	1.4
Moss	0.3	–	–
<i>Muehlenbeckia australis</i>	0.1	–	–
Orchids	0.1	–	–
<i>Paraxilla</i>	<0.1	–	–
<i>Ripogonum scandens</i>	1.0	–	1.4
<i>Rubus</i>	0.3	–	0.1
<i>Uncinia</i>	<0.1	–	–
<b>NOT IN PLANTS</b>			
Ground/air feeding	2.0	–	3.7

<sup>1</sup> only totals 94.2% in original reference.

**Detailed studies** In ORONGORONGO VALLEY, NI (24 faecal samples from adults, mist-netted Oct. 1973–Aug. 1976; Moed & Fitzgerald 1982; data estimated from graph): **Plants** Unident. c. 4% freq. **DICOTYLEDONS:** Loganiaceae: *Geniostoma ligustrifolium* c. 8 fru., sds. **Animals** **SPIDERS** c. 96: Opiliones c. 4. **INSECTS:** Coleoptera: beetles c. 71; Curculionidae c. 29; Elateridae c. 8; Diptera c. 42; Ephemeroptera c. 4; Hemiptera: bugs c. 33; Cixiidae c. 17; Hymenoptera: wasps c. 42; Formicidae c. 4; Lepidoptera: ads c. 50, larv. c. 67; Neuroptera c. 8; Orthoptera: Gryllacridoidea c. 38; Plecoptera c. 4.

**Other records** **Plants** Fruit<sup>5,9</sup>. **GYMNOSPERMS:** Podocarpaceae: *Dacrydium cupressinum* fru.<sup>7</sup>. **DICOTYLEDONS:** Araliaceae: *Pseudopanax edgerleyi* fru.<sup>7</sup>; *P. simplex* fru.<sup>7</sup>; Cornaceae: *Griselinia littoralis* fru.<sup>7</sup>; Cunoniaceae: *Weinmannia racemosa* fru.<sup>7</sup>. **Animals** **SPIDERS**<sup>2,8,9,10</sup>. **INSECTS:** Ads<sup>3,8,10</sup>, larv.<sup>3,5,10</sup>, eggs<sup>5</sup>: Coleoptera<sup>1,4</sup>; Diptera ads<sup>3</sup>, larv.<sup>4</sup>: Calliphoridae<sup>4</sup>; Chironomidae<sup>4</sup>; Hemiptera<sup>9</sup>: Aphididae<sup>4,10</sup>; Hymenoptera: wasps<sup>4</sup>; Lepidoptera: larv.<sup>5</sup>; ads<sup>1,6</sup>. **Other matter** Cooked rice<sup>11</sup>.

**REFERENCES:** <sup>1</sup> Stidolph 1939; <sup>2</sup> Abraham 1951; <sup>3</sup> Turbott 1967; <sup>4</sup> Horning & Horning 1974; <sup>5</sup> St Paul 1975; <sup>6</sup> Falla *et al.* 1981; <sup>7</sup> O'Donnell & Dilks 1989; <sup>8</sup> Moon 1992; <sup>9</sup> Heather & Robertson 1997; <sup>10</sup> Oliver; <sup>11</sup> CSN 9.

**Young** Fed by both parents; for c. 17 days in nest (15–18 days) and for 3–4 weeks after fledging. Nestlings fed every 5 min or so, usually in bouts of feeding that lasted 30–45 min (Soper 1963; Gill 1982a,b). At Kowhai Bush, fledgelings first caught own food 18 days after fledging, but were also fed by parents for up to 35 days after fledging (Gill 1982a). At Kowhai Bush, feeding rates of a brood of three (B/3) and a brood of four (B/4) nestling Warblers were greater than rate of feeding a single Shining Bronze-Cuckoo nestling; for nestling Warblers, feeding rates were 5 visits/h for B/3 and ten visits/h for B/4 on Days 1–3 of nestling life; 21 visits/h for B/3 and 22 visits/h for B/4 on Days 16–18; rate of feeding of cuckoo 6.5 visits/h on Days 1–3 and 15 visits/h on Days 16–18 (n=36 h of observations of B/4, 17 h of B/3, and 41 h of single Cuckoo); rates were always higher for broods of Warblers than single Cuckoo at any time during nestling period (Gill 1982a).

**Detailed studies** At KOWHAI BUSH (173 items from stomachs of 19 nestlings  $\geq 10$  days old; Gill 1983a): **MOLLUSCS:** Stylommatophores 3.5% no. **SPIDERS** 22.0. **INSECTS:** Unident. 9.2; Coleoptera 5.2; Diptera 12.1; Hemiptera 3.5; Lepidoptera: larv. 41.6; ad. moths 2.9. **Other records** Food offered to young includes: spiders, ants, moths and caterpillars (Soper 1963; Gill 1982b).

**Intake** Nestlings  $\geq 10$  days old were fed insects 1–35 mm long; maximum number of items recorded in stomach of a nestling 31 (n=19 stomachs) (Gill 1983a).

**SOCIAL ORGANIZATION** Well known: breeding studied in detail at Kowhai Bush, Kaikoura, SI, for three seasons from 1976–77 to 1978–79 (Gill 1980a, 1982a, 1983a). **BREEDING SEASON** (late July to Jan.): In territorial pairs (Gill 1978, 1980a, 1982a) and, at Kowhai Bush, not recorded in mixed-species feeding flocks Sept.–Dec. (Dean 1990). **NON-BREEDING SEASON:** At Kowhai Bush, Mar.–July, foraged in small groups of 3–6 birds, and often associated with flocks of other small insectivorous species (see Food); in winter, territorial behaviour absent or weak, though birds lured in by replay of taped calls; gathered in groups of up to 12 with

little antagonism. Recent progeny do not accompany adults in winter (Gill 1980a, 1982a). In another study at Kowhai Bush, in non-breeding season, foraged in pairs or small monospecific flocks, and often in mixed-species feeding flocks (see Food); often foraged just behind main body of flock, and appeared to follow flight-calls of Brown Creepers (Dean 1990). On Little Barrier I., in July, more likely than not to be found in a mixed-species feeding flock; noted six times on edge of mixed-species flocks and once in middle (McLean *et al.* 1987). For species in mixed-species feeding flocks, see Food; also occasionally occur in flocks with New Zealand Tomtits *Petroica macrocephala* (Dean 1990; NZRD). McLean & Rhodes (1991) noted that Grey Warblers did not form monospecific flocks and, *contra* above observations, were usually solitary.

**Bonds** Monogamous (Gill 1978, 1980a, 1982a). During 3-year study, one pair bred together for 3 years, another pair for 2 years (then both disappeared), and one pair for 1 year, then female bred with another male for next two seasons, and male eventually bred with another female; at least four pairs remained together for more than one season. At least four changes in partners observed, all involving nearest neighbours, within 100 m. Sometimes changed mates for reasons other than death or emigration of previous partner, but rarely within a breeding season (Gill 1980a, 1982a). Members of pairs often seen together outside breeding season (Gill 1980a). **AGE OF FIRST BREEDING:** At Kowhai Bush, some young males held territories in breeding season after fledging, but not known if they had mates, though at least one did; such males with mates thought to be rarely successful in first breeding season. One male bred successfully in second year after fledging. One probable female noted in breeding population 2 years after fledging (Gill 1980a, 1983a). **Parental care** Only female incubates and broods; both sexes feed nestlings and fledgelings (Gill 1982a, 1983a). After fledging, young of early broods of season usually stay together for 1–3 weeks and are fed by both adults, though male often does most feeding if only two young fledge; for next 1–3 weeks, male often attends young alone, while female occasionally leaves to build second nest; when with family group, she often eats food she collects and ignores, or drives off, her begging young (Gill 1978, 1980a, 1983a); one female fed young on day she laid second clutch (Gill 1980a). One female moulted while mate still fed single young that had fledged 18 days before (Gill 1983a). Occasionally, parents divide broods between them; both parties stay near each other, but each juvenile begs to, and receives food from, only one parent. Twice an adult Warbler was seen feeding an unrelated juvenile in addition to its own (Gill 1983a). **INDEPENDENCE OF YOUNG:** Young fed for 28–35 days after fledging, with some up to 38 days; young catch some of their own prey after 18 days (Gill 1980a, 1982a); also said to be fed for 3 weeks after leaving nest (Falla *et al.* 1979; Oliver). Usually show increasing signs of independence c. 30 days after fledging, when begging declines, parents become aggressive towards their young, and young begin to move farther from the group (Gill 1980a). Once independent, most juveniles disperse from natal area or die (Gill 1980a, 1982a). Often disperse quietly and secretively, though sometimes chased from territories by resident adults; however, often they are tolerated by their parents (Gill 1983a). Usually have left parents by winter (Gill 1982a). During study at Kowhai Bush, of young that fledged, six of 100 birds were recruited into breeding population: one bird (probable female) seen near

natal territory; four males had established territories 2.3, 0.8, 0.7 and 0.6 km from their natal territories; and one male was found on territory 0.4 km from where it was banded as a juvenile (Gill 1982a, 1983a).

**Breeding dispersion** Nest solitarily (Gill 1978, 1980a, 1982a). Distance between concurrent nests of neighbouring pairs in tall dense forest, 72 m (11.0; 57–95; 10); in stunted open forest, where territories larger, 112 m (23.5; 71–154; 14) (Gill 1980a). On Motuhoropapa I., Noises Grp, 13–14 territories in area of 9.5 ha (Cunningham & Moors 1985). **Territories** During breeding season (late July to Jan.), both members of pair defend all-purpose territory, driving away any conspecifics other than their own dependent young (Gill 1978, 1980a, 1982a). Young, apparently unpaired males also sing and defend territories against neighbours (Gill 1983a). Defence of territories apparently stops after breeding; in winter, territories seem to expand into overlapping home-ranges, but adults are still sedentary (Gill 1980a, 1982a). In pairs, male apparently more active in defence near boundaries, while both sexes defend near nest (Gill 1980a, 1982a); female sometimes stop incubating or brooding to chase intruder near nest (Gill 1982a). Boundaries determined by contest with neighbours, and conspecifics seem to trespass at any opportunity (Gill 1980a, 1982a). Some overlap of adjacent territories (Gill 1980a). Mean size of territories 0.68 ha (0.34; 0.25–1.73; 34) with largest being seven times that of smallest; size varies with habitat. Possible that boundaries of some territories change during breeding season. In breeding season each year at Kowhai Bush, banded birds used same territories, with any changes in boundaries or partner involving nearest neighbours from distances of <100 m (Gill 1980a, 1982a); on Motuhoropapa I., Noises Grp, boundaries of territories changed little between years (Cunningham & Moors 1985). Once, chased a Rifleman *Acanthisitta chloris* and snapped bill at it (Stidolph 1939). In mixed-species feeding flocks, very occasionally chased by Brown Creepers (Dean 1990). **Home-range** Birds stay in home-ranges outside breeding season; breeding territories seem to expand into home-ranges that overlap with those of other warblers, with adults moving up to 100 m beyond their breeding boundaries. Of 52 birds banded in study area in winter, 18 (35%) held territories there during next breeding season, all within 100 m of where they were banded (Gill 1980a, 1982a).

**Roosting** No information.

**SOCIAL BEHAVIOUR** Quite well known from breeding studies described in Social Organization. Behavioural responses to cuckoos near nest also studied (McLean & Rhodes 1991). Male and female distinguishable by behaviour: only adult males give full Song, whereas females and independent juveniles, at most, only give Subsong; males perform Wing-fluttering Display that is rarely seen in females; and only female builds nest, incubates or broods, thus any birds entering nests (cf. merely perching at entrance) are females (Gill 1983a).

**Agonistic behaviour** Usually not pugnacious (Stidolph 1943). **Territorial advertising** Males sing to advertise ownership of territories (Gill 1980a, 1983a); sing throughout year (Marples 1944; Gill 1982a, 1983a), though intensity varies, with rate of Singing probably directly reflecting level of territorial behaviour (Gill 1980a); Song seems weakest in winter, with full Song increasing through winter to a maximum in spring and summer (see Voice), coinciding with peaks of laying (Gill 1982a; Gill *et al.* 1983). Sing at all stages of repro-

ductive cycle: vocal when accompanying female to and from nest during building; and sing while attending fledgelings (Stidolph 1925; Gill 1980a). Males sing from both prominent and insignificant perches (Gill 1980a). Approach in response to replay of taped calls and imitation (see Voice). **Attack** Males fight to defend territories (Gill 1983a). **CHASING:** At territorial boundaries, most disputes settled by rapid chases in wide circles where Chattering calls are heard. Chasing often begins with two birds giving a spiralling flight up to 20 m above canopy, and ends several tens of seconds later, with antagonists separating c. 20 m from starting point. Third and fourth birds, possibly females, sometimes join in (Gill 1980a). Territorial boundary disputes tend to involve chasing rather than physical contact (Gill 1980a, 1982a). **Fighting** Rivals sometimes fight in spring (Stidolph 1939). In May, two apparent males fought in presence of a female for most of day; tumbled over ground with bills locked together, and chased each other into the air, sometimes bill to bill with tails spread; all fighting was silent, except for clicking of bills; female sometimes joined chase, giving shrill calls and pecking at antagonists (Stidolph 1943). When two males fighting, they sometimes paused to sing (Stidolph 1943). **Alarm** Respond to replay of taped alarm calls of native species involved in mixed-species feeding flocks (McLean & Rhodes 1991). When handled by banders, adults raised feathers of crown (Gill 1983a). Song may also be used in alarm, e.g. short Songs given in response to model Shining Bronze-Cuckoo (McLean & Rhodes 1991); short snatches of Song from male (and short Trills from both sexes) when observer within 2 m of nest (Stidolph 1939); and agitated Song (in succession to Twitter) said to be given in anger or distress (St Paul 1975). At Kowhai Bush, males sang at or near their nests in response to disturbance from other species of birds, especially Bellbirds *Anthornis melanura* and New Zealand Robins *Petroica australis*, or humans (Gill 1980a).

**Sexual behaviour** Some singing by males possibly sexual in function (see above). Spreading of wings and tail is a common display at all stages of nesting cycle, and possibly reinforces pair-bond and synchronizes activities of pair (Gill 1983a). **WING-FLUTTERING DISPLAY:** Male vigorously flaps half-outstretched wings while advancing along a perch; occurs at all stages of breeding and given mainly in presence of female; rarely seen in females (Gill 1983a). **NEST-SITE SELECTION** thought to be associated with following behaviour: female flies in wide circles, constantly twittering and with male close by; she then collects material and flies to twig, closely followed by male, who perches 10–20 cm away; female leans backwards, almost hanging, for 4–5 s with head and body vertically aligned, tail spread and wings outstretched; male does likewise while female, still hanging, binds material round twig with her bill, then resumes normal perching position. Male then perches normally and sings before both birds leave; sequence often repeated after a few minutes (Gill 1983a). **NEST-BUILDING:** Female collects nesting material and builds nests, with male often accompanying her to and from nest (Stidolph 1939; Bull 1943; Gill 1980a, 1982a, 1983a; Oliver), though later in season, female often builds alone as male tends fledgelings (Gill 1983a); said that male sometimes carries material but female builds it into nest (Falla *et al.* 1979; Oliver). Stidolph (1939) noted that male sings while quivering wings, while female builds nest. Courtship feeding between adults not seen at any stage of nesting cycle (Gill 1982a). Females often join males between bouts of incubation (Gill 1983a). **Copulation** At Kowhai

Bush, seen late Oct. to mid-Dec.; once, 14 days before first eggs laid, once on day first egg laid, and once on day third egg laid; one apparently fruitless copulation seen 1 month before male began to moult. Occurs on ground or on perches, some of which nearly vertical. Mounting lasts <10 s, but is usually repeated, with male alternately balancing on female's back by constantly fluttering his wings and perching beside her. Female moves her tail to allow cloacal contact, sometimes while holding nesting material or food in bill; Chattering given on at least one occasion by female (Gill 1980a, 1983a).

**Relations within family groups** During incubation or when feeding nestlings, parents approach nest cautiously and indirectly (Gill 1983a); during incubation, female flies rapidly to perch 5–10 m from nest, then immediately enters nest (McLean & Rhodes 1991). Male always delivers food directly to young, never when female on nest (Gill 1980a, 1982a).

**BEHAVIOURAL DEVELOPMENT OF YOUNG:** Newly hatched young rest on abdomen in foetal or 'egg' position, doing little other than raising head to gape. On Day 4, show signs of grasping lining of nest, and give faint cheeping (begging calls) in the hand. On Day 7, young able to right themselves when inverted; when at rest, grip with toes, hold wings against body and hunch head without raising it. On Day 8, shuffle in nest and can be heard cheeping from 5 m away. On Days 8–12, start to raise head, look sideways and responsive to visual stimuli. On Day 12, able to grasp twigs but not raise own weight; if made to perch, rest on belly. After Day 12, give single cheeps almost continuously, and rapid cheeping when parent arrives with food (Gill 1983a). Fledgelings give short peeps when parents absent, which turn into whines as parents approach with food (McLean & Waas 1987). Sometimes nestlings crowd entrance and beg vigorously, forcing parent to deliver food from adjacent twig. When removed from nest, older nestlings sought cover of dark cavities, but near fledging, stayed in light and gaped at objects thrust close to their bills (Gill 1983a). After leaving nest, young said to have distinctive calls in addition to begging call (Falla *et al.* 1979). Young Shining Bronze-Cuckoos in nests with young Warblers briefly compete for food before pushing Warblers out (Gill 1979, 1983c). For reaction of parents to begging calls of Shining Bronze-Cuckoos, see HANZAB 4 and McLean & Rhodes (1991).

**Anti-predator responses of young** When handled: 2–3 days after hatching, nestlings struggled by stroking legs, and clenching and unclenching toes; on Day 4, started cheeping; on Day 5, squealed (protest calls). On about Day 13, raised feathers of crown when bill measured. When parents away from nest, young nestlings lay prostrate, pressed against one another and camouflaged with lining of nest; if handled, clung to floor of nest, and if dislodged, squealed loudly. When approached, nestlings usually never left nest suddenly, unless about to fledge anyway (Gill 1983a), though nestlings that had not been handled much sometimes left if unduly disturbed (Gill 1982a).

**Parental anti-predator strategies** At nest, some birds tame and confiding when people near, others not (Stidolph 1939). Sing in response to people near nest (Gill 1980a). One pair fed young when camera c. 2 m from nest (Stidolph 1939); another female allowed small nestlings to be removed beneath her while she continued to brood (Gill 1983a). When nestlings squeal in alarm, parents usually respond immediately, both bill-clicking, growling and giving agitated trilling while they hover, perch and swoop to within centimetres of the squealing young; similar responses given in defence of fledgelings (Gill 1983a). In experimental

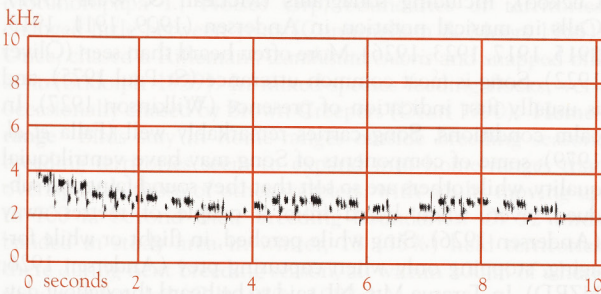
study of reaction of parents to Shining Bronze-Cuckoos near nests, when models of a European Greenfinch *Carduelis chloris* and a Bronze-Cuckoo were placed near nests during incubation, Warbler parents responded to Cuckoo as a threat. Usual reaction of female returning to nest was to move away from nest and inspect model; and females become more agitated when Cuckoo was present than when Greenfinch present; one remained still on perch 2 m from Cuckoo and 0.5 m from nest for 16 min, even though Cuckoo was removed after 1 min; female then moved head, but stayed on perch for a further 9 min, when male arrived. If male arrived with female, he usually gave alarm calls and swooped at model of Cuckoo; only one female gave alarm calls, and none swooped. Such reactions by males were not usually made to model of Greenfinch. When model of Cuckoo was placed near nest for 1 min, return to nest by female was delayed significantly; during this delay, some females inspected site where Cuckoo model had been, and gave alarm calls or short Songs. The next incubation stint was also significantly longer, and at end of stint, female stayed close to nest, rarely moving >15 m away (McLean & Rhodes 1991). At Kowhai Bush, there seemed to be no evidence of antiparasitic behaviour, such as abandoning parasitized nests, removal of parasite's egg, or burying entire clutch under fresh nesting material and laying again (Gill 1983c).

**VOICE** Song quite well known, but other vocalizations poorly known. Detailed studies of breeding, including information on calls (Gill 1980a, 1982a, 1983a); of singing through year (Marples 1944; Cunningham 1955); and of begging calls of young (and of young of parasitic Shining Bronze-Cuckoo), including sonagrams (McLean & Waas 1987). Calls in musical notation in Andersen (1909, 1911, 1913, 1915, 1917, 1923, 1926). More often heard than seen (Oliver 1922). Song is most common utterance (St Paul 1975), and is usually first indication of presence (Wilkinson 1927). In calm conditions, Song carries remarkably well (Falla *et al.* 1979); some of components of Song may have ventriloquial quality, while others are so soft that they sound faint and subdued, even when heard from a couple of metres away (Andersen 1926). Sing while perched, in flight or while foraging, stopping only when capturing prey (Andersen 1926; NZRD). In Tararua Mts, NI, said to be heard throughout day, but months of visit not stated (Wilkinson 1924). Song at its best, louder and most persistent in spring, especially during courtship and construction of nest (Buller 1888; McLean 1911; Stidolph 1925, 1939; Marples 1944); a Maori saying regarding laziness is *I hea koe i te tangihanga o te riroriro* ('Where were you at the crying of the riroriro?'), a reference to Song in spring, the season for planting (Colenso 1880). At Dunedin, SI, Song heard throughout year, though there is a marked decline in winter; main peak in Sept. or Oct., falling to a minimum in Dec. or Jan., and reaching another peak in Feb. or Mar., with a subsequent decline in winter (Marples 1944). At Masterton, NI, Song occasional in May, and increases through winter to maximum in last half of Sept., corresponding with laying; there is a second but smaller peak in latter half of Nov., corresponding with laying of second clutches, after which declines to a second minimum in Jan., when breeding stops, and then increases to an unexplained slight peak in Mar. (Cunningham 1955; Gill 1980a). Only adult males give full Song, whereas females and independent juveniles at most give occasional tuneful Subsongs (Gill 1983a). **GEOGRAPHICAL AND INDIVIDUAL VARIATION:** Song



varies regionally (Stidolph 1939; Marples 1944); some such variants described below. Individual birds may be identified by their Songs (Stidolph 1939). **RESPONSE TO PLAYBACK:** Respond to imitation (Buller 1888), and attracted by recordings of Song, even in winter, but quickly become accustomed to a particular recording (Gill 1980a, 1982a, 1983a). **NON-VOCAL SOUNDS:** When two males were fighting, clicking of bills audible (Stidolph 1943). In response to squeals of nestlings being handled, parents clicked bills (and also uttered Trills and Growls), while swooping, hovering or perching within centimetres of nestlings (Gill 1983a). One bird snapped its bill at a Rifleman (Stidolph 1939).

**Adult SONG:** Song (sonagram A) variously described as: soft, sweet trilling warble, sometimes subdued, regular and cricket-like (Buller 1888); cheery trilling notes (Wilkinson 1924); long plaintive, rambling indeterminate trill, at c. 8 notes/s, usually lasting c. 5 s, but sometimes as long as 12 s (Andersen 1909, 1911, 1926; Marples 1944); and shrill trilling (St Paul 1975). Do not weave several themes into one Song, but rather appear to have a number of themes, and sing sometimes one, sometimes another, lengthening Song merely by repetition (Andersen 1926). May be broken off suddenly when apparently not complete (St Paul 1975). Varies regionally: near Wairarapa, NI, high-pitched *chee-ree* and low-pitched *chee-ree*; near Wellington, NI, *chee-ree-e re-rare-re*; and near Paekakariki, NI, *che-reeeeeeee* on a descending scale (Stidolph 1939). Song is given only by males and is important in maintaining territories (Gill 1980a). May also be used in alarm or during aggressive encounters (see Social Behaviour). **SUBSONG:** Occasional tuneful subsongs are uttered by females and independent juveniles (Gill 1983a).



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

**TWITTER:** Constant twittering given when a female apparently selects nest-site (Gill 1983a). Shrill or rapidly repeated twitter (perhaps succeeded by agitated Song), in anger, distress or agitation (St Paul 1975; NZRD). Faint, cheerful twittering conversation, sometimes barely audible, may be uttered by two foraging birds (Andersen 1926); small twitter given when recovering dropped beetle (Stidolph 1939). Shrill twitter (as well as repeated short, shrill little cries) given by female observing two males who were fighting (Stidolph 1943). **TRILL:** Short trill from each sex when feeding, often when alighting on branch (Stidolph 1939). Both sexes gave short trills (and male short snatches of Song) when observer within 2 m of nest (Stidolph 1939). In response to squeals of nestlings being handled, parents trilled in an agitated fashion (see above) (Gill 1983a). **GROWL:** In response to squeals of nestlings being handled, parents growled (see above) (Gill 1983a). **CHATTER:** A distinctive chattering call accompanies chasing during boundary disputes, but whether given by bird

in pursuit or being pursued not known (Gill 1980a). **HARSH CHATTER:** Harsh chattering given during copulation, by female on at least one occasion (Gill 1980a, 1983a). **DOWNSLURRED CALLS:** Short downslurred calls (and Song) given by male, while female apparently laying (Gill 1983a). **Other calls** Repeated short shrill little cries (as well as Twitter) given by female observing two males who were fighting (Stidolph 1943). Calls given in alarm (as well as short Songs), but not described further, given in response to model Shining Bronze-Cuckoo (McLean & Rhodes 1991).

**Young** When 4 days old, faint cheeping, a begging call, uttered when handled; from 5 days, give loud squeal of protest if taken from nest; older nestlings give single cheeps, breaking into rapid cheeping whenever a parent arrives with food (Gill 1983a). Newly fledged young utter an incessant but scarcely audible piping note (Buller 1888). Dependent fledgelings give short *peeps* when parents absent, becoming longer whines as parent approaches with food; *peep* of one dependent fledgeling: length of note 40 ms, interval between notes 450 ms, uttered 3.1 notes/s, main frequency 7.78 kHz and frequency range 3.65–8.1 kHz; whine of same fledgeling: length of note 50 ms, interval 350 ms, 3.5 notes/s, main frequency 7.78 kHz and frequency range 3.65–8.25 kHz (McLean & Waas 1987). Dispersing juveniles can often be distinguished by their quietness (Gill 1983a).

**BREEDING** Well known; detailed study of breeding biology and parasitism by Shining Bronze-Cuckoo, over three seasons from 1976 to 1979 at Kowhai Bush, Kaikoura, SI (Gill 1980a, 1982a,b, 1983a,c). Solitary and monogamous (Gill 1982a).

**Season** Throughout range, breeding recorded mid-June to Jan. (Stidolph 1925, 1939; Gill 1980a, 1982a; Oliver; see below). Throughout range, of 55 records in NZ NRS and a few published breeding reports (Stidolph 1939; Gill 1980a; CSN 1), most indicate laying between mid-Aug. and early Dec., with exceptional cases in mid-June, July and early Jan. At Kowhai Bush, laying recorded over 15–16 weeks (with laying of first clutches spread over at least 5 or 6 weeks; see below), between last week in Aug. and third week in Dec., but with bimodal distribution; total time from first building to last fledging 27 weeks. Laying by week for 1976–77 and 1977–78 seasons summarized in Table 2. When nests divided into categories of early in season (before 23 Oct.) and late in season (after 23 Oct.), which probably reflect first and second clutches respectively: laying of first clutches was spread over 5–6 weeks, but later nests were less synchronous, as some birds were replacing unsuccessful earlier nests while others were continuing uninterrupted. At Kowhai Bush, most building early Aug. to late Nov., though exceptional cases in early June, July and late Dec. indicate that sometimes breed very early, even while day-length is still decreasing (Gill 1980a). Bimodal distribution obvious at Kowhai Bush, but obscured in data from throughout range, otherwise seasonal pattern appears similar across range (Gill 1980a).

**Site** Nest in a variety of native and introduced trees, shrubs and, sometimes, vines, usually among outer branches and foliage and, at least at Kowhai Bush, with preference for small-leaved species. From NZ NRS, nests were in at least 40 different plant species, including 16 exotics (n=130 nests); 35% were in Manuka *Leptospermum scoparium*, 11% in Golden Gorse *Ulex europaeus*, 7% in *Coprosma* and 5% in Matagouri *Discaria toumatou* (Gill 1983a). At Kowhai Bush, recorded nesting in 19 species of trees and shrubs (including

five exotic species), mostly small-leaved species and especially Kanuka *Kunzea ericoides*, which was dominant plant in area; of 129 nests, most (69%) were in plants with leaves <2 cm long, including 33% in Kanuka and 26% in three small-leaved exotic Golden Gorse, Montpellier Broom and Broom *Cytisus scoparius*. Plants used include: those WITH LEAVES <2 CM LONG, such as *Coprosma propinqua*, Mingimingi, Montpellier Broom, Broom, *Helichrysum aggregatum*, Kanuka, Manuka and Golden Gorse; those WITH LEAVES 2–4 CM LONG, such as Putaputaweta *Carpodetus serratus*, Traveller's Joy *Clematis vitalba*, *Coprosma propinqua* × *robusta*, Kohuhu *Pittosporum tenuifolium* and Sweet Briar *Rosa rubiginosa*; and those WITH LEAVES >4 CM LONG such as Karamu *Coprosma robusta*, Tutu *Coriaria arborea*, Akeake *Dodonaea viscosa*, Mahoe *Meliccytus ramiflorus*, Akiraho *Olearia paniculata* and Tarata *Pittosporum eugenioides*. Suggested that probably preferred small-leaved species because attachment of nests was easier, camouflage was better where branching was dense, and because spines of gorse and needle-like leaves of *Leptospermum* and Mingimingi deterred predators. Nearly all nests at Kowhai Bush (94% of 92 nests) were attached to live vegetation, and the exceptions, while attached to dead twigs, were often surrounded by live foliage from adjacent branches (Gill 1983a). Also reported in Tawa *Beilschmiedia tawa*, willow *Salix*, *Muehlenbeckia*, *Macrocarpa*, eucalypts, Stinkwood *Coprosma foetidissima*, *Cyathodes* growing beneath beech trees, and in a white rata vine growing against trunk of Ribbonwood *Hoheria glabrata* (Stidolph 1923, 1939; Moncrieff 1932; Sibson 1947; Pennycook 1949; Weeks 1949; St Paul 1975; Gill 1983a; Oliver; CSN 3). Nests sometimes well concealed, but sometimes in very open situations and visible at considerable distance (Stidolph 1939). **ORIENTATION:** Direction of entrance was found to be non-random, but not directly related to direction of prevailing wind (Gill 1980a, 1983a). **SELECTION OF SITE:** In three cases, nest at first site chosen was not finished, and new nests were built 30, 36 and 52 m away (Gill 1983a). For further details of behaviour when selecting site, see Social Behaviour. **DISPERSION:** At Kowhai Bush, concurrent nests of neighbouring pairs were closer in one habitat than another: mean distance of 72 m (11.0; 57–95; 10) apart in tall dense Kanuka forest, and 112 m (23.5; 71–154; 14) apart in stunted open Kanuka forest, the difference being associated with different sizes of territories (see Habitat, Social Organization). Distance between early and late nests of same pair was 47 m (29.5; 16–111; 15) in tall dense forest and 48 m (23.2; 26–85; 5) stunted open forest, and difference not significant (Gill 1980a). **SITE-FIDELITY:** Said that certain birds prefer particular sites, and that possible to identify owners of nest from its position, e.g. one pair invariably built nest 0.76–0.91 m above ground in middle of a 1.8 m tall Manuka, while another pair always

built c. 4.6 m above ground on end of Manuka branch (Stidolph 1939). **MEASUREMENTS (m):** From NZ NRS, 2.7 (2.80; 0.3–21.3; 135). At Kowhai Bush: all nests, 3.2 (1.93; 0.7–9.0; 103) (Gill 1983a); height of nest 3.5 (2.25; 0.8–8.5; 42); of these, early nests were built significantly higher than late nests: early in season, 4.5 (2.06; 0.9–8.5; 29), and late in season, 2.5 (2.05; 0.8–8.0; 13). Said to nest 0.6–7.5 m above ground (Stidolph 1939; Oliver). Height of nest-plant: At Kowhai Bush, 4.4 tall (2.46; 1.2–11; 97) in subcanopy or shrub layer, below canopy 9.5 (2.61; 4.4–17.0; 94) tall; early in season, nest in plants 5.1 (2.47; 1.2–11.0; 60) tall, and late in season, in plants 3.3 (2.01; 1.2–8.5; 37) tall. Early in season, ratio of height of nest to height of canopy 0.45 (0.28; 0.08–1.00; 58); late in season, 0.27 (0.22; 0.06–0.94; 36). Ratio of height of nest to height of nest-plant varied with habitat: in stunted open Kanuka forest with no understorey, nest closer to canopy than in dense Kanuka forest; ratio of height of nest to height of canopy 0.60 (n=22 nests in stunted open forest, 5–12 m high, on stony soils), 0.36 (n=24 nests in dense forest, 7–13 m high, on silty-sandy soils) and 0.34 (n=29 nests in dense forest, 10–15 m high, on silty soils) (Gill 1980a, 1982a). In comparison between first and subsequent nests of same pair in same season, eight of 22 pairs were in same species of nest-plant; 16 of 22 late nests were lower than corresponding earlier nests, and 13 of 17 were in shorter trees; the ratio of height of nest to height of tree was lower for ten of 17 late nests; and the ratio of height of nest to height of canopy was lower for 14 of 17 late nests (Gill 1983a).

**Nest, Materials** Nests vary in size and shape: pear-shaped or bottle-shaped, some with suggestion of a tail; some have a distinct roof or hood over side entrance, which is nearer top of nest than bottom (Stidolph 1939). At Kowhai Bush, tails were present on 63% of 89 nests, and either hung freely or were involved in attachment of nest; 94% of 88 nests had hoods; and 14% of 81 nests had a ledge that extended from lower rim of entrance (Gill 1983a). Once, hood deteriorated into flap over entrance, and another was attached to a twig (Stidolph 1939). Outer layer of nest formed from dark brownish grey-green fabric made from a framework of rootlets and grass stems filled out with fine matter, such as moss and wool, and bound together with spider web; some have layer of wool or *Clematis* seeds between outer layer and lining (Gill 1983a). Usually made from pieces of bark and dry grass, 2.5–12.7 cm long, rootlets, moss, spider web and spider egg-sacs, and lined with feathers, plant-down or 'fern fur' (Stidolph 1939). Materials recorded (Kowhai Bush and NZ NRS combined) include: moss, spider web and egg-sacs, lichen, wool, hair from horses, cows, deer and people, feathers, leaves (including leaf-skeletons and pine-needles), grass-stems, scales and fibre from ferns, twigs, bark, rootlets, plant-down, downy catkins of willow, decayed wood,

**Table 2.** Laying by week for 1976–77 and 1977–78 seasons at Kowhai Bush. Figures in parentheses are known second clutches (included in total) (from Gill 1980a, 1983a; Gill *et al.* 1983).

	AUG.					SEPT.					OCT.					NOV.					DEC.		
	25	1	8	15	22	29	6	13	20	27	3	10	17	24	1	8	15						
1976–77	–	6	25	22	11	4	5	4	0	0	1	8(2)	9(7)	10(0)	4(3)	2(1)	1						
1977–78	10	10	16	17	6	3	6 <sup>A</sup>	3 <sup>B</sup>	3(3)	14(7) <sup>C</sup>	15(8) <sup>D</sup>	10(6)	7(3)	4	4	–	–						
TOTAL	10	16	41	39	17	7	11	7	3	14	16	18	16	14	8	2	1						

A–D: Known number of replacement clutches (included in total): A 4 clutches; B 3; C 1; D 3.

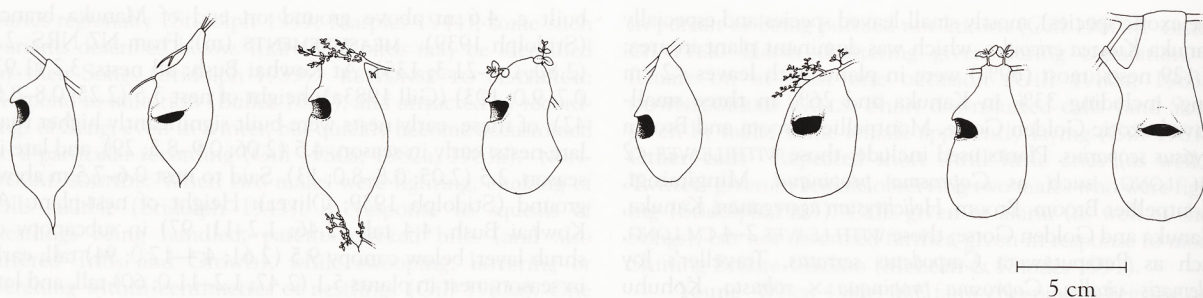


Figure 1. Examples of nest shapes (Source: Fig. 3, Gill 1983a)

fine creepers and scraps of paper; lining includes feathers (one at Kowhai Bush contained 255 feathers), downy seeds and scales of tree-ferns (Gill 1983a). One nest was lined mostly with feathers of European Greenfinch, another contained a few pheasant *Phasianus* feathers, and another had feathers of Pukeko *Porphyrio melanotus* (Stidolph 1939). One nest was made almost entirely of scales from trunk of tree-fern, with moss added to exterior (Stidolph 1939); another was mostly of moss, dry rootlets and stems, and lined with white feathers; hood was conspicuous and built almost entirely from dry rootlets (Stidolph 1925). At Kowhai Bush, 46% of nests were pensive, with rest secured at many points in a matrix of surrounding twigs: 25% had significant lateral attachments only, 16% were attached both laterally and below and 13% were secured below but not laterally (Gill 1982a, 1983a); said that nests are almost always braced in some way (Stidolph 1939). **ROLE OF SEXES IN BUILDING:** Only female collects material and builds nest; usually accompanied by male, at least early in season; later, male may attend fledgelings while female builds alone; female flies directly to nest after collecting material (Stidolph 1939; Bull 1943; Gill 1980a, 1982a, 1983a; Oliver; see Social Behaviour). Said that male sometimes carries material, but female incorporates it into nest (Falla *et al.* 1979; Oliver). Once, female seen pulling small pieces of bark from a tree and arranging them in her bill; on arrival at nest, much material protruded from both sides of bill. **CONSTRUCTION:** Nest built from top down: once support has been started, bird perches on it and adds material to bottom, hanging downwards or sideways, till nest reaches desired length; bird then builds body of nest, pushing sides outward and adding lining. Sometimes stay at nest for only 2–3 s, and may pay several visits in as many minutes, then leave for 10–15 min to forage (Stidolph 1939). Material gathered from up to 30–60 m from nest (Stidolph 1939). Early nests (see season above) built on average in 22 days (16–27; 7); other nests, between Aug. and Oct., built in c. 3 weeks, with a possible minimum of 12 days; entrance and central cavity formed after 5–10 days. Late nests (see season above) built about three times more quickly than early ones; of six late nests, five took 7 days to complete and another 9 days; once, lining material was added after first egg laid. New nests built for each clutch; male often absent, caring for young of previous brood, during construction of late nests (Gill 1980a, 1982a). Also said that takes about a week to build nest (Stidolph 1939; Oliver), though apparently complete nests are often left for 2 weeks before laying (Stidolph 1939; see Laying). Take up to four times longer to build nests than other native passerines, but nest is large relative to size of bird (Gill 1980a, 1982a). **SIMILARITY OF FIRST AND SECOND NESTS OF A PAIR:** At Kowhai Bush, nine of 14 nest pairs were pensive to a

similar degree; presence of hood was consistent in 13 pairs; and presence of ledge consistent in eight of ten pairs; direction of entrance was similar in 13 of 15 pairs; external depth was within 1 cm in six of seven pairs; presence of beard was similar in only six of 12 nest pairs (Gill 1983a). **MEASUREMENTS (cm):** Summarized in Table 3. An average nest 14 long  $\times$  7 wide, with diameter of entrance 3 (Gill 1982a, 1983a); said to have external height 16.5, external diameter 8.9 and entrance diameter 2.5 (Stidolph 1939). At Kowhai Bush, deepest entrance (6.0) was also widest (3.5), and smallest was  $2.0 \times 2.0$ ; exceptionally low-slung nest had external depth of 21.0 (Gill 1983a). One had external diameter 8.9, external height 12.1; diameter of entrance 3.2, hood over entrance 1.0 (Stidolph 1925). **WEIGHT:** 9.7 (5.6–18.0; 23), heavy relative to weight of adult birds (Gill 1980a).

**Eggs** Pale pink or white, with reddish-brown spots or speckles, usually concentrated, and sometimes forming a more or less distinct ring, at large end (Stidolph 1939; Gill 1980a, 1982a; Oliver). Speckling varied both within and between clutches, from almost none to intensive, and blotches ranged from minute to c. 1.5 mm wide; occasionally, eggs were speckled uniformly (Gill 1983a). Early writers reported pure white eggs, attributed to young birds or separate species, but these are not mentioned in recent literature and none found at Kowhai Bush (Gill 1983a). Shell is translucent and slightly pink when fresh, but becomes chalky white and opaque with incubation (Gill 1983a). **MEASUREMENTS:** At Kowhai Bush, 17.1 (0.77; 15.8–18.8; 31)  $\times$  12.08 (0.39; 11.3–13.0; 32) (Gill 1980a); longest egg was among the narrowest ( $18.8 \times 11.4$ ), and shortest was among the widest, ( $15.8 \times 12.2$ ), but no statistical correlation between length and width (Gill 1983a). Late eggs were significantly ( $P < 0.01$ ) wider than early eggs (12.23 cf. 11.96), but not significantly different in length (17.21 cf. 16.95) (Gill 1983a). Also given as  $15.5 \times 11.8$ ,  $17.5 \times 12.5$  (Oliver). Shining Bronze-Cuckoo

Table 3. Measurements of nests at Kowhai Bush (from Gill 1983a).

NEST DIMENSION	MEASUREMENT (CM)
Width of entrance	2.9 (0.33; 2.0–3.5; 61)
Depth of entrance	2.8 (0.68; 2.0–6.0; 61)
External depth	14.0 (1.65; 10.0–16.5; 58) <sup>A</sup>
Internal depth below entrance	4.0 (1.08; 2.0–6.0; 27)
External frontal diameter	7.2 (0.72; 5.5–8.5; 56)
External lateral diameter	7.5 (0.81; 6.0–9.0; 55)
Length of tail	6.6 (3.85; 2.0–19.0; 35)
Length of hood	2.9 (0.87; 1.5–4.5; 49)

<sup>A</sup> Excludes low-slung nest of 21.0 mm.

eggs in Warbler nests measured  $18.7 \times 12.6$  (Gill 1980a, 1983a). **WEIGHT:** Large relative to size of bird. Within 6 h of laying 1.49 (0.08; 1.4–1.6; 9); mean weight on day before hatching 1.13 (0.04; 1.1–1.2; 7); eggs lost c. 24% of their weight during incubation.

**Clutch-size** Usually three or four, rarely two or five (Stidolph 1939; Gill 1980a). At Kowhai Bush, overall clutch-size was 3.93 (0.31; 3–5; 60); C/3  $\times$  5, C/4  $\times$  54 and C/5  $\times$  1 (excluding two apparent clutches of two and a few of three, suspected to be incomplete through loss of eggs); no significant difference in clutch-size between nests in stunted open Kanuka forest with patchy understorey (mean clutch-size 4.0; n=17) and tall dense Kanuka forest with low dense understorey (mean 3.91; n=21); also no significant difference in clutch-size early in season 3.97 (0.28; 3–5; 39) and late in season 3.86 (0.36; 3–4; 21) (Gill 1980a). Of records in NZ NRS: 91 clutches contained up to four eggs and only two contained five (Gill 1982a).

**Laying** At Kowhai Bush, laying interval 2 days (n=67) with one exception, an apparent interval of 3 days (or egg laid after 11:30 on Day 2); from NZ NRS, laying interval 2 days  $\times$  3, and between 2 and 3 days  $\times$  2 (Gill 1980a). Also said that eggs not always laid on successive days (Stidolph 1939). At Kowhai Bush, for nests early in season, which usually first clutches, interval between completion of nest and laying of first egg 4.3 days (2–8; 12), but interval for nests later in season (n=3) only 1–2 days (Gill 1980a, 1982a). At Kowhai Bush, three eggs known to have been laid within 1 h of sunrise; one record in NZ NRS included laying of fourth and final egg between 08:00 and 16:00. At Kowhai Bush, once spent 9 min in nest before taking 1.5 min to lay third egg (beginning at 06:45) and staying 7.5 min after laying; once, after female flushed from nest, she returned 15 min later (at 06:29) and spent 25.5 min in nest before taking 1 min to lay fourth egg, and spent 9 min in nest after laying; once, was flushed from three eggs at 06:18 but had laid final egg and left nest by 07:06 (Gill 1980a). Usually double-brooded (Gill 1980a); at Kowhai Bush, all pairs followed closely had at least two broods, and 16 pairs laid 37 clutches in a season, giving mean of 2.3 nesting attempts/year (Gill 1982a). Apparently sometimes lay three broods (Stidolph 1923), but length of season makes it very unlikely that three broods could be reared in a season (Gill 1982a). At Kowhai Bush, twice, re-laid 10 and 12 days after abandoning first clutch, and also re-laid in four other instances between 22 and 88 days after desertion; mean interval between fledging of first brood and initiation of second clutch was 23 days: 14 days (one fledgeling); 15–20 days (two fledgelings), 42 days (three fledgelings); and 20 and 35 days (four fledgelings) (Gill 1980a, 1982a).

**Incubation** (All from Kowhai Bush [Gill 1980a]): Begins soon after laying of last egg. Where at least one individual of a pair was marked, only assumed female (based on behaviour) incubated, and was not seen to be fed by other bird. Of 342 observations, birds spent 68% of time incubating, with time spent on nest apparently decreasing during first 80% of period before increasing slightly; proportion of time on nest in five 4-day intervals within incubation period: 72.2%, 71.6%, 67.2%, 60.3% and 67.9%. Though little data available, order of hatching appears to follow order of laying, though early eggs appear to start developing before incubation begins. Of 20 clutches of C/4 checked daily, modal pattern (35%) of clutches was for three eggs to hatch on one day and last egg on next day; twice, all four eggs hatched on

same day; hatching occurred over 2 days 11 times; and hatching over 3 days occurred seven times; mean spread of hatching was 1.4 days (0.3–2.1 days). **INCUBATION PERIOD:** 19.5 days (1.25; 17.3–21.3; 14) after last egg laid, though first eggs were in nest longer than others and persisted for 24 days on average (thus outside range shown) with second egg 22.2 days and third egg 20.6 days (Gill 1980a). 17–19 days (Oliver).

**Young** Altricial, nidicolous. When newly hatched, 68% of nestlings had pink skin and 32% had greyish skin; skin slightly darker where pterygiae later formed. Nestlings hatch with dense white down on dorsum, mostly on head and back (Stidolph 1939; Gill 1980a, 1983a); see Plumages and Bare Parts for further details, and Gill (1980a) for details of development of all tracts. Only females brood (Gill 1982a), but both sexes feed nestlings and remove faecal sacs (Stidolph 1939; Gill 1982a,b). Often, adults appeared to prod nestlings to stimulate defecation, and nestlings revolved in nest and presented their rumps at nest-entrance (Gill 1983a). Faecal sacs taken 6–15 m from nest where some, perhaps all, were dropped (Stidolph 1939; Gill 1983a); dried faecal sacs also accumulated in lining of nest (Gill 1983a). At Kowhai Bush, faecal sacs were removed on 30% of 376 visits (32% of visits by males, 29% of visits by females). Single Shining Bronze-Cuckoo nestlings were brooded more often but fed less often than unparasitized broods of three or four (Gill 1980a, 1982b; see Food). In nests containing a Shining Bronze-Cuckoo nestling, faecal sacs were removed on only 14% of 189 visits (12% of visits by males, 15% of visits by females), even though Cuckoo nestlings were visited less often; suggested that overall effort required to rear a Cuckoo nestling is less than that required to rear a brood of Warblers, though Cuckoos probably brooded till 18 days old while Warblers brooded till 10.7 days old, possibly (but not necessarily) negating energy savings for females but not males. Bouts of brooding of both Warblers and cuckoos usually from <1 min to c. 30 min, though nestling Warbler once brooded for >38 min; mean time spent brooding 6.2 min (5.59; 63) for Warblers and 10.2 (7.73; 47) for Cuckoos. Bouts of brooding that were ended by arrival of male (with food) were significantly shorter ( $P < 0.05$ ) than those when female left the nest spontaneously (c. 63% of uninterrupted bouts; n=110); bouts ended by male occurred on 66% of occasions (n=67) for Warblers and 71% of occasions (n=53) for Cuckoos; female usually resumed brooding shortly after male had fed nestlings. Young fed by male more often than by female early in nestling period, probably because female spent much time brooding (Gill 1982b). At Kowhai Bush, no nests were known to have been deserted due to handling, because nestlings were handled carefully; one female even allowed nestlings to be taken from under her; nestlings handled regularly did not fledge prematurely. One nest that came away from its attachment was wired up 30–40 cm away and parents continued to feed nestlings (Gill 1983a). Once a pair was seen feeding young in nest that had fallen to ground (CSN 7). **Growth WEIGHT:** Weights during nestling period summarized in Table 4 (for daily weights, see Gill [1982a]). Weight of two at hatching, 0.8 and 1.15 g; of 83 nestlings weighed within 24 h of hatching, 14 were 1.0 g and seven were 0.85–0.95 g; these lighter young thought to have hatched recently. Individual nestlings reached maximum weights of 6.7–8.9 g at 10–17 days old; nestlings from broods of two were lightest during first half of nestling period, but significantly heavier at peak weight and on fledging than those from broods of three and four (which were not significantly different from each other). Analysis of

nestling composition suggested that loss of weight before fledging was from loss of water. Broods of four Warblers always weighed more than single Cuckoo nestlings at same stage, but not to extent that two Cuckoos could have been raised (Gill 1982b). **MEASUREMENTS** (mm): Length of wing and tarsus on day before fledging 40.0 (2.31; 25) and 22.0 (0.82; 47) respectively; wing-length was 76% of adult wing-length, but length of tarsus was same as that of adult (Gill 1980a, 1982a).

**Fledging to independence FLEDGING PERIOD:** 17.2 (0.86; 15.0–18.5; 52) (Gill 1982a); 17–19 days (Oliver). Fed by both parents for 28–35 days after fledging; first caught own prey 18 days after fledging, but begged from parents for up to 38 days (Gill 1982a; Oliver; see Food, Social Organization). Shining Bronze-Cuckoos were also fed for a similar period after fledging (Gill 1982b), up to 28 days (Gill 1982c). For 1–3 weeks after fledging, early broods usually stayed together and were fed by both parents, though male often did most feeding if only two young fledged; for next 1–3 weeks, when female re-nesting, fledgelings were cared for by male only. Sometimes male cared for two fledgelings and female cared for other one or two fledgelings. Twice, unrelated juveniles were fed in addition to own (Gill 1980a, 1983a). For further details see Food and Social Behaviour: Relations within family group.

**Success** At Kowhai Bush, of 265 eggs in 73 nests, 70% hatched and 38% produced fledgelings; of 185 nestlings, 54% fledged. Early and late nests were equally likely to contain nestlings, but fewer late nests than early nests produced fledgelings: for early nests ( $n=40$  nests) hatching success was 77.3%, nestling success 65.5% and breeding success 50.7%; for late nests ( $n=33$  nests): 60.0%, 34.8% and 20.9%; and for all nests: 69.8%, 54.1% and 37.7% (Gill 1982a). There were also seasonal differences in breeding parameters, with relatively high mortality of nestlings in 1976–77 and of eggs in 1977–78, but fledging rates were similar in both years (1.74 and 1.71 fledgelings/nest, respectively); in 1976–77, of 109 eggs, 43% yielded fledgelings, while in 1977–78, of 123 eggs, 34% yielded fledgelings (Gill 1983a). Of nests with eggs at Kowhai Bush, 42% produced at least one fledgeling; of 44 adequately documented records in NZ NRS, 20 nests fledged at least one young or seemed likely to (Gill 1982a). Survival of fledgelings while dependent on parents was high: of 48 banded nestlings, only two did not survive first 9 days after fledging, at least 39 (81%) survived to 18 days, and at least 26 (54%) survived  $\geq 25$  days. Once independent, most fledgelings disappeared from natal area; of 89 nestlings and six free-flying juveniles that were banded, only six were later known to hold territories; and of 44 banded fledgelings in main study area only two joined adult population there (Gill 1982a). Infertility of eggs more common in early clutches

**Table 4.** Weights of nestlings over nestling period (from Gill 1982a, which see for daily weights).

AGE (DAYS)	WEIGHT (g)
0	1.18 (0.16; 0.9–1.6; 57)
1	1.54 (0.21; 1.2–2.1; 63)
5	4.04 (0.45; 2.4–4.7; 57)
10	6.85 (0.52; 5.7–8.0; 52)
15	7.20 (0.49; 6.5–8.9; 47)
16	7.09 (0.53; 6.0–8.4; 45)
17	7.02 (0.64; 6.0–8.1; 20)

than late ones, as was death of nestlings in nest without obvious cause (Gill 1983a). Eggs were occasionally cracked or broken by observer during study, but only once did this cause clutch to be deserted (Gill 1980a). **PREDATORS:** At Kowhai Bush, loss of at least 12 of 38 nests (32%) attributed to introduced mammals, probably Stoats *Mustela ermina* and Black Rat *Rattus rattus* (Gill 1982a). Potential but unconfirmed avian predators include Australian Magpies *Gymnorhina tibicen*, Sacred Kingfishers *Todiramphus sanctus* and Shining Bronze-Cuckoos (one of which had an egg, probably of a Warbler, in its gizzard, and one observed eating a Grey Warbler egg) (Michie 1948; Gill 1982b,c). Predation by mammals was probably responsible for most losses of eggs; of 79 eggs that failed to hatch: 31% disappeared without trace; 18% were thrown from nest (including nine [11%] that were probably tossed out of nest by strong wind); another 3% were found broken in nest; 10% were infertile; 17% contained dead embryos; and 21% were destroyed by Shining Bronze-Cuckoos. Predators were greatest single cause of nestling mortality; of 72 nestlings that did not fledge, predators took 28% (nest destroyed, nestlings mutilated or both) and 24% disappeared without trace, possibly from predation; 17% were evicted by Cuckoos; 5% left nest prematurely, possibly after being disturbed by predators; 23% died in nest from unknown causes; and two 'runts' (3%) failed to obtain sufficient food (Gill 1982a,c, 1983a). Many nests have back or bottom torn out, or disappear entirely, but not known which predator responsible (Stidolph 1939). Said that destruction of some nests possibly by the birds themselves, as found for Brown Gerygones *Gerygone mouki* (Moncrieff 1932). **CUCKOOS:** When present, a Shining Bronze-Cuckoo nestling will throw out all other contents of nest at 3–7 days old (usually through entrance). No first nests and only 55% of late nests were parasitized, and parasitism only reduced production of fledgeling Warblers from late nests by 17% (Stidolph 1939; Gill 1980a, 1983c). Of 40 active nests, in 1976–77 to 1978–79 breeding seasons, that were considered available for parasitism, 22 were parasitized, with overall frequency of parasitism 55%. Similarly, of 61 nests recorded in NZ NRS that held eggs after mid-Oct., 14 (23%) were parasitized and 19 (31%) were definitely not; the outcome of the remainder not known (Gill 1983c). Records of parasitism by Long-tailed Cuckoo *Eudynamis taitensis* not substantiated and probably based on confusion with Shining Bronze-Cuckoo (Stidolph 1939; HANZAB 4). **PARASITES:** Nearly 40% of 37 nests at Kowhai Bush developed infestations of the blood-sucking mite *Ornithonyssus bursa*, but this figure possibly inflated by potential transmission via bag used to weigh nestlings during study (Gill 1983a).

**PLUMAGES** Prepared by J.S. Matthew. Natal down present at hatching. Fledge in juvenile plumage. Extent of post-juvenile (first pre-basic) moult not known; if complete, attain adult (first basic) plumage; if partial, attain adult-like first immature (first basic) plumage and then undergo a complete first immature post-breeding (second pre-basic) moult to adult plumage. After attaining adult plumage, a complete post-breeding (pre-basic) moult each cycle produces successive adult plumages with no change in appearance. Sexes alike. Plumage description based on examination of skins of eight adults (NMNZ), photos and sketches of juveniles (D.J. Onley), and other sources as cited.

**Adult** (Definitive basic). **HEAD AND NECK:** Most of forehead, crown, nape and hindneck, grey-olive (43) in most

birds, olive-brown (30) or brownish (c123) in some. Sides of lower forehead, light grey (c85) or pale grey (86), not forming pale supraloral area (pace Ford 1986). Sides of neck, grey-olive (43) or brown (c123), grading to pale grey (86) towards throat. Lores, black-brown (119) directly in front of eye, tapering narrower towards bill. Feathers extending narrowly behind eye, black-brown (119), combining with lores to form short black-brown (119) eye-stripe, not extending far behind eye. Eye-ring, off-white (ne) above and below eye, darker (black-brown 119) in front of and behind eye; in some, upper and lower edges of eye-ring form indistinct and narrow whitish arcs above and below eye, but these not always present (pace Ford 1986). Narrow strip of feathers from sides of lower forehead to above ear-coverts, light grey (c85) or pale grey (c86), forming indistinct and diffuse pale supercilium, paler than top of head, but similar to or slightly paler than ear-coverts. Ear-coverts and narrow strip of feathers below eye, grey-olive (43) or brownish (c123) with exposed pale-grey (86) bases. Malar area, chin and throat, off-white (ne) or pale grey (86), usually slightly paler than ear-coverts; some have very faint pale-yellow (157) tinge and, in some, malar area slightly darker (light grey c85) and indistinctly flecked whitish. Several short, fine black (89) bristles protrude from above gape, base of forehead and interramal area. **UPPERPARTS:** Mantle, back, scapulars and rump, uniform olive-brown (30) or grey-olive (43). Uppertail-coverts, brown (c123) with olive (c51) fringes to some. All feathers of upperparts have concealed grey (87) bases. **UNDERPARTS:** Breast, light grey (85) or greyish (c84) with faint pale-yellow (c157) suffusion in centre in some birds; breast darker and grayer than in other gerygones. Belly and flanks, white, with faint pale-yellow (c157) suffusion in some; some also have a few light-grey (85) blotches or light-grey (85) suffusion on sides of belly and flanks. Cause of variation in amount of yellow on underparts not understood, but possibly related to age or wear. Undertail-coverts, white. Feathers of thighs, brown (28) with lighter brown (223D) fringes. Axillaries, white or pale yellow (157). All feathers of underparts have concealed dark-grey (83) bases. **UPPERTAIL:** Rectrices, black-brown (119), grading to olive-grey (c42) or pale straw-yellow (c56) towards base of outer webs of t1-t4 and grading to whitish towards base of both webs of t5 and t6; t2-t4 have broad (to 9 mm wide on t4) white subterminal band on inner web, extending to outer web on t3 and t4 in some; and t5 and t6 have broad (to 13 mm) white subterminal band on both webs, white outer edges and narrow dark-brown (121) tips which are broader on outer webs. Shafts, light brown (239) (see Fig. 2). **UNDERTAIL:** Patterned as uppertail, but ground-colour dark brown (c121); and shafts, white. **UPPERWING:** All marginal and median coverts, dark brown (121) with olive (c51) fringes. Greater secondary coverts, dark brown (121) with olive (c51) fringe at tips and on outer webs. Greater primary coverts, dark brown (121) or black-brown (119) with olive (c51) fringe to outer webs. Feathers of alula, dark brown (121) or black-brown (119); two shortest feathers fringed olive (51). Greater primary coverts and alula contrastingly darker than rest of upperwing. Remiges, dark brown (121), though tertials slightly darker, black-brown (c119) with: olive (51) outer edges that grade to paler, off-white (ne) distally on outer primaries; and off-white (ne) inner edges, which do not extend as far distally on outer primaries. Outer edges of remiges combine to form rather broad and diffuse pale-olive (c51) panel on folded wing. Shafts of remiges, red-brown (221B). **UNDERWING:** All marginal and median coverts, white with partly exposed

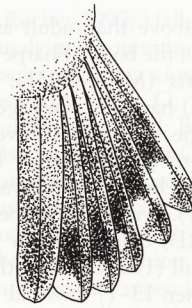


Figure 2. Pattern of uppertail

brown (28) bases and pale-yellow (c157) fringes in some birds. Greater secondary coverts, white. Greater primary coverts, light grey-brown (119D) or pale grey (86). Remiges patterned as upperwing, but ground-colour brownish grey (c79); outer webs normally concealed.

**Nestling** Natal down present at hatching (Gill 1983a); dense and white; occur in eight main patches (ocular, coronal, abdominal, occipital, secondary, humeral, femoral and dorsal), and two vestigial patches (crural and jugular). Gill (1983a) stated that teleoptile (pin) feathers not necessarily preceded by neossoptile (down) feathers. See Gill (1980a) for detailed account of development of feather-tracts.

**Juvenile** Little known. Based on single skin (NMNZ 1672) that is possibly a first immature with part of juvenile plumage retained, photos of recently fledged bird (B. Chudleigh) and photos and sketches of two birds in varying stages of post-juvenile moult (D.J. Onley). Photos and published observations suggest that juvenile plumage varies, particularly in extent of yellow on head and underparts (see below). Similar to adult, but differing by: **HEAD AND NECK:** Feathers extending from upper rear edge of eye to above ear-coverts, straw-yellow (c57), forming indistinct straw-yellow (c57) hind-supercilium. Lores, paler greyish (c84); eye-stripe very indistinct; and face appears rather plain compared with adult. Eye-ring, off-white (ne) or pale yellow (c157), broken narrowly by greyish (c84) feathers in front of and behind eye; forms narrow off-white (ne) or pale-yellow (c157) arcs above and below eye. Malar area, ear-coverts and feathers extending narrowly below eye, greyish (c84), tinged straw-yellow (c57); and malar area and area below eye faintly flecked whitish. Chin and throat, off-white (ne), tinged straw-yellow (c57) at sides of throat. **UPPERPARTS:** Brownish (c123), grading to yellowish brown (ne) on rump and uppertail-coverts. Upperparts lack olive tone of adult and feathers are softer and more loosely textured. **UNDERPARTS:** Breast and flanks, off-white (ne), tinged straw-yellow (ne) at sides; breast apparently not grey as in adult, but one photo (B. Chudleigh) shows recently fledged bird with faint grey (ne) suffusion across upper breast. Amount of yellow on flanks said to vary individually (D.J. Onley) and not known if different from adult. **UPPERTAIL:** Rectrices slightly narrower and more acute at tip. **UPPERWING:** Fringes of all coverts and outer edges to remiges, yellow-brown (c24), broader on tertials and inner secondaries.

Juvenile apparently distinguishable from adult till c. 2 months old (Gill 1980a, 1983a); when <2 months old, face is suffused yellow, eye-ring often apparent and pale yellow, and tail paler than adult (Gill 1983a).

Published descriptions (Barnett 1985) also suggest that juvenile plumage varies: young (presumably referring to

juvenile) 'brownier above than adult and washed with pale yellow on the sides of the body' (Sharpe 1879); juveniles have yellow on underparts (Meise 1931); immature (probably referring to juvenile) has paler plumage than adult, and yellow is absent on the abdomen (Oliver); immature (again probably referring to juvenile) has belly and undertail-coverts, white; and breast, grey washed olive at sides (Ogilvie-Grant 1907). Eye-ring described as yellowish (Meise 1931), yellow (NZRD) or pale yellow in some (Heather & Robertson 1997); Gill (1983a) stated that feathers of orbital region are yellow when 13–17 days old.

**First immature** (First basic). Little known. Apparently retains all juvenile primaries and secondaries (D.J. Onley); otherwise not known if distinguishable from adult.

**Aberrant adult plumage** Skin (NMNZ 9928) of leucistic bird has white plumage with pale-yellow (157) suffusion to back and rump; and pale-yellow (157) outer edges to greater secondary coverts and remiges.

**BARE PARTS** Based on examination of photos (Barnett 1985; Haddon 1990; unpubl. B. Chudleigh; D.J. Onley; also standard sources), information from museum labels (NMNZ), information from 14 adults, 28 first immatures and 34 juveniles captured on SI (D.J. Onley), and other sources as cited. **Adult** Bill, black (89); also described as blackish grey (NMNZ) or dark brown (Sharpe 1879). Orbital ring, greyish (ne). Iris, red (210, 14); also described as red (Gill 1983a), or brown, dark brown or light yellow-brown (NMNZ), but not known if latter adults or first immatures. Legs and feet, black (89); also described as brownish black (NMNZ) or dark brown (Sharpe 1879). Soles described as pale grey (NZRD). **Nestling** Following from Gill (1983a) and NZRD: Bare skin of hatchlings pink in 68% of nestlings and grey in 32%. Bill pink or grey with black tip. Gape white at hatching, usually yellow by 3–4 days old, and always yellow or cream by 5–6 days old; Stidolph (1939) described gape as yellow, but age not stated. Legs and claws described as pink at first, dark grey-pink by 7–8 days old, and greyer by 11–12 days old. **Juvenile** Gill (1980a) stated that juvenile distinguishable till c. 2 months old. Differences from adult: Bill, grey-black (82) with pinkish-brown (219D) base to lower mandible and basal half of tomtia; also described as dark grey with black tip (Gill 1983a) or black with brown tomtia (D.J. Onley). Gape, cream (c54) or pale yellow (c157), slightly swollen; also described as white at hatching, later bright yellow (NZRD). Palate described as yellowish (Gill 1980a, 1983a). Iris, dark brown (c119A); also described as brown (Ogilvie-Grant 1907; Meise 1931; NZRD; D.J. Onley); during post-juvenile moult, iris becomes progressively redder from lower edge upward (Gill 1980b, 1983a; D.J. Onley). Legs and feet, grey-black (82); also described as grey or dull grey-pink (Gill 1980a, 1983a). Soles, pale buff (123D); also described as paler than legs (Gill 1983a). **First immature** Little known. First immatures captured on SI, Mar.–Sept. (after finish of post-juvenile moult) with iris described as red and brown (D.J. Onley).

**MOULTS** Based on examination of skin of 16 adults (NMNZ); 22 adults, 13 first immatures and 62 juveniles or birds undergoing post-juvenile moult captured on SI (D.J. Onley); and other sources as cited. **Adult post-breeding** (Third and subsequent pre-basic). Complete. Primaries moult outward, starting at p1. Active moult of primaries recorded Jan. (2 of 2; PMS 11, 18) and Feb. (2 of 2; PMS 34, 44); seven of eight in Mar. and Apr. had all primaries new; of 23 from

May to Nov., 22 had all primaries worn or slightly worn. Meise (1931) and Gill (1983a) recorded moult of primaries from Jan. to Mar. Combined results indicate that moult of primaries occurs Jan. to Mar., but recorded as early as Dec. (D.J. Onley). Secondaries moult inward; one with PMS 34 had following secondary moult-pattern: N<sup>1</sup>4<sup>1</sup>2<sup>1</sup>O<sup>3</sup>; one with PMS 44 had nearly finished moult of secondaries but had not yet started moult of tertials; one with PMS 11 had not yet started moult of secondaries or tertials. Moult of tail recorded from bird that had finished moult of primaries, with t2–t6 new and t1 growing; one, with PMS 19, had not yet started moult of tail. Timing of moult of wing-coverts and body much as primaries; one finishing moult of body and marginal coverts in mid-Feb., after end of moult of primaries; moult of body recorded Jan. to June. **Post-juvenile** (First pre-basic). Little known. Apparently partial; involves all or most feathers of body, rectrices and tertials; moult of greater secondary coverts recorded from one; no records of moult of secondaries or primaries. Usually occurs Jan.–May, but recorded as early as Nov. (D.J. Onley). First basic plumage adult-like (Gill 1983a; NZRD). Moult of tertials and rectrices recorded Jan. to Mar.; moult of tertials apparently starting at s8 or s9. Sequence of replacement of rectrices varies: started at t1 in eight of 12, at central or outer rectrices in others. Banded juveniles with active moult of tail recorded early Feb. (Gill 1983a). **First immature** (Second pre-basic). No information. Timing and extent probably similar to adult post-breeding.

**MEASUREMENTS** (1) NI and SI, skins, adults (NMNZ). (2) NI, skins, adult males (Keast & Recher 1997).

	MALES	FEMALES
WING	(1) 52.7 (1.93; 50–55; 13) (2) 53.4 (1.1; 8)	47, 49, 51 –
TAIL	(1) 49.3 (2.59; 45–53; 13) (2) 45.0 (2.80; 8)	43, 45, 48 –
BILL S	(1) 11.9 (0.30; 11.4–12.4; 13) (2) 11.9 (0.30; 8)	11.2, 11.6, 11.6 –
HIND TOE C	(2) 8.4 (0.30; 8)	–
TARSUS	(1) 19.5 (0.70; 18.4–21.2; 13)	19.4, 20.0, 20.3

Live, unsexed: (3) Kowhai Bush, SI, ages not given (Gill 1980b). (4) Orongorongo Valley, NI, ages combined; Bill W = width of bill measured at base of exposed culmen; Bill D = depth of bill measured at base of exposed culmen (Robertson *et al.* 1983). (5–7) SI (D.J. Onley): (5) Adults; (6) First immatures; (7) Juveniles.

	UNSEXED
WING	(3) 52.7 (1.92; 48–57; 59) (4) 52.4 (1.69; 48–57; 111) (5) 54.0 (2.14; 50–58; 23) (6) 53.2 (1.99; 50–57; 28) (7) 53.0 (2.16; 46–58; 49)
TAIL	(3) 51.5 (2.97; 46–59; 54) (4) 49.3 (2.28; 44–58; 84)
BILL S	(3) 12.6 (0.65; 10.8–13.7; 59)
CULMEN	(4) 8.7 (0.63; 7.0–10.0; 86)
BILL W	(3) 3.1 (0.21; 2.6–3.5; 59)
BILL D	(3) 2.4 (0.11; 2.1–2.6; 59)
TARSUS	(3) 21.8 (0.80; 20.1–23.5; 38) (4) 20.0 (0.90; 18.0–24.0; 65) (5) 20.3 (0.70; 19.4–21.1; 6) (6) 20.2 (0.58; 19.3–20.3; 12) (7) 20.1 (0.71; 18.4–21.5; 23)

**WEIGHTS** (1) NI and SI, adults, from museum labels (NMNZ).

	MALES	FEMALES
(1)	6.0 (0.63; 4.9–7.0; 9)	6.3

Live, unsexed: (2) Kowhai Bush, SI, adults captured autumn and winter (Gill 1982a); (3) Orongorongo Valley, NI, ages combined (Robertson *et al.* 1983); (4) NI and SI adults, from museum labels (NMNZ); (5–7) SI (D. Onley): (5) Adults; (6) First immatures; (7) Juveniles.

	UNSEXED
(2)	6.4 (0.39; 5.7–7.2; 50)
(3)	6.4 (0.72; 5.0–8.0; 112)
(4)	5.5 (1.15; 4.0–7.2; 6)
(5)	6.5 (0.36; 5.8–7.0; 21)
(6)	6.6 (0.58; 5.7–7.8; 28)
(7)	6.9 (0.56; 5.6–8.7; 49)

**STRUCTURE** Tip of longest primary reaches about half-way along tail when wing folded. Ten primaries: p6 longest; p10 20–24 mm shorter, p9 7.0–9.5, p8 1.5–3.0, p7 0–1.5, p5 0–1.0, p4 1.5–3.5, p3 3.0–6.0, p2 5.0–8.0, p1 6.0–10.0. Slight emargination to outer webs of p5–p8; and slight emargination to inner webs of p7–p10. Ten secondaries, including three tertials; tip of longest tertial does not reach tip of p1 on folded wing. Tail fairly long, slightly rounded at tip when folded; 12 rectrices; t1 longest, t2–t4 0–2 mm shorter than t1, t5 2–5, t6 6–10; rectrices rounded at tips in adult, more acute at tip in juvenile. Bill fairly long compared with most other gerygones (Keast & Recher 1997); about three-quarters length of head; fairly slender; upper mandible decurved at tip; gonys inclined slightly upward. Nasal groove about one-third length of exposed culmen. Rictal bristles longer than most other gerygones; Keast & Recher (1997) stated that mean length of rictal bristles 6.6 mm (0.30; 8). Tarsus fairly long compared with most other gerygones, compressed laterally; scaling holothecal. Tibia fully feathered. Middle toe longest, rather long compared with other gerygones except Chatham Island Warbler *Gerygone albofrontata*; mean length, including claw 12.6 mm (0.91; 11.1–13.4; 5); inner and outer toes 65–75% length of middle; hindtoe c. 75%. Hindclaw 3–4 mm long.

**SEXING** No differences in plumage and not known if differ in size. Only females develop brood-patch (Heather & Robertson 1997).

**AGEING** Juvenile distinguishable by bare parts and plumage (see Field Identification and Plumages). First immature resembles adult, but retains juvenile primaries and secondaries, these often appearing more worn in autumn and winter compared with those of adult. First immatures have red and brown coloration to iris, the iris becoming progressively redder, from lower edge upward, with age; iris probably entirely red by c. 1 year old.

**GEOGRAPHICAL VARIATION** None known. Some early studies (Meise 1931; Mack 1953) considered Grey Warbler *G. igata* conspecific with Brown Gerygone *G. mouki*, but this unequivocally rejected in most other studies (Parker *et al.* 1985; Ford 1986; Sibley & Monroe 1990; Christidis &

Boles 1994; Keast & Recher 1997; Hall; DAB). Ford (1986) conducted cladistic analyses on morphological characters in gerygones and his results suggest a close phylogenetic relationship between Brown Warbler *G. igata* and Chatham Island Warbler *G. albofrontata* and Brown Gerygone *G. mouki*. Ford (1986) also suggested that *G. igata* evolved from *G. mouki*-like ancestors that first arose in Aust. but emigrated and colonized islands of sw. Pacific Ocean. General characters (DAB; this study) separating *G. igata* from *G. mouki* are: face, throat and breast, grey (whiter on throat and breast in *G. mouki*); indistinct and dull supercilium (white and distinct in *G. mouki*); varying yellow coloration to underparts (*G. mouki* lacks yellow on underparts); bill fairly long and slender (shorter and stouter in *G. mouki*); and songs differ markedly (see Voice of each species).

Insufficient museum skins to compare measurements of populations from NI and SI, but data from live birds (Gill 1980b, 1983a) suggests no significant differences in measurements. Examination of skins of seven adults from NI and seven adults from SI (this study) reveals no discernible geographical variation in plumage. Ogilvie-Grant (1907) tentatively divided populations on NI and SI into four species. Later studies (Meise 1931; Ford 1986; NZRD; Peters; DAB) recognize only single monotypic species from NZ.

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**Volume 6, Plate 11**

Grey Warbler *Gerygone igata* (page 319)  
1 Adult; 2 Juvenile; 3 Adult

Chatham Island Warbler *Gerygone albofrontata* (page 334)  
4 Adult male; 5 Adult female; 6 Putative juvenile (yellow variant); 7 Juvenile (pale variant)

Norfolk Island Gerygone *Gerygone modesta* (page 341)  
8 Adult; 9 Juvenile