Order PASSERIFORMES

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

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

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

The Passeriformes divide into two main groups:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Family PETROICIDAE   Australasian robins

Small to medium-sized and often brightly coloured passerines. Size ranges from Red-capped Robin *Petroica goodenovii* (length 11 cm, weight 8–9 g) and Garnet Robin *Eugerygone rubra* (length 10–11.5 cm) to Southern Scrubrobin *Drymodes brunneopygia* (length 19–22 cm, weight 31–37 g). The Petroicidae comprises 38–46 species in 11–17 genera (Wolters 1975–82; Sibley & Ahlquist 1990; Sibley & Monroe 1990; Peters; DAB); DAB recognizes 15 genera in the family, including *Eugerygone* of New Guinea, but excluding *Culicicapa* of Wallacea and se. Asia and *Amalocichla* of New Guinea. As circumscribed by DAB, family essentially confined to Aust.–New Guinea region, with only five species extending farther: Golden-bellied Flycatcher *Microeca hemixantha* endemic to Tanimbar Is in Wallacea, and four species of *Petroica* on islands of sw. Pacific Ocean, including three endemic to NZ, and Scarlet Robin *Petroica multicolor*, widespread, on Solomon Is, Vanuatu, Banks Is, Fiji, Samoa, Norfolk I. and Aust. (Sibley & Monroe 1990; Coates *et al.* 1997; DAB), though DAB splits Aust. and islands forms of Scarlet Robin. In HANZAB region, 23 species in eight genera; DAB tentatively divided the Petroicidae into three subfamilies; these and their component genera (combining arrangements of Christidis & Boles [1996] and DAB) are:
EOPSALTRIINAE: *Poecilodryas* (3 species in genus, 1 in HANZAB region), *Heteromyias* (2, 1), *Plesiodryas* (1, 0), *Gennaeodryas* (1, 0), *Peneothello* (4, 0), *Tregellasia* (2, 2), *Eopsaltria* (5, 4) and *Melanodryas* (2, 2). DAB places *Heteromyias*, *Plesiodryas* and *Gennaeodryas* in *Poecilodryas*, and places Mangrove Robin *Eopsaltria pulverulenta* in monotypic *Peneoenanthe*.
PETROICINAE: *Monachella* (1, 0), *Microeca* (6, 3), *Eugerygone* (1, 0), *Petroica* (10, 8) and, probably, *Pachycephalopsis* (2, 0).
DRYMODINAE: Monogeneric *Drymodes* (2, 2).

The name Eopsaltriidae has been used for this family (e.g. Sibley & Ahlquist 1990; Peters) but Petroicidae has priority (Bock 1990; Christidis & Boles 1994). Formerly placed with Old World flycatchers (Muscipicapidae), whistlers (Pachycephalidae) or monarch flycatchers (Dicruridae) (e.g. Schodde 1975) but evidence from DNA–DNA hybridization (Sibley & Ahlquist 1985, 1990) and protein allozyme (Christidis & Schodde 1991) studies confirm that they are not closely related to any of these and should be treated as a distinct family. *Drymodes* also formerly placed with turdine thrushes (Muscicapidae) (e.g. Mayr 1963; Diamond 1972; Storr 1973; Peters) or timaliine babblers (Sylviidae) (e.g. Mayr 1941; Rand & Gilliard 1967) but results of DNA–DNA hybridization studies show they are part of the Petroicidae (Sibley & Ahlquist 1980, 1982). Nearest relatives not certain; they are part of a particularly old and divergent lineage (DAB) and evidence from various molecular techniques is conflicting. Results of DNA–DNA hybridization studies suggest a relationship with the Corvoidea (Sibley & Ahlquist 1990) whereas results of protein allozyme studies suggest a relationship with the Meliphagoidea (Christidis & Schodde 1991).

Body shape rather rounded and stocky, with large and rounded head. Bill usually short, straight and varyingly broad, though typically not deep, and with prominent long rictal bristles at base of bill; maxilla notched. Wings usually rounded at tips, with ten primaries and, usually, nine primaries (including three tertials). Tail short to moderately long, with square tip; long in *Drymodes*; 12 rectrices. Tarsus usually moderately long to long, slender. Fossae at head of humerus, single and trabeculated (pachycephaloid in form). Horns of vomer articulated and dorsoventrally flattened, and protrude forward of apically inflated maxillo-palatine processes. Narial and orbital cavities openly aperturate. Temporal fossae much reduced, with short post-orbital and zygomatic processes and small, almost unwinged ectethmoid plate that tapers towards jugal bar without reaching it. Free lachrymals missing (Coates *et al.* 1997; DAB). The three subfamilies further characterized by the following features (after DAB). In the Eopsaltriinae, inter-orbital bar usually missing; vomerine horns are very large, oblong plates about the size of the maxillo-palatines, bilobed at tip and constricted at base; and temporal fossae larger than in the other two subfamilies. The Petroicinae retain fine inter-orbital bar; tiny, almost awl-shaped vomerine horns that are only a fraction of the size of the maxillo-palatines; and temporal fossae are small. The Drymodinae differ from the other two subfamilies in slender form; apparent lack of vomerine horns; and ossified inter-orbital bar.

In adult plumage, upperparts usually rather plain grey, brown or black, but underparts often brightly coloured. Sexes alike in most species but *Petroica* and *Eugerygone* sexually dimorphic in plumage, with brightly coloured males (pink to red on underbody) and plainer females. Most species have distinctive wing-markings, typically a large pale wing-bar across bases of primaries (see Fig. 1). Fine to broad pale or brownish streaking or spotting common in juvenile plumage. All species appear to undergo partial post-juvenile (first pre-basic) moult shortly after
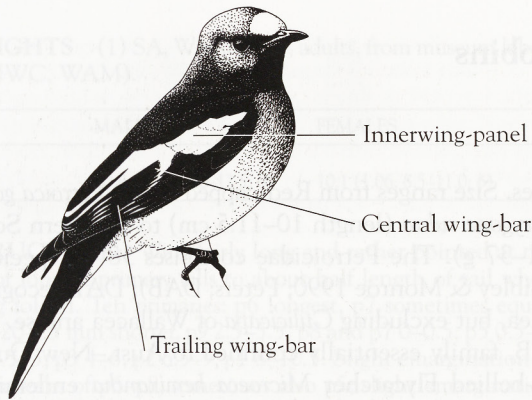
Figure 1(a). Pattern of folded wing of adult male Scarlet Robin (Source: Fig. 1, Rogers 1993)
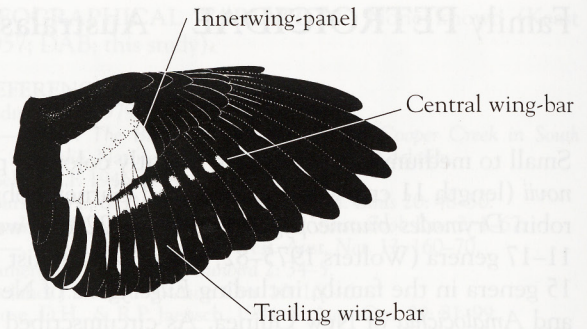
Figure 1(b). Pattern of spread wing of adult male Scarlet Robin (Source: Fig. 1, Rogers 1993)

fledging to an adult-like first immature plumage. After attaining adult plumage, undergo a single complete post-breeding (pre-basic) moult annually, with no change in appearance. Primaries moult outwards.

The following summary of biology and ecology based largely on *HANZAB* species accounts (q.v.), Rand & Gilliard (1967), Watling (1982), Coates (1990), Coates *et al.* (1997) and other references as cited.

Throughout family range, occupy most wooded habitats, from coasts to uplands, including alpine regions, and in all bioclimatic zones. In Aust., widely distributed in wet to dry sclerophyll forests and woodlands, usually dominated by eucalypts, including wet and dry forests through to arid and semi-arid woodlands and shrublands. In Aust. and New Guinea, many species in various rainforest associations and, in New Guinea, in lowland to montane forests. A few species inhabit mangroves (e.g. Mangrove Robin, Golden-bellied Flycatcher). NZ *Petroica* found in variety of native forests, mostly dominated by podocarps or beech *Nothofagus*, and coastal and subalpine shrubland. River Flycatcher *Monachella muelleriana* of New Guinea inhabits fast-flowing rocky streams. Many species use ecotone between wooded and open habitats, including agricultural and grazing land, with some species in such habitats more often in non-breeding season (e.g. Flame *Petroica phoenicea* and Scarlet Robins). Also use modified habitats, such as regrowth native forests following logging or fire, or plantations of introduced pines.

Most species resident or sedentary, though many undertake some local or dispersive movements. Populations of several species in se. Aust. migrate altitudinally, breeding at high altitudes and wintering in lowlands. Several Aust. species seasonally migratory or partly migratory, most notably several Aust. *Petroica*, which breed in SE, including Tas., in spring–summer, and migrate to winter in N, with movement generally aligned with e. Aust. coast (see Chan 2001; Griffioen & Clarke 2002; and species accounts). Some species (e.g. Flame Robin), show a high degree of site-fidelity, returning to same breeding areas and wintering grounds in subsequent years (Robinson 1990; see species accounts).

Primarily insectivorous, though several species occasionally also take seeds. Many species join mixed-species feeding flocks. Arboreal and terrestrial; many primarily arboreal, particularly *Microeca*, though most recorded at least occasionally foraging on ground; others largely or wholly terrestrial (e.g. scrub-robins *Drymodes*, some *Poecilodryas*, *Heteromyias*). Most foraging by perch-and-pounce method, perching on vantage point before catching prey by sally-striking or sally-pouncing onto ground, then returning to perch to eat prey; many species (particularly within Eopsaltriinae) commonly cling sideways to tree-trunks and other vertical surfaces, remaining stationary for long periods scanning for prey. *Microeca* flycatchers mostly sally-strike at aerial prey. Terrestrial species mainly glean prey from ground or low vegetation.

Social organization well known from detailed studies of several species, especially Flame Robin, New Zealand Robin *Petroica australis*, New Zealand Tomtit *P. macrocephala* and Hooded Robin *Melanodryas cucullata* though most species much less well known. Most occur in pairs or small family groups throughout year, though some form flocks in non-breeding season. Typically socially monogamous, with long-term bonds, though extra-pair copulation known in Hooded Robin. Co-operative breeding reported in *Melanodryas*, *Tregellasia* and *Eopsaltria*, with helpers assisting in feeding nestlings and defence of territory. Social behaviour quite well known for a few species, but poorly known in most (as social organization). During breeding season vigorously defend territory, especially area immediately round nest. Some sexual behaviour described, including song-flights in *Microeca*, and wing-flicking displays in Hooded Robin. Courtship feeding occurs in most genera studied. In HANZAB region, distraction displays reported in all genera, except *Microeca*.

In general, not noisy and not noted songsters. Vocalizations of most species pleasant but repetitious whistling, piping, squeaking, trilling or buzzing notes (Chisholm 1960; Rogers 1993; Pizzey & Knight 1997; Coates 1990; see species accounts). Songs apparently function in advertising and defending territories, in attracting a mate and maintenance of pair-bond; may also be used as contact call and in other circumstances (e.g. see Scarlet Robin).

Most nest as solitary pairs, but several species breed co-operatively (see above). Nests cup-shaped, often with pieces of bark, lichen or moss attached to outside, typically aligned vertically, so that nests well-camouflaged against branch or trunk. Most nests built in fork in tree or shrub, but some built in hollows, and scrub-robins nest on ground. Construction usually by female only. Eggs varyingly oval; usually creamy white, pale green or pale blue, often spotted or blotched with brown. Clutch-size usually 1–4, but clutches of up to six have been recorded in some species (e.g. New Zealand Tomtit). In most species, only female incubates, though both sexes observed incubating in scrub-robins. Incubating female usually fed by male. Incubation usually takes 14–20 days. Both parents, and any helpers present, usually feed nestlings and nestlings. Young of most species take 12–22 days to fledge.

Many species have been adversely affected by clearance, fragmentation and degradation of habitat. In Aust., Norfolk I. Scarlet Robin *Petroica multicolor multicolor* and Tiwi I. Hooded Robin *Melanodryas cucullata melvillensis* considered vulnerable (and six other taxa of Least Concern) (Garnett & Crowley 2000). Black Robin of NZ endangered.

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Petroica australis **New Zealand Robin**

Turdus australis Sparrman, 1788, *Mus. Carlsonianum* pt 3: no. 69 — Dusky Sound, South Island, New Zealand.

The specific name alludes to the type-locality, from Latin *australis*, southern (from *auster*, the south).

OTHER ENGLISH NAMES Robin; Bush Robin; North or South Island Robin.

POLYTYPIC Nominate *australis*, SI, NZ; *longipes* (Garnot, 1827), NI, and Little Barrier and Kapiti Is, NZ; *rakiura* Fleming, 1950, Stewart I. and associated outlying islands, NZ.

FIELD IDENTIFICATION Length c. 18 cm; wingspan not known; weight 35 g. Large, rather robust A'asian robin with long slender dark legs and upright stance. Largest *Petroica* robin in NZ; larger and bulkier than New Zealand Tomtit *Petroica macrocephala*, with heavier bill and much longer and stronger legs. Mostly grey-black or dark grey, with varying fine pale streaking on upperparts and varying whitish breast and lower underparts, with extent and prominence of pale streaking and pale areas of underparts varying with sex and subspecies. Sexes usually differ slightly in adults (and usually separable when members of pair seen together); sexes appear similar in juveniles. No seasonal variation. Juvenile separable. Immatures usually inseparable from adult in field (very similar to respective sexes of adult in nominate *australis*, and like adult female in subspecies *longipes*; not known in subspecies *rakiura*; time taken to develop adult plumage may also differ between subspecies [see Geographical Variation]). Slight geographical variation; three subspecies, differing mainly in extent and prominence of pale streaking and colour and extent of pale area on underbody. Nominate *australis* and subspecies *rakiura* apparently very alike in plumage (see Geographical Variation); in subspecies *longipes*, pale streaking more distinct and more extensive than in nominate, and pale area on lower breast and belly smaller. **Adult male** SI, STEWART I. AND ASSOCIATED ISLANDS: Head and neck, slate-black, with fine pale streaking on ear-coverts, chin and throat; and narrow white eye-ring, slightly broken in front of and behind eye. Can raise feathers of crown, with a distinct line between raised feathers and normal feathers across nape, giving helmeted appearance. Small white frontal patch on lower forehead (separated from bill by narrow dark band), size and shape of which can be varied. Rest of upperbody, slate-black. Uppertail brownish black, slightly browner than upperbody. Folded wing, brownish black, with faint and ill-defined pale-grey wing-bar across inner primaries and secondaries; in flight, upperwing appears blackish, with diffuse narrow pale grey wing-bar across bases of remiges (petering out on inner primaries). Breast, belly, vent and undertail-coverts, white to yellowish white or cream, fairly sharply demarcated from dark throat in straight line across upper breast; flanks and sides of breast, dark grey, and birds often have some dark-grey patches or smudging from mid-flanks onto pale sides of belly. Thighs, brownish grey. Undertail, black-brown. Underwing, dusky, with diffuse whitish wing-bar across bases of remiges, as on upperwing. Bill usually black, though some show fine pale cutting edges; gape usually black, but buff in some. Iris, black-brown. Legs, grey-black to olive-brown; feet similar or pale yellow-brown, with yellow or orange-yellow soles. NI, AND LITTLE BARRIER AND KAPITI IS: Broadly similar to SI males but appearing much scruffier; differ from SI adult males by: Head and neck faintly streaked whitish; and have fine whitish speckling in front of and above eye, which can combine with streaking behind eye to give suggestion of diffuse narrow supercilium in some. Upperbody faintly streaked whitish. Chin, throat and most of breast, dark slate-grey, streaked whitish, leaving smaller and varying pale area on centre of lower breast and belly, which is also usually whiter and less sharply demarcated from dark breast and flanks (latter also streaked whitish). **Adult female** Very similar to respective adult males above and some, especially single birds, probably difficult to distinguish from them. Differ from adult males by: dark head, neck, upperparts and dark of underparts tend to be very slightly paler and greyer; whitish streaking on head and neck slightly more distinct; and whitish to cream area of breast and belly usually less extensive, less sharply demarcated from dark of foreparts, and often slightly scruffier in appearance. Blackish bill often has paler grey-brown base to lower mandible. **Juvenile** Not well known. Similar to respective adult females but browner overall. Differences from adult females: whitish frontal patch small or obsolete; dark areas of plumage are browner, with more prominent pale streaking on crown, hindneck and upperbody; wing-bar is browner; pale patch on breast and belly usually smaller and underbody washed brownish grey on chin, throat and more strongly brown on breast and flanks, grading to buff or brownish wash on vent and undertail-coverts. **Immature** Retain juvenile remiges, alula and greater upperwing-coverts, and some immatures possibly separable from adults in close view by browner wing-bar and contrast between old retained juvenile plumage of wing and new immature plumage of rest of wing and body. Otherwise inseparable.

Similar species None. Much larger and bulkier than **New Zealand Tomtit**, with noticeably longer legs, characteristic upright stance and terrestrial foraging behaviour (Tomtit is smaller, daintier, more pot-bellied and less terrestrial). Robins also lack broad white wing-bar across bases of remiges on folded wing and white in outer rectrices (both prominent in Tomtit in all plumages other than on Snares Is); and Robin is also more extensively dark below (cf. mainly whitish underbody of Tomtit). Calls also clearly different (see Voice of respective accounts).

Seen singly, in pairs and, occasionally, family parties. Generally tame and confiding, often flying down to inspect leaf-litter at feet of observers. Alert and active, typically seen hopping over forest floor, often stopping to tremble one foot to flush insects or to flick aside litter and stand upright to spot any invertebrates that may be disturbed; also scan for prey from low perches, from which pounce onto ground prey. Also forage by gleaning insects from foliage or from under bark on branch or trunk of tree, and occasionally by hover-gleaning in

understorey and foliage near ground or, more rarely, by capturing flying insects on wing. When foraging, often flick wings and occasionally flick tail upward; long legs distinctive when on ground.

HABITAT Native forests and, sometimes, tall scrub or introduced pines. Occur from sea-level to tree-line (McLean 1911; Moncrieff 1932; Wilkinson & Wilkinson 1952; Flack 1973; Child 1975; St Paul 1976; Duncan *et al*. 1999; see below). At Kowhai Bush, near Kaikoura, prefer forest without extensive coarse ground cover, and often recorded in clearings or on old tracks; do not occur in extensive areas without trees or where trees widely scattered with a grassy understorey or sparse ground cover (Flack 1979).

Mainly in various native forests, mostly podocarp *Podocarpus* or beech *Nothofagus* associations, often mixed with hardwoods such as rata *Metrosideros* and Kamahi *Weinmannia racemosa*, and usually with a diverse and complex understorey (Guest 1975; Elliott & Ogle 1985; Brown 1997; CSN). In surveys in L. Sumner State Forest Park, n. Canterbury (137 plots, each surveyed once using a 5-min count), recorded in: (1) mixed beech forest dominated by Red Beech *Nothofagus fusca* and Mountain Beech *N. solandri*, with mixed subcanopy of Silver Beech *N. menziesii*, *Coprosma foetidissima*, *C. parviflora* and Prickly Shield-fern *Polystichum vestitum* (recorded in 31% of 55 plots surveyed in this habitat); (2) forest of Red Beech–Mountain Beech mixed with Broadleaf *Griselinia littoralis* and *Coprosma pseudocuneata* (19%, 16 plots); (3) forest of Mountain Beech–Silver Beech with *Olearia lacunosa* and *Pseudopanax simplex* in shrub layer, and diverse ground cover (13%, 15 plots); and (4) forest of Mountain Beech of simple structure, occasionally with *Coprosma pseudocuneata* and *Polystichum vestitum* present (3%; 31 plots). Not recorded in dry Mountain Beech–Broadleaf forest, with canopy of Mountain Beech and subcanopy of Broadleaf and *Coprosma linariifolia*, and understorey dominated by *C. pseudocuneata* and *Polystichum vestitum* (Wilkinson & Guest 1977). On Kapiti I., inhabit moist gullies dominated by Pukatea *Laurelia novaezelandiae* mixed with bush lawyer *Rubus*, Supplejack *Rhipogonum scandens* and Kohia *Tetrapathaea tettranda* forming dense canopy with many epiphytes, and ground cover of ferns and much leaf-litter (Wilkinson & Wilkinson 1952). Occasionally inhabit dry Manuka *Leptospermum scoparium* and Kanuka *Kunzea ericoides* scrub or forest (McLean 1911; Wilkinson & Wilkinson 1952; Flack 1973; Powlesland 1981a, 1983b; Pierce 1994; Duncan *et al*. 1999; CSN 21, 23, 37), sometimes mixed with beech (Moncrieff 1932). On Moturua I., Bay of Islands, NI, mainly occur in Kanuka scrub with varying ground cover; one pair recorded in dry acacia scrub with dense ground cover (Pierce 1994). On islands in Marlborough Sounds, occur in mixed Kanuka–coastal broadleaf forest, especially Mahoe *Melicytus ramiflorus* and Kohekohe *Dysoxylum spectabile* (M. Aviss). Also occur in Kanuka and Manuka regrowth (Wilkinson & Wilkinson 1952; Duncan *et al*. 1999; CSN 29; *contra* CSN 5). **MODIFIED HABITATS**: Sometimes recorded in plantations of exotic pines *Pinus*, usually Monterey Pine, often with understorey of ferns, including Bracken *Pteridium esculentum*, and *Pomaderris*, though sometimes without shrubs in understorey (Weeks 1949; Gibb 1961; Turbott 1967; Duncan *et al*. 1999; CSN). Said to sometimes occur in gardens (NZRD).

DISTRIBUTION AND POPULATION Endemic to NZ. **NI** N of 37°S, only recorded on Moturua I., Bay of

Islands (see below), and Little Barrier I. More widespread but patchily distributed farther S, mostly in s. and e. Waikato, Volcanic Plain, Wanganui and e. Taranaki, S or E of line from around Te Aroha, through L. Arapuni and lower reaches of Tongaporutu R., to near Patea; mainly occur E to Urewera NP, in w. East Coast, and S to line joining sites W of Wairoa, Tarawera, s. Kaweka Ra. and Kakatahi. Very rarely recorded farther S, such as in Ruahine Ra. and, farther S still, on Kapiti I., and, very occasionally, on adjacent mainland (NZ Atlas; CSN). **SI** Sparsely scattered in Marlborough Sounds; more widespread in e. Marlborough, centred on Kaikoura Ras, S to lower reaches of Conway R. Very occasionally recorded in inland Canterbury; and isolated populations occur on Otago Pen. and in n. Southland, SE of L. Wakatipu. Widespread on Stewart I. A few scattered records in s. Southland, between Waihoaka and site W of L. Poteriteri, but more widespread in Fiordland, from between Edwardson and Dusky Sounds, N to near Awarua Bay. A few scattered records in s. Westland, and an isolated population farther N from near Okarito, N to L. Brunner. Very widespread in n. Westland and throughout Nelson, E to Spencer, St Arnaud and Richmond Ras (Duncan *et al*. 1999; NZ Atlas; CSN).

Breeding Probably throughout range.

Introductions An unknown number successfully released onto Ulva I. in either late 19th or early 20th century, but these later extirpated by Cats (Guthrie-Smith 1914). Five birds introduced to Moturua I., Bay of Islands, from Inner Chetwode I. in 1973 (Anon. 1998); another six birds introduced from Rotorua district, Apr. 1983 (CSN 32); and a further 16 introduced from Mamaku Plateau, Bay of Plenty, in Feb. 1986 (Pierce 1994); a survey of Moturua I. in June 1987 located 14 birds; in 1989, seven birds; and in June 1994, a minimum of 23 (Pierce 1994; CSN 38). Five birds introduced to Allports I., Marlborough Sounds, from Kowhai Bush, Kaikora, in 1973; and a total of 11 introduced to Maud I., Marlborough Sounds, from Outer Chetwode I., in 1983 (Anon. 1998). In June 1991, 13 birds released onto Mokoia I., L. Rotorua; population had increased to >100 by 1994 (Pierce 1994). In Apr. 1992, 44 Robins translocated to Tiritiri Matangi I. from Mamaku Plateau, near Rotorua; by Sept.
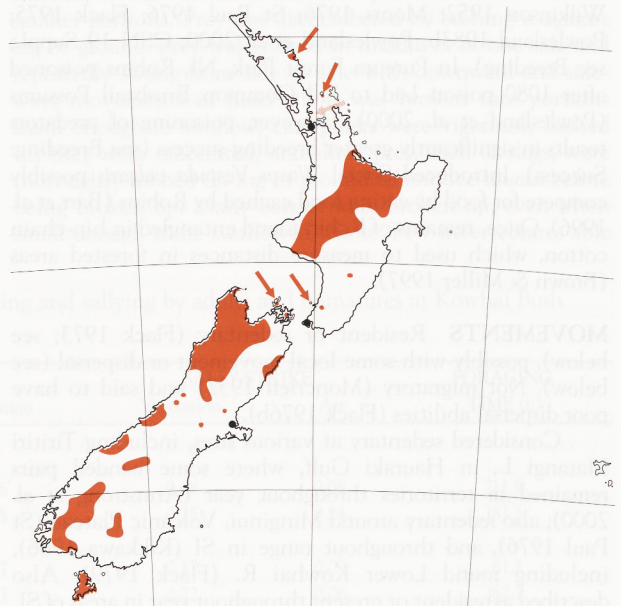
1992, 33 remained (Armstrong 1995; Armstrong *et al.* 1995). Said to have been introduced to Waingaro, but no details available (CSN 35).

Change in range, populations Formerly widespread on mainland at time of European settlement (NZCL), but range has subsequently contracted (Heather & Robertson 1997; Oliver; see Threats and Human Interactions). Decline in numbers noticed by 1870s (Turbott 1967) and species had disappeared from n. and s. NI by early 1900s (Heather & Robertson 1997). Formerly 'plentiful' in Canterbury and elsewhere throughout SI in 1880s but had declined by early 1900s (Guthrie-Smith 1914). Rarely recorded near e. coast of SI by early 1930s (Moncrieff 1932). In mid-1960s, declines recorded in several areas, such as round Te Whaiti and S. Mamaku (CSN 19 Suppl.). Near Kaikoura, banded population declined from 94 to 16 in 1970s (Powlesland 1983b). On Kapiti I., marked increase in numbers noticed between 1924 and early 1950s (Wilkinson & Wilkinson 1952); and numbers there increased rapidly after Common Brushtail Possums were eradicated from the island in the 1980s (Heather & Robertson 1997). At Lower Hollyford, a few birds recorded in mid-1970s after an absence of several years, possibly recolonising area from Eglinton Valley after having been wiped out by Stoats *Mustela erminea* a few years earlier (CSN 23).

THREATS AND HUMAN INTERACTIONS Declines in populations and contraction of range (see above) thought to be result of loss and degradation of forest habitat and introduction of mammalian predators (Heather & Robertson 1997; Oliver). Said to persist in fragmented forest after clearing (Moncrieff 1932), though many areas of apparently suitable forest no longer support the species (Fleming 1950; see above). Comparison of populations in logged and unlogged forests near Karamea, SI, during winter, found significantly smaller populations in logged forests (Onley 1983). Absent from treeless areas that are regularly grazed, but may recolonize these sites after grazing animals removed and vegetation allowed to regenerate (Wilkinson & Wilkinson 1952). Eggs, young and adults taken by introduced mammalian predators, particularly rats, mice, mustelids and Common Brushtail Possums, and possibly Cats (Wilkinson & Wilkinson 1952; Moors 1976; St Paul 1976; Flack 1975; Powlesland 1983b; Powlesland *et al.* 2000; CSN 19 Suppl.; see Breeding). In Pureora Forest Park, NI, Robins poisoned after 1080 poison laid to kill Common Brushtail Possums (Powlesland *et al.* 2000). However, poisoning of predators results in significantly greater breeding success (see Breeding: Success). Introduced Social Wasps *Vespula vulgaris* possibly compete for food by eating food cached by Robins (Barr *et al.* 1996). Once, remains of Robin found entangled in hip-chain cotton, which used to measure distances in forested areas (Brown & Miller 1997).

MOVEMENTS Resident or sedentary (Flack 1973; see below), possibly with some local movement or dispersal (see below). Not migratory (Moncrieff 1932) and said to have poor dispersal abilities (Flack 1976b).

Considered sedentary at various sites, including Tiritiri Matangi I., in Hauraki Gulf, where some banded pairs remained in territories throughout year (Armstrong *et al.* 2000); also sedentary around Minginui, Volcanic Plateau (St Paul 1976), and throughout range in SI (Kikkawa 1966), including round Lower Kowhai R. (Flack 1979). Also described as resident or present throughout year in areas of SI,

such as round Kaikoura (Flack 1973; Powlesland 1981b, 1983a,b), e. Fiordland (CSN 33), Westland (Moncrieff 1929), Buller R. Drainage Basin, including near Reefton (Dawson *et al.* 1978) and Ohikanui Valley (Wilson *et al.* 1988), and Nelson (Moncrieff 1932). Also present throughout year on Kapiti I., off Waikanae, NI (Wilkinson 1927; Wilkinson & Wilkinson 1952).

At Kowhai Bush, Kaikoura, SI, sometimes wander into neighbouring territories (Flack 1973, 1979); and territories said to break down to some degree when birds moulting at end of breeding (Flack 1976a). Significant increase in population near Reefton, SI, in Apr. 1974 thought to be from movement of young birds (Dawson *et al.* 1978). Post-breeding dispersal into Charleston area, SI, in winter, arriving in small numbers in Nov. and staying till July (CSN 33, 35).

Banding Of 730 banded in NZ, 1950–1974, 218 recoveries (29.9%) (Robertson 1975). Of 3158 banded 1950–96, 173 recoveries (all nominate *australis*), 1988–93 (Cossee 1989, 1991, 1993, 1995, 1997, 1998a,b; Cossee & Wakelin 1991).

FOOD Invertebrates and fruit. **Behaviour** Terrestrial and arboreal; mainly forage close to or on ground. On ground, forage in soil, among litter and debris, and from low vegetation; above ground, forage in cracks, crevices and holes, and among foliage. Search for prey by perch-hunting (sit and wait) from elevated perches, such as branches, boulders or tree-trunks; and collect most prey by gleaning (McLean 1911; Wilkinson 1927; Fleming 1950; Wilkinson & Wilkinson 1952; Turbott 1967; Powlesland 1981b; Oliver; and as below). DETAILED STUDIES: At Kowhai Bush, SI, Aug. 1976–July 1978 (Powlesland 1980a, 1981b); at Kowhai Bush and on Outer Chetwode I., Apr.–June 1978 (Powlesland 1981a); on Nukuwaiata I., Chetwodes Grp, 21–23 Mar. 1993 (McLean *et al.* 1994); and on Little Barrier I., Nov. 1967–Oct. 1968 (Gravatt 1969, 1971). Territorial. Mostly forage in pairs, and occasionally singly (Wilkinson & Wilkinson 1952; St Paul 1976; Oliver; see Social Organization). Not reported feeding in association with other species. However, sometimes forage close to people, hopping round their feet in search of prey; also seen to forage round timber-felling operations (McLean 1911; Oliver 1922; Moncrieff 1932; Anon. 1947; St Paul 1976; CSN 1, 2). FORAGING HEIGHTS: At Kowhai Bush, when gleaning from vegetation, most foraging within 2 m of ground; of 29.1 h of observation of foraging from vegetation: 23.8% of time spent feeding 0.1–0.6 m above ground; 13.0% 0.7–1.1 m; 18.4% 1.2–1.6 m; 15.1% 1.7–2.1 m; 9.0% 2.2–2.6 m; 7.2% 2.7–3.1 m; 4.6% 3.2–3.6 m; 3.7% 3.7–4.1 m; 1.8% 4.2–4.6 m; 1.8% 4.7–5.1 m; and 1.6% >5.1 m; heights of perches used to scan for prey probably similar to heights at which recorded feeding (Powlesland 1981b); mean height of foraging in vegetation 1.48 m (0.1–8.0; 500 foraging obs.) (Powlesland 1980b). On Nukuwaiata I., of 42 observations of foraging: 81% on ground; *c.* 7% at 0.1–20% of canopy height (height of canopy not stated); and *c.* 12% >40% of height of canopy. On Little Barrier I., of 43 observations of foraging: 88.4% on ground; 2.3%, 0.1–1.5 m above ground; 2.3%, 1.6–3.0 m; and 7.0%, >4.5 m. FORAGING SITES: At Kowhai Bush, mostly foraged on ground, less often in vegetation and occasionally in air. On ground, foraged in soil, among leaf-litter, on rotten logs and in low vegetation that could be reached from ground. When foraging in vegetation above ground, searched crevices, fissures, holes, among dead foliage and tangles of

vines, accumulated debris in axils between branches and trunks of trees, and in rough bark; of 19.8 h of observations of foraging, when foraging above ground in vegetation, mostly foraged from tree-trunks, by perching either on branch or the trunk itself: 39.5% of time spent foraging from branches; 58.2% from trunks; 2.0% from decaying tree-stumps; and 0.3% from foliage (Powlesland 1981b). On Nukuwaiata I., of 42 observations of foraging: 74% among leaf-litter; 10% on bare ground; 14% on bark of trees; and 2% on dead wood. Mostly scanned for prey from elevated perches: mostly trunks and branches of trees (55%), but also small branches and twigs (7%), and ground (38%). On Little Barrier I., of 42 observations of foraging, most on ground (90.5%), mainly among leaf-litter; less often foraged from tree-trunks and shrubs. FORAGING METHODS: Search for prey by perch-hunting (sit and wait), and collect most prey by gleaning (Powlesland 1981b; McLean *et al.* 1994; see below). Scan for prey from elevated perches, especially large and small branches and boulders, though, if no such perches available, will cling vertically to tree-trunks. If no prey detected after scanning, usually fly to another perch and scan from there. At Kowhai Bush, forage by hopping and stepping over litter and vegetation, or scanning from elevated vantage points. Move litter and bark aside only to collect prey that has been seen retreating beneath them. Movement of feet, wings and tail apparently disturb prey and enhance its detection. Foot-movement comprised either continuous or discrete pulses, with feet used alternately; when among dry leaf-litter, rustling caused by trembling feet was audible. Foot-trembling mainly used when foraging on ground, but occasionally also when foraging on branches. All foraging Robins said to use foot-trembling, and some juveniles made these movements within 12 days of leaving nest (Powlesland 1981b). Nearly 88% of searching by hops and steps along ground (n=18,727 movements), the rest being flights between foraging sites; 66% of flights (n=2289 flights) ended with Robins landing on branches, 30% on ground and 4% on tree-trunks (Powlesland 1981b). At Kowhai Bush, of 12.8 h observations of foraging during incubation, males spent 93.7% of foraging time searching for prey; not seen systematically turning over leaf-litter, but relied largely on prey being visible (Powlesland 1981b). Elsewhere, such as on Little Barrier I. and Kapiti I., said that regularly turn over leaves with bill in search of prey (Wilkinson 1927; Gravatt 1971; Oliver). On Nukuwaiata I., when moving between perches in search of prey, made mean of 7.1±7.7 moves/min, covering mean distance of 2.1±1.29 m in mean of 24.2±16.71 s. At Kowhai Bush, mostly fed by gleaning; of 923 h observations of foraging: 33.8% of foraging time spent scanning; 61.3% gleaning on ground; 4.5% gleaning from vegetation; and 0.4% sallying, including 0.3% sally-striking

Table 2. Time taken to kill, dismember and eat some common prey items (after Powlesland 1981b).

PREY ITEM	LENGTH OF ITEM (cm)	TIME (min)
Cicadas *Amphipsalta zelandica*	3–4	2.2 (0.71; 1.0–4.0; 27)
Earthworms	<4	0.3 (0.06; 0.1–0.9; 16)
Earthworms	4–14	1.3 (0.32; 0.4–2.4; 13)
Earthworms	>14	6.0 (11.81; 3.4–13.6; 14)
Stick insects	8–15	1.8 (1.32; 0.4–4.6; 25)
Slugs	2–4	2.5 (1.46; 0.4–4.8; 14)
Snails	1.5–3.0	5.1 (0.17; 4.6–5.5; 3)
Tree Wetas *Hemidenia femorata*	3.5–5	5.0 (3.45; 2.8–8.4; 10)

from vegetation and 0.1% sally-striking in air; for details of monthly distribution of foraging methods throughout study period, see Powlesland (1981b). On Nukuwaiata I., foraged mainly by gleaning; of 42 observations of foraging: 71% by gleaning, which included scratching leaf-litter, probing and turning over (raking) leaves; also fed by sallying, including 19% sally-pouncing and 10% sally-striking on vegetation; none seen sally-striking in air (McLean *et al.* 1994). At Kowhai Bush, during non-breeding season, time spent scanning for prey and gleaning and sally-striking for prey differed significantly between adults and immatures (see Table 1): adults and immatures spent similar proportion of time gleaning from vegetation and sally-striking in air, but adults spent more time scanning and sally-striking at hard substrates, and immatures more time gleaning on ground (Powlesland 1980a). Observed feeding on larvae of small aquatic insects from shallow water, shaking the case free before eating larvae (Veitch 1970). HANDLING OF PREY: At Kowhai Bush, of 12.8 h observations of foraging, 6.3% of time spent handling and eating prey. Time taken to kill, dismember and eat prey depended on size of prey and any defence used by prey (see Table 2); small items (<5 mm long) were swallowed whole and appeared to be killed by crushing them between mandibles; larger invertebrates were killed by quick stabbing and pinching movements of bill and, once prey had been stabbed, it was carried to secluded place to be broken into smaller portions. Prey was dismembered by bashing it against log or ground: prey was grasped in middle or at one side and repeatedly swung from side to side with downward and sideways movements of head till it was broken into portions small enough to swallow; caterpillars were vigorously bashed till they were macerated, and slimy prey, such as slugs, were thoroughly rubbed on log or ground to remove mucus before being broken up. Many berries were broken up, even when small enough to be swallowed whole. Few invertebrates able

Table 1. Proportion of time spent scanning for prey, and gleaning and sallying by adults and immatures at Kowhai Bush during non-breeding season (after Powlesland 1981b).

	SCANNING	GLEANING		SALLY-STRIKE		FORAGING
		Ground	Vegetation	Vegetation	Air	TIME (h)
ADULTS						
1977	36.09	56.59	6.76	0.48	0.08	211.9
1978	37.92	58.14	3.65	0.25	0.04	183.3
IMMATURES						
1977	28.03	64.94	6.77	0.17	0.09	81.1
1978	29.97	66.02	3.73	0.22	0.06	162.7

to defend themselves against attack by Robins; ground-dwelling beetles were usually ignored, possibly because of their strong exoskeleton, though they were occasionally attacked and eaten; stick insects and wetas occasionally deterred attacks by waving their long spiny legs. When foraging for soil-burrowing prey such as earthworms, used 'head-cock' and 'bill-pounce' methods: when potential burrow found, Robin stood still, cocking its head from side to side; if prey seen, bird straightened its head and pounced forward with both feet off ground, thrusting its bill into burrow with much force and speed; bill-pounces repeated whenever prey retreated out of reach or worm broke into two pieces, leaving a portion remaining in hole (Powlesland 1981b). SEASONAL VARIA-TION: At Kowhai Bush, Dec. 1976–Mar. 1977 and Dec. 1977–Mar. 1978, foraged for c. 72% of time during Jan.–Mar. 1977 (n=122 h of obs. of foraging) and c. 80% during Jan.–Mar. 1978 (92 h); significantly more time spent foraging (P<0.01) Jan.–Mar. than in either Dec. 1976 (46% of 5.2 h) or Dec. 1977 (60% of 21.5 h) (Powlesland 1983a). At Kowhai Bush in winter, when soil moist, most time spent gleaning on ground; gleaning from vegetation was also more important in winter than in other seasons. Frequency of scanning and sallying declined during winter, possibly because aerial and arboreal prey less numerous and active at that time of year. Time spent using various foraging methods changed markedly between winter–spring and summer. Amount of time spent scanning and sallying increased with increase in numbers of aerial and arboreal invertebrates; more time spent sallying for flying insects in summer than at other times of year (for quantitative details, see Powlesland 1981b). Diet also varied seasonally: during winter and spring, when soil moist, earthworms, slugs, snails and larvae of March Fly *Philia negrostigma* dominated diet; by late spring to early summer, numbers of moth and butterfly adults and larvae eaten increased; during Jan., cicadas *Amphipsalta zelandica* emerged in large numbers, and were taken almost exclusively by some Robins; few cicadas remained by early Apr., and Robins fed more often on stick insects; when autumn rains invigorated soil-inhabiting invertebrates, stick insects were mostly ignored. Also fed on fruit in autumn and summer; and, during autumn, fungi (mushrooms and toadstools) were broken up to gain access to small invertebrates living in them (Powlesland 1981b). TIMES OF FORAGING: At Kowhai Bush, temporal pattern of foraging behaviour by adults was similar in breeding and non-breeding seasons. Time spent gleaning above ground rather constant during day, with slight increase in mid-morning and late afternoon. Time spent gleaning on ground rather constant from mid-morning to mid-afternoon, but less time spent on ground in early morning and late afternoon; scanned more often in early morning and late afternoon than at other times of day. Diurnal patterns of foraging behaviour by adults and immatures were similar during non-breeding season, except that immatures scanned less often than adults in early morning and late afternoon (Powlesland 1981b). In separate populations at Kowhai Bush and on Chetwode I., males on Chetwode I. spent significantly more time foraging (94% of 62.9 h of foraging obs.) than males on mainland (82% of 45.3 h). Temporal pattern of time spent foraging also differed between the two populations: on Chetwode I., time spent foraging remained constant throughout day (c. 91% of foraging time in six equal periods) except in late morning (c. 86% of time); at Kowhai Bush, foraged less often in early and mid-morning (c. 74% of time in early morning; 78% in late morning) than later in day (c. 85% of time) (Powlesland 1981a).

CACHING OF FOOD: Often store food (Moncrieff 1929; Fleming 1950; Soper 1963), usually on top of logs or among moss growing on large branches (St Paul 1976). In captivity, when offered a worm, a Robin ate part of it and broke the rest into pieces and piled them in corner of cage (Moncrieff 1932). In populations at Kowhai Bush and on Chetwode I., stored food each day; males on Chetwode I. spent less time storing food (c. 0.5% of 62.9 h of foraging obs.) than males at Kowhai Bush (c. 1% of 45.3 h of foraging obs.) (Powlesland 1981a). At Kowhai Bush, stored only invertebrates; prey stored singly, at different sites, and either whole or in pieces; prey too large to be carried in flight was broken up before it was stored. Use a variety of sites, mainly axils between branches and trunks of trees, but also stumps, holes and crevices; sites used only once. As males dominant over mates, female often moved out of sight before caching food. However, sometimes birds of either sex immediately ate food stored by their partner or, sometimes, moved it to a new site. Caching occurred most often Apr.–July. Mean height of storage site was 2.85 m (1.54; 0.3–8.0; 293), significantly higher than mean height at which Robins foraged in vegetation (1.48 m; see Foraging heights, above). Mean time taken to store an item 24 s (4–150; 340); of 40 items stored, 58% disappeared, and assumed to have been retrieved on same day. Of 269 items of food stored in non-breeding season (Jan.–July): earthworms comprised 69.8%; slugs 6.3%; stick insects 5.2%; cicadas 4.1%; beetle larv. 3.7%; tree wetas 2.6%; ground wetas 2.6%; snails 1.9%; caterpillars 1.5%; flatworms 1.1%; spiders 0.4%; cockroaches 0.4%; and flies 0.4% (Powlesland 1980b). CASTING OF PELLETS: (All from Powlesland 1979.) Before egesting a pellet, usually retire to secluded perch and rest for c. 1 min with plumage slightly fluffed up. Just before pellet ejected, bill opened once or twice, possibly in response to movement of pellet up the esophagus, then bill opened wide and head shaken as pellet ejected. Three times a Robin was seen egesting pellet in 2–3 small portions, produced c. 1 min apart. Average measurement of pellets, 12.9 mm (8.0; 8.9–20.4; 43) × 7.3 mm (0.005; 6.2–8.9); mean dry weight 123 g (0.2; 45.7–305; 64). Pellets only very occasionally cast in early morning, but rate of egestion fairly constant during rest of day, with slightly greater rate in middle of day. Rate of egestion higher in Jan.–Mar. than at other times of year. Pellets mostly contained remains of fruit and invertebrates: fruit eaten mainly during non-breeding season; of 13 pellets from adults in breeding season (Aug.–Dec. 1977), only 8% contained seeds of fruit; in non-breeding season (Apr.–July 1977 and Jan.–July 1978), 39% (n=28 pellets) from adults and 64% (n=25 pellets) from immatures (n=25) contained seeds. Pellets also contained remains of insects, especially cicadas, but in winter, when insects were scarce, also contained earthworms, slugs, snails and insect larvae.

Detailed studies At KOWHAI BUSH (observations and qualitative listing of food items; Powlesland 1981b): **Plants** (Fruit unless stated.) MONOCOTYLEDONS: Liliaceae: *Astelia fragrans*. DICOTYLEDONS: Araliaceae: *Pseudopanax arboreus*; Coriariaceae: *Coriaria arborea*; Cornaceae: *Corokia cotoneaster*; Epacridaceae: *Cyathodes fasciculata*; Escalloniaceae: *Carpodetus serratus*; Pittosporaceae: *Pittosporum eugenioides*; Polygonaceae: *Muehlenbeckia australis*; Rosaceae: *Rubus fruticosus*; Rubiacea: *Coprosma rhamnoides*; *C. robusta*; *C. propinqua*; Violaceae: *Melicytus ramiflorus*. **Animals** ANNELIDS: Oligochaetes. MOLLUSCS: Gastropods. SPIDERS. INSECTS: Coleoptera: unident. beetles; Carabidae: *Mecodema*; *Megadromus wallacia*; Diptera: Bibionidae: *Philia negrostigma*;

Hemiptera: Cicadidae: *Amphipsalta zelandica*; *Kikihia subalpina*; Lepidoptera: ads, larv.; Orthoptera: Stenopelmatidae: *Hemiandrus*; *Hemideina femorata*; Phasmatodea: Phasmatidae: *Acanthoxyla*; *Clitarchus*.

Other records Fungi BASIDOMYCETES: Tricholomataceae: *Armillaria limonea*[13]. **Plants** Fruit[11,17]. DICOTYLEDONS: Corynocarpaceae: *Corynocarpus laevigatus* fru.[2]; Meliaceae: *Dysoxylum spectabile* fru.[2]; Rosaceae: *Rubus parvus* fru.[18]; Solanaceae: *Solanum aviculare* fru.[2]. **Animals** ANNELIDS: Oligochaetes[2,3,6,8,10,11,14]. **MOLLUSCS:** Gastropods[11]. DILPOPODS[6]. **SPIDERS**[10,14]. **INSECTS**[1,2,3,4,6,8,11,14]: Coleoptera[2]; Hemiptera: Cicadidae[10]: *Amphipsalta zelandica*[11]; Hymenoptera: Formicidae[6]; Isoptera[15]; Lepidoptera; ads, larv.[10]; Orthoptera: Anastostomatidae and Rhophadophoridae[10]; Phasmatodea[10]; Trichoptera[9]. Also said to take amphipods (Crustacea)[12]. **Other matter** Bread crumbs[1,2,4, 5,7,15,17]; biscuits and cake[1,6]; butter[6,16]; pieces of meat (venison)[7]; boiled eggs[3].

REFERENCES: [1] McLean 1911; [2] Wilkinson 1927; [3] Moncrieff 1932; [4] Fleming 1950; St Paul [5] 1959, [6] 1976; [7] Edgar 1961; [8] Turbott 1967; [9] Veitch 1970; [10] Flack 1973; [11] Powlesland 1979; [12] Heather & Robertson 1997; [13] Medway 2000; [14] Oliver; CSN [15] 2, [16] 7, [17] 9, [18] 19.

Young Nestlings fed by both parents. Fledgelings fed by both parents, though role of parents varies with size of brood and whether pair attempting to re-nest; broods of more than one fledgeling usually divided (see Social Behaviour: Relations within family group, and Breeding: Young, Fledging to independence). At one nest in Eglinton Valley, SI, male did all feeding of chicks in first week, either feeding young directly or passing food to female to feed to chicks; after *c.* 10 days both parents foraged and fed young (Soper 1963).

No detailed studies on diet of young; recorded being fed insects (Parkin & Parkin 1952; St Paul 1959), including Isoptera (St Paul 1959). No further information.

SOCIAL ORGANIZATION

Reasonably well known, with detailed studies that cover aspects of social organization: on Kapiti I. (Wilkinson & Wilkinson 1952), at Pureora Forest Park, NI (Powlesland *et al.* 2000) and Tititiri Matangi I. (Armstrong *et al.* 2000); and at Kowhai Bush, near Kaikoura, SI, in 1970s (Flack 1973; Powlesland 1983b). Normally occur singly or in pairs (McLean 1911; Oliver 1922; Wilkinson 1927; Wilkinson & Wilkinson 1952; Elliott & Rasch 1994; CSN); sometimes reported in small family groups of up to five (St Paul 1959; CSN 36) and, rarely, up to seven (CSN 23, 39). Do not join other species to forage (McLean 1911).

Bonds Appear to be both socially and sexually monogamous; in genetic study of 21 families, no extra-pair genetic contribution was detected (Ardern *et al.* 1997), though, in one study, males had large cloacal protuberances (relative to their size), which is usually characteristic of polygynous birds (Armstrong *et al.* 2000), but no further data. Pairs usually maintain bond for life but some females change mates within or between breeding seasons (Maloney & McLean 1995; Armstrong *et al.* 2000). Pairs remain together throughout year, but territories appear loosely held and often partitioned with little interaction between pair in non-breeding season (Soper 1963; Flack 1973, 1976b; Armstrong 1995; Armstrong *et al.* 2000). Claimed, probably wrongly, that pair-bond breaks down in non-breeding season (St Paul 1976). SEX-RATIO: Most mainland populations are male-biased, sometimes as high as 60–67% males (Powlesland 1997). In study of translocated populations, four groups were translocated from Mamaku Plateau, NI, to Tiritiri Matangi I., NI (from which Robins were previously absent) in Apr. 1992; initial groups caught on Mamaku Plateau had sex-ratios of 67–70% males (Armstrong 1995); on Tiritiri Matangi I., after translocation, ratio was 79% male in 1992–93, 70% in 1993–94, 61% in 1994–95, 60% in 1995–96, 62% in 1996–97 and 55% in 1998–99; sex-ratio of recruits into population apparently close to 1:1 (Armstrong *et al.* 2000). Occasional sequential polyandry recorded: female lays clutch with new male while previous mate still rearing fledgelings (Armstrong *et al.* 2000). One record of polygyny: in NI, a male paired with two females on adjoining territories, after all three birds had lost mates earlier in season; of these, one female raised brood successfully (Powlesland *et al.* 2000). Of 53 pairs present in study area in Pureora Forest Park at start of breeding season in Sept., 37 (70%) still together 7 months later, after breeding (Powlesland *et al.* 2000). One bachelor paired with female who was at least 13 days into incubation when she lost mate; new male fed female and her brood (Powlesland *et al.* 2000). DOMINANCE: Adult males dominant over their mates (Flack 1973; Powlesland 1980b, 1981a); dominance relationships also reported among juveniles (Flack 1973). Dominance probably expressed by display (see Frontal Spot and Crown Displays below). **Parental care** Only female incubates and broods; nestlings fed by both parents (for details see Breeding). Fledgelings fed by both parents, though role of parents, especially attendance by female, appears to vary with size of brood and whether, and how quickly, female attempts to re-nest. After fledging, broods of more than one usually divided, each parent taking charge of one or two young and, if number of juveniles odd, males usually feeding extra young; single fledgelings usually attended and fed by male only. When multiple broods raised in one season, male continues to feed young of one brood till next clutch hatches (see Breeding: Fledging to independence for details). Lone adult males sometimes feed unrelated dispersing juveniles, though may also act aggressively towards juveniles (Armstrong *et al.* 2000). DEPENDENCE AND DISPERSAL OF YOUNG: Fledgelings usually fed for 3–7 weeks after leaving nest, but period can vary greatly according to circumstances (see above, and Breeding: Fledging to independence). Fledgelings dependent for mean of *c.* 5 weeks (4.5–7) after fledging (Wilkinson & Wilkinson 1952; Flack 1973; Armstrong *et al.* 2000). At Kowhai Bush, number of days parents fed juveniles varied greatly; if parents re-nested, juveniles usually fed till next clutch hatches, or soon after it hatches: single fledgeling often fed for a few days after subsequent clutch hatched but driven from territory *c.* 24 days after it fledged; if re-nesting fails, fledgelings could be fed for up to 50 days before they were ousted from territory (Powlesland 1983b). On Tiritiri Matangi I., earliest a juvenile no longer fed by parents was 4.5 weeks after fledging; the latest 7 weeks after fledging (n=34 broods of fledgelings); earliest young seen at another location was 7.5 weeks after fledging, and the latest a juvenile seen in its natal territory was 10 weeks (Armstrong *et al.* 2000).

Breeding dispersion Territorial throughout year (Moncrieff 1929, 1932; Wilkinson & Wilkinson 1952; Soper 1963; Maloney & McLean 1995; Oliver). However, sometimes move through territories of other Robins to bathe (Flack 1973); and can forage outside own territory in autumn (Powlesland 1980b). At Kowhai Bush, territories roughly 2–3 ha in area (from 1 to 5 ha); boundaries stable from year to year if occupants of neighbouring territories survive (Flack 1973, 1976b; Powlesland 1983b). On mammal-free Outer

Chetwode I., Marlborough, territories 0.2–0.6 ha in area (Flack 1976b). In some dense populations (such as on Outer Chetwode I.), males so aggressive towards mates that members of pair inhabit different parts of joint territory (Flack 1973; Powlesland 1981a). After independence, young males disperse and establish themselves in 'subterritories', maintaining exclusive use of small areas of habitat, sometimes coexisting with resident adult pairs; timing usually coincides with onset of adult post-breeding moult when less emphasis on territorial defence by adults (Hay 1975). Juveniles take up home-ranges at some distance from natal territory; some juvenile females were 'adopted', at least fed by, unmated adult territorial males within a few weeks of independence (Flack 1973). On mammal-free islands, over 70% of young alive in winter failed to establish a breeding territory, but stayed in population as non-breeders (Flack 1975). **Roosting** No information.

SOCIAL BEHAVIOUR Reasonably well known. Detailed studies on SI near Kaikoura and on Outer Chetwode I. (Flack 1973, 1976a,b; Powlesland 1981a, 1983a). Often considered tame; and usually quiet and unobtrusive (McLean 1911; Oliver 1922; Moncrieff 1932; Wilkinson & Wilkinson 1952; St Paul 1959; Edgar 1961; Soper 1963; Maloney & McLean 1995; CSN 23), but also said to be shy and secretive in some areas (Heather & Robertson 1997). Often rest in early afternoon (Moncrieff 1932). Proportion of time spent on maintenance behaviours varied between populations; suggested that in populations with less abundant food, birds spent more time foraging and less on maintenance behaviour and reproduction (Powlesland 1981a). In Jan. 1958, near Mt Arthur, SI, seen to immediately approach, seize with bill, and shake out a lighted match placed on track nearby (Breed 1974), though claim that species 'puts out bushfires' (Breed 1974) an exaggeration. Disgorge pellets of undigested food after retiring to sheltered perch (see Food). Foot-trembling, wing-flicking and, in some birds, tail-flicking appear to be used to flush prey near bird (Powlesland 1981b; see Food). **Comfort behaviour** (From Powlesland [1983a] unless stated.) STRETCHING: (1) *WING-LEG-STRETCH*: Wing and leg on same side of body extended downward and backward, and tail fanned towards same side; (2) *BOTH-WINGS-STRETCH*: Both wings raised briefly over back so that tips touch; neck stretched forward at same time, with bill parallel to ground; (3) *BOTH-LEGS-STRETCH*: Both legs are extended, so that body raised from perch; (4) *JAW-STRETCH*: Neck stretched forward and mandibles held wide open for a few seconds, then closed; usually followed by scratching of head and neck. SHAKING: (1) *BODY-SHAKE*: Feathers ruffled, then body quickly shaken from side to side; sometimes head also shaken and tail fanned or wagged; appears to function to remove water from plumage and rearrange feathers after foraging or bathing; (2) *HEAD-SHAKE*: With feathers of head and neck usually ruffled, head stretched forward and pointed upward to 45° and rotated several times around long axis; occurs most often after drinking, feeding or bathing and appears to function in cleaning bill and feathers of solid particles or water; and (3) *TAIL-WAG*: Slightly fanned tail shaken from side to side several times, mainly after bathing and defecation, apparently to remove foreign material. HEAD-SCRATCHING: Bird brings leg from behind lowered wing so that claw can scratch feathers of head; either scratches one part of head persistently or several parts in sequence. Sometimes preceded by transferring oil, via bill, from preen-gland to claw. BILL-WIPING: Bill drawn, from base to tip, against branch or ground, often after feeding, apparently to remove foreign matter from bill and facial bristles. TOE-NIBBLING: Bill brought down to feet or feet raised to bill, and bird pecks at toes. Probably functions to relieve irritation, e.g. in birds, usually juveniles, with swellings caused by bird pox (Flack 1973), or to remove foreign matter. PREENING: (1) *NIBBLE-PREENING*: Often preceded by fluffing of plumage; one or several feathers drawn through bill, from base to tip, often nibbling them with bill. Remiges brought forward towards bill and at first held at base in bill; rectrices cocked, fanned upward and angled slightly to one side, to facilitate preening. (2) *OILING*: Tail cocked to one side, then head turned to same side and bill, chin and crown rubbed over preen-gland, then rubbed over other parts of body. Usually occurs when drying after bathing. BATHING: Crouch with head partly immersed in water to c. 3 cm deep; then shake head; water scooped over back and tail by ducking head then quickly raising body; body-plumage ruffled, with wings thrashed in and out of water, splashing droplets over bird. Body often rolled from side to side as wings move. Often bathe after eating large items of prey. Bathe during rain, and, once, in wet grass. Will traverse other territories to bathe. After bathing, dry off on sheltered perch, using vigorous movements of wings along side of body. Each bath lasted mean of 1.4 min (1.2; 0.2–6.2; 58) and birds spent mean of 3.0 min drying (2.6; 1.1–14.7; 56). Overall, spent 0.5% of time bathing and drying, and averaged nearly one bath per day. Bathe throughout year. ANTING: With plumage sleeked, tail brought forward, and folded wing held slightly forward and out. Bird holds an invertebrate in bill and wipes it quickly along each underwing alternately; between wipes, invertebrate manipulated in bill and finally it is eaten. Overall, spent mean of 0.04% of time anting; each invertebrate used for mean 7 s (0.1; 3–21; 25), and bouts, using several invertebrates in succession, lasted 3 min (4.3; 0.4–13.5; 7). Anting recorded throughout year, though episodes involving multiple prey, only recorded Dec.–May. Kinsky (1957) noted that ants were picked up from underneath and passed along edges of primaries. SUNNING: Performed by adults, mostly in middle of day, Dec.–Feb., after breeding and before moult. Lean to one side, with tail and exposed wing fanned, contour feathers ruffled and head positioned so that one eye turned towards sun. Bird keeps still except when turning to expose shaded side to sun. In intense sunlight, birds pant. Sunning often followed by preening, scratching and shaking. Sunning often occurred in bouts with birds moving in and out of direct sunlight; each period in direct sunlight was termed an exposure; sunning exposures averaged 2.1 min (2.2; 0.1–16.3; 172); each bout of sunning averaged 2.6 exposures (2.4; 1–12; 65) and lasted 5.6 min (5.2; 0.1–29.8; 65) (Powlesland 1983a). RESTING: In resting posture pull head to body, fluff contour-feathers, depress tail slightly and flex legs; perch with one leg tucked into feathers, or sometimes sit on branch; sometimes close eyes (Powlesland 1981a).

Agonistic behaviour Male does most defence of territory (Armstrong 1995). Birds less aggressive towards neighbours than to unfamiliar Robins (Armstrong et al. 1995). Song mostly uttered by unmated males to attract mates (see below) but also uttered in boundary disputes or in response to Song of neighbour; in paired males, main function of Song probably to proclaim ownership and defence of territory. Uttered in most months of year, but frequency least when moulting, and at that time, probably use Downscale Call in place of Song (Hay 1975; Powlesland 1983b). Downscale Call: Probably

functions in defence of territory, advertisement of territorial boundaries, or spacing of birds during moult when territorial boundaries are less well defined and when full Song rarely uttered; Downscale Call apparently given in similar situations to Song, but with no element of mate attraction (Hay 1975; Powlesland 1983b; see Voice). Adult males use Downscale Call when ousting immatures that have set up subterritories when adults in moult (Powlesland 1983c). Downscale Call often interactions with neighbours preceded or followed by (27% of calls investigated; see Voice), e.g. birds responded to Downscale Call of neighbour by moving towards it or by giving similar call (Powlesland 1983b). Downscale Call given most often in Apr. and rarely in breeding season; possibly not used while breeding so that location of nest not revealed (Powlesland 1981a, 1983c). Downscale Calls also used to maintain contact between pairs and in establishment and maintenance of pairs (see below). Soft Aggressive Chuck Call: Uttered in purely aggressive situations (Hay 1975; Flack 1976a; see below). Aggressive Downscale Call uttered in situations of intense aggression, being most common during boundary conflicts, and heard most often in winter, when these are most intense (Hay 1975; Powlesland 1981a, 1983b). FRONTAL SPOT DISPLAY: When not displaying, patch of white feathers on lower forehead forms a narrow white line or crescent. During Frontal Spot Display, feathers of forehead and crown are drawn backward so as to expose greater extent of white on forehead, resulting in more prominent round white spot; the spot can be flashed by rapidly moving feathers back and forth. During display the crown feathers are sleeked back, and the angle of bill and position of head varies (cf. Crown Display) (Flack 1976a). Mostly used in interspecific interactions (see below), or in response to mildly alarming stimuli (see Alarm below), but can occur in some aggressive interactions with conspecifics (Wilkinson & Wilkinson 1952; Flack 1973, 1976a). Frontal Spot Display given during aggressive intraspecific interactions, usually briefly upon initial encounter when facing opponent, and often by young bird in presence of territorial adult; also given when flying away from attacker or upon landing, or when facing away from attacker; it is often an appeasement response by subordinate birds under attack. Of 19 aggressive encounters involving Frontal Spot Display, Display given seven times by aggressor and 12 times by subordinate or intruding bird. At Kaikoura, one adult male attacked his recently independent son by flying at him with fully displayed spot; when the juvenile acted submissively the vigour of attacks was reduced; male also flashed spot from up to 7 m away before flying at juvenile; at one time, the juvenile flashed spot and male abruptly ceased aggressive approach. On Outer Chetwode I., three different adult males were seen to flash frontal spot briefly as they attacked intruders (Flack 1976a). Sometimes flash frontal spot when hunting on ground (Flack 1973). CROWN DISPLAY: During this display the feathers of forehead and crown are drawn forward so that feathers of crown are raised, with frontal spot often largely or wholly hidden; males raise feathers of crown higher than females, such that they can have somewhat helmeted appearance. Same feather-tracts involved as in Frontal Spot Display, but feathers are moved in opposite direction. Display directed at other Robins, usually in aggressive interactions, such as in territorial boundary disputes and in defence of territory; mostly given when initiating aggression. Often given by adult male exhibiting dominance over females or immatures. Display sometimes also given by pair feeding on ground near each other (Flack 1973, 1976a; Powlesland 1981a). WING-

LIFTING: Birds raise wings to varying degrees (Flack 1976a), though display not further described; usually performed by males in aggressive circumstances outside breeding season, e.g. in boundary disputes during territorial defence (Flack 1973; Powlesland 1981a). AGGRESSION BETWEEN MEMBERS OF PAIR: Males often aggressive towards mate (see Social Organization), and male sometimes takes prey from mate in non-breeding season (Powlesland 1981b). When male chased female, he often gave Squeak and Soft Aggressive Chuck Call, and female gave submissive Begging Call (see below) (Hay 1975). OTHER INTRASPECIFIC DISPLAYS AND POSTURES: Flack (1976a) lists several other behaviours without details or circumstances of use: (1) Flights in which tail held tightly folded so that pale undertail-coverts show at sides and above tail; apparently given during intraspecific disputes; (2) Puffing pale plumage of breast out, forward and laterally; (3) Puffing up plumage of back and other parts of body; and (4) perching in sleek upright posture. One adult male adopted upright posture and puffed out feathers of breast to drive his young son from territory, though male continued to feed his female offspring (Moncrieff 1932). BOUNDARY DISPUTES: Boundary disputes involve several of the aggressive behaviours and vocalizations described above. During one such boundary dispute between territorial male and neighbouring territorial female: male performed Frontal Spot Display, flashing frontal spot several times at female, then gave Crown Display; with body-plumage fluffed up and crown feathers raised, he hopped and flew parallel to female while giving extended Wing-lifting (Flack 1976a). Also raise undertail-coverts and engage in bill-snapping during boundary disputes (Powlesland 1981a). Song, Downscale Call, Soft Aggressive Chuck Call and Loud Chuck Call all reported during border disputes (see above, and Voice). CHASING: Used in variety of circumstances, including during territorial boundary disputes (Moncrieff 1932); during interspecific interactions (see below); and when territorial adult males chased immatures from territories (Powlesland 1983b); also used in sexual behaviour (see below). Chases usually accompanied by vocalizations such as Soft Aggressive Chuck Call, Twitter Squeak and bill-snapping, but sometimes silent; chases usually preceded by Frontal Spot Display, after which birds often crouch, partly spread tail and lower wings before pursuing opponent from up to 20 m away (Hay 1975; Flack 1976a). **Fights** Sometimes peck at face of another bird, in apparent dispute over food item (CSN 23). Once, seized neck-feathers of another, which called in distress and was then driven away (McLean 1911). **Submission** BEGGING CALL: Often given in submission (Hay 1975). SUBMISSIVE POSTURES: Bird crouches with wings fluttering and uttering Begging Call; usually given by young before attaining adult plumage and in presence of adult, but sometimes given by adults (Hay 1975; Flack 1976a). Sometimes hunch back, lean forward into horizontal position and flick tail downward while giving Begging Calls (Flack 1976a). Once, bird (probably adult male) stood on ground in semi-erect posture, but slightly crouched, with wings lowered and with tip of fanned tail touching ground, giving impression of submissiveness (Edgar 1961); possibly same 'wing drooping' display referred to by Maloney & McLean (1995). **Alarm** Large predators, such as Stoats, scolded from safe distance, using Loud Chuck Calls, for up to 15 min (Hay 1975; Flack 1976a; Powlesland 1981a). Frontal Spot Display given in response to mildly alarming stimuli, e.g. on sudden encounter with person (Flack 1973). Distress Squeal uttered in situations of extreme stress, e.g. when handled, or when

bird was pinned on its back during conflict with Bellbird *Anthornis melanura* (Hay 1975). INTERSPECIFIC INTERAC- TIONS: Frontal Spot Display usually directed at other species including Bellbird, New Zealand Tomtit, Grey Fantail *Rhipidura fuliginosa*, Rifleman *Acanthisitta chloris*, Brown Creeper *Mohoua novaeseelandiae*, Silvereye *Zosterops lateralis*, and people (Flack 1976a). Loud Chuck Calls given in response to predators (see Alarm). Near Kaikoura, SI, usually ignored other species of bird (Flack 1976a), though some- times attack and drive away other species that enter territory or come close to nest (Flack 1976a; Oliver; see Relations within family group, below), e.g. a Grey Fantail was forced onto its back on ground (Moncrieff 1931). In reactions to other species, almost always give Frontal Spot Display (see below) and often chase and use bill-snapping (Powlesland 1981a). In Jan. 1957 at D'Urville R., SI, flew at and chased a Brown Hare *Lepus capensis* through trees (Breen 1959). On Outer Chetwode I., males aggressively defend food-caches from other species such as Bellbird (Powlesland 1981a). Phrases of Song sometimes given when chasing other species, such as Rifleman, Brown Creeper and Silvereye (Flack 1976a).

Sexual behaviour Song appears to function mainly to attract a mate; males sing throughout year, though least often during moult. Unpaired males sang more often than males with mates, singing regularly till they mated; and at all times of breeding season, unmated males sang for a greater proportion of time than paired males. Once a male finds a mate, regular singing stops abruptly, except after boundary disputes (Fleming 1950; Hay 1975; Powlesland 1983b,c; see Voice). Downscale Calls, while mainly used in agonistic situations, particularly territorial defence (see Agonistic behaviour), also used between members of pair, probably to maintain contact; 25% of Downscale Calls used between members of pair. Downscale Call also given when selecting nest-site (Hay 1975; Powlesland 1983b). Downscale Calls given most often in Apr. and rarely during breeding season (Powlesland 1983c). At Kowhai Bush, chases between members of pairs seem to be involved in pair-formation and reinforcement of pair-bond (Powlesland 1981a; see Agonistic behaviour, above). Begging Call given by female during courtship (Hay 1975). COURTSHIP DISPLAYS: In apparent courtship displays by unpaired males, directed at paired females at edge of territory, male spread wings, performed Frontal Spot Display (see above) and attempted to get behind female (Armstrong *et al.* 2000). In another possible sexual display on Little Barrier I., a female flew silently from nest to perch sideways on tree- trunk where she slowly fluttered wings, raising them vertically above back like butterfly (Parkin & Parkin 1952); same dis- play also performed on ground (St Paul 1976). **Courtship feeding** Males feed females throughout the breeding season, but particularly while nesting (nest building, pre-laying period, laying, incubation), usually on a perch near nest (Parkin & Parkin 1952; Wilkinson & Wilkinson 1952; Powlesland 1983b; Armstrong *et al.* 2000); while brooding during heavy rain, female occasionally accepted food from male rather than feed nestlings (Powlesland 1983b). Short segments of Song often given by male before feeding his mate (Wilkinson & Wilkinson 1952; Hay 1975; Soper 1976). Sometimes female begs from mate before receiving food (Armstrong *et al.* 2000). Once, male called female off nest to feed her, but then acted aggressively towards her; the female then begged from the male while performing Frontal Spot Display (see above); she was then fed while still performing Frontal Spot Display (Flack 1976a). For rates of feeding of female during different

stages of breeding, see Breeding. CONTACT: Downscale Call probably functions in maintenance of contact between pairs (as well as in territorial advertisement); in response to Downscale Calls, partner often responded by giving same call, by moving towards its mate, or by doing both (Hay 1975; Powlesland 1983b; see Voice). Contact Chuck Call often given while foraging, especially when near other birds, such as mate or offspring (Hay 1975).

Relations within family group Only female incubates and broods; nestlings fed by both parents, male either feeding nestlings directly or passing food to female to feed to nestlings (for details see Breeding). Nestlings beg with Begging Calls (see Voice), which usually also involves use of wings (Flack 1973). Brooding female begs for food for nestlings from male by rotating on nest while vigorously flapping wings; male then brings food to nest and female stands up to reveal nestlings, which male then feeds (Flack 1973). Short seg- ments of Song often given by both sexes when carrying food to older nestlings and to fledgelings (Wilkinson & Wilkinson 1952; Hay 1975; Soper 1976). Call-away Song is a very rapid form of Song, often given by adults when young are fledging; typically, young move towards sound, but if they remain in the nest they are not fed, and adults move round nest singing till the young leave it (Hay 1975). FLEDGELINGS: Fledgelings often sit in separate trees; beg for food with Begging Calls (see Voice) and by shaking one wing only (Wilkinson & Wilkinson 1952), or by opening bill and spreading each wing alternately (Moncrieff 1932). Contact Chuck Call often given by adult just before feeding dependent juveniles (Hay 1975; see Voice). Downscale Call given when feeding juve- niles, when possibly assists in maintenance of contact between parent and young (Hay 1975; Powlesland 1983b). Fledgelings fed by both parents, though role of parents, especially attendance by female, appears to vary with size of brood and whether, and how quickly, female attempts to re-nest. Broods of more than one fledgeling usually divided, with male and female each feeding specific juveniles, at least until female re-nests; if there is an odd number of offspring, male usually feeds extra one; if brood of one, male provides all care while female re-nests. If pair raises multiple broods in season, male continues to feed young of one brood till next clutch hatches (for details see Breeding: Fledging to indepen- dence). **Anti-predator responses of young** At one nest watched for much of nestling period, young remained still during approach by human observer (Parkin & Parkin 1952). From 14 to 21 days old, nestlings escape predators by jump- ing from nest (Flack 1973). Fledgelings often remain well hidden in dense vegetation for first few days after leaving nest (Powlesland *et al.* 2000). **Parental anti-predator strategies** Use epiphytes to camouflage nest (Powlesland *et al.* 2000). Parents do not feed fledgelings when potential threat nearby (Powlesland *et al.* 2000). DISTRACTION DISPLAYS: Several displays described. Performed by both sexes. Usually, bird hops and flies between perches round nest and intruder, often dropping towards ground; at first, wings and tail partly spread as bird moves round threat, often facing it at close range. As intensity of display increases, wings are fully spread and held above back with tail fully fanned and slightly depressed (similar to Butterfly Flight, see below), and bird usually leans forward. Also commonly use Frontal Spot and Crown Displays during distraction displays. When unob- structed, all elements of display are symmetrical (Flack 1976a). Utter low piping note during distraction display (Buller 1888). *BUTTERFLY FLIGHT*: Performed by both sexes

as part of distraction display at nest; bird flies up and lands just above intruder's head, raises fully spread wings and fanned tail, then floats gently down past intruder's face (to within c. 1 m), turning and spiralling with eyes always looking at intruder, before landing on ground and pirouetting slowly back and forth (Parkin & Parkin 1952; Soper 1963; St Paul 1976). OTHER DISTRACTION DISPLAYS: Parent sometimes flies to ground and feigns injury, trailing her wings to distract human intruder (McLean 1911; St Paul 1976). Once, when observers within 1 m of nest, a male picked up a twig or two, flew downhill and dropped the material before returning towards observers (Wilkinson & Wilkinson 1952). ATTACKS: Adults occasionally attack people at or near nests with eggs or young, flying directly at, and to within c. 30 cm of, their heads; at nest, can also land and peck intruder's hands (McLean 1911; Wilkinson 1927; Parkin & Parkin 1952; Flack 1976a; St Paul 1976). Do not defend nests against predation by Black Rat (Brown 1997). For period of dependence of young, see Social Organization.

VOICE Well known. Two detailed studies, both near Kaikoura, SI: of seasonal and diurnal variation of vocalizations (Powlesland 1983c), and the other of vocalizations (Hay 1975), and which includes sonagrams. Calls rendered in musical notation in Andersen (1909, 1918, 1926). Often quiet (McLean 1911; Oliver 1922). ANNUAL PATTERN: From Jan. to July, Downscale Call given more than Song, but from July to Dec. Song given more than Downscale Call. Males sing throughout year, but least often in Jan. and Feb., when moulting; after Feb., frequency of use of Song increases till Apr., decreases in May, and then increases to a peak in Oct. During adult moult, the type of Song heard commonly is practised Song of juveniles (see below), distinguished from adult Song by a more fluid note structure in phrases. Substantial alterations sometimes occur in the Song repertoire of an individual over a year: some basic sequences of phrases remain, but there are occasionally additions and deletions of note-types, and changes in the frequency with which different note-types occur. There was a trend for greater overall uniformity of Song in population as season progressed (Hay 1975). DIURNAL PATTERN: At Kaikoura, Song heard at any time of day, though more often in early morning (Hay 1975; Powlesland 1983c); on Outer Chetwode I. there was no such pattern (Powlesland 1981a). At Kaikoura, observations in May–June, Aug.–Nov. and Dec.–Jan. failed to show any dawn chorus from birds. However, dawn chorus heard on Outer Chetwode I. in Oct. (though not Feb., July or Dec.), in which 4–5 birds sang intermittently with pauses, sometimes several at once, sometimes singly, often continuously for 15–20 min; chorus started later on a rainy morning (Hay 1975). DIFFERENCES BETWEEN SEXES: Females not heard to give full Song, but often utter Subsong, mostly when selecting nest-site (Powlesland 1983c). Female said to sing phrases of Song before feeding older nestlings or fledgelings (NZRD). INDIVIDUAL DIFFERENCES: Downscale Call varies individually, and possibly allows recognition of individuals (Hay 1975). LOCAL AND REGIONAL VARIATION: Song varies geographically (Fleming 1950). Songs of population at Kaikoura did not show a consistent variation with location; the repertoire of an individual did not appear to be influenced by those of its neighbours, as similarity between Songs of males did not decrease as the distance between them increased. Songs in other parts of SI comprised a large number of notes not comparable to those used at Kaikoura. Mean duration of interval

between notes was also consistently different between populations (Hay 1975). In Apr.–June, birds from Kaikoura and from Outer Chetwode I. spent similar proportions of time uttering calls other than Song; at this time at Kaikoura, Song given mostly by unmated males, but on Outer Chetwode I. Song not heard (Powlesland 1981a). RESPONSE TO PLAYBACK AND IMITATION: Attracted by replay of Song, Loud Chuck Call, or Downscale Call; also by squeaks and whistles, and by knocking of sticks together or against a tree (Moncrieff 1932; Hay 1975; Flack 1976a; Powlesland *et al.* 2000). NON-VOCAL SOUNDS: Bill-snapping indicates a high level of aggression, and accompanies chasing of birds of own or other species, though sometimes given when stationary (Flack 1976a; Powlesland 1981a). Also snap bills when sallying for insects (Hay 1975).

Adult SONG: A series of phrases, each consisting of a number of identical notes, uttered in a sequence which is neither random nor fixed. A phrase of one type of note sometimes followed by any of a number of other phrases of other types of note, but certain phrases more likely to be uttered in sequence. In population at Kaikoura, 114 types of note distinguished, with mean repertoire of 23.6 types of note per individual (Hay 1975). Song (from SI) described as *tĩnk, tĩnk, tĩnk, tink, tink, tink, tonk, tonk, tonk, tonk, tonk, tonk*, with first three phrases louder, higher pitched and longer, followed by shorter, flatter calls, with *tonks* sounding more wooden than rest (M. Aviss). Song described as beautiful, sweet, cheerful, musical and powerful, a joyous little melody, which is a prolonged outpouring of rather staccato notes, rising and falling in pitch, and of surprising volume for the size of the bird (Reischek 1887; McLean 1907, 1911; Wilkinson 1927; Moncrieff 1932; Soper 1976). Song of subspecies *longipes* said to be superior to that of nominate *australis* (Guthrie-Smith 1914; Wilkinson 1927; Moncrieff 1932). Bouts of Song can continue for up to 30 min (Guthrie-Smith 1914; Wilkinson 1927). Sonagram **A** shows part of a Song. Much variation in amount of singing, both spontaneous and induced by playback, between individuals of similar status, e.g. between paired males in adjacent territories. Unpaired males sing more often than males with mates, singing regularly till they obtain a mate, when regular singing stops abruptly: at all times of breeding season (Aug.–Dec.), unpaired males sang for a greater proportion of the time than paired males; in 1977 breeding season, unpaired males sang c. 55 bouts/day, each with mean duration of 4.7 min; singing rates of paired males not given (Hay 1975; Powlesland 1983c). Main function of Song appears to be to attract a mate (Powlesland 1983c). However, Song, or parts of Song, uttered in variety of circumstances, particularly by males during and after boundary disputes, which is when paired males utter most Song
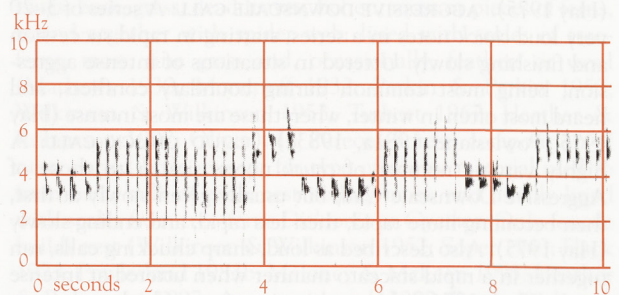
A L.B. McPherson; Kaikoura, SI, Oct. 1983; P107

(Powlesland 1983c); phrases of Song also sometimes given when chasing other species, such as Rifleman, Brown Creeper and Silvereye (Flack 1976a); and short segments often given by both sexes when carrying food to older nestlings and to fledgelings, and by male before feeding mate (Wilkinson & Wilkinson 1952; Hay 1975; Soper 1976). CALL-AWAY SONG is a very rapid form of Song, often given by adults when young are fledging; typically, young move towards sound, but if they remain in nest they are not fed, and adults move round nest singing till the young leave it (Hay 1975). SUBSONG: A quiet non-stereotyped form of Song, with notes and phrases given randomly, in contrast to their ordered arrangement in full Song (Hay 1975; Powlesland 1983c). Described as delightful (St Paul 1976), but audible to only a few metres. Except in pre-laying and laying stages, males rarely utter Subsong in breeding season; females give most Subsong when selecting nest-site. The proportion of time devoted to Subsong is greatest in summer, during moult, when often given while foraging (Powlesland 1983c). DOWNSCALE CALL: A series of very loud notes, descending in frequency, starting in rapid succession and finishing slowly; Call lasts 3–4 s. Each note is short and covers a broad range of frequencies (Powlesland 1983c). As loud as or louder than Song. Varies individually, allowing individual recognition (Hay 1975). Though uttered several times an hour, never repeated immediately. Probably uttered more often by males than by females (Hay 1975), *contra* very rarely given by females (Powlesland 1983c). Usually given by solitary birds; and heard most often outside breeding season, though uttered when selecting nest-site and when feeding juveniles (Hay 1975; Powlesland 1983c). From late Jan. to May, heard almost to the exclusion of Song (Hay 1975). Of 273 Downscale calls investigated, in 24% of cases the partner responded by giving same call, by moving towards its mate, or by doing both; in 27% of cases there were interactions with neighbours before or soon after the call, e.g. birds responded to Downscale Call of neighbour by moving towards it or by giving similar call (Powlesland 1983c). Likely functions are advertisement of territory, spacing of birds during moult, and the maintenance of contact between pairs, and possibly between parent and young (see Social Behaviour). CALLS BASED ON CHUCK SOUNDS: CONTACT CHUCK CALL: A quiet single *chuck* note, with a musical tone. Often given while foraging, especially when near other birds, such as mate or offspring; also given just before feeding dependent juveniles (Hay 1975). A short chirp, given as a contact call (Falla *et al.* 1979) probably same call. SOFT AGGRESSIVE CHUCK CALL: Similar to Contact Chuck Call. Several given in sequence, but without any temporal pattern. Uttered in purely aggressive situations, and associated with displays and chases (Hay 1975; Flack 1976a). TWITTER: A series of high-pitched *chuck* notes at regular intervals. Usually given by pursuer in chases (Hay 1975). AGGRESSIVE DOWNSCALE CALL: A series of 3–20 very loud *chuck* notes in a series, starting in rapid succession and finishing slowly. Uttered in situations of intense aggression, being most common during boundary conflicts, and heard most often in winter, when these are most intense (Hay 1975; Powlesland 1981a, 1983c). LOUD CHUCK CALL: A highly varying number of *chuck* notes, similar to those of Aggressive Downscale Call, but usually given slowly at first, then becoming more rapid, then less rapid, and ending slowly (Hay 1975). Also described as loud, sharp chucking calls, run together in a rapid staccato manner when uttered at intense levels (Flack 1976a). Uttered in situations of high stress, e.g. in presence of a predator, for up to 10–15 min (Hay 1975;

Flack 1976a; Powlesland 1981a). Repeated spluttering note (McLean 1911) and angry chittering, uttered during border disputes (Soper 1976), probably same call. CALLS BASED ON SQUEAKING SOUNDS: SQUEAK: A quiet squeak heard infrequently during mild aggressive encounters, especially between members of a pair. Usually given in conjunction with light *chuck* notes and begging calls, normally by the male as he chases the female. CALLS BASED ON HARSH SOUNDS: BEGGING CALL: A harsh, high-pitched call, with frequency modulation, given in submission, and by female during courtship. DISTRESS SQUEAL: A varyingly loud harsh squeal or screech, uttered in situations of extreme stress, e.g. when handled, or when bird was pinned on its back during conflict with Bellbird (Hay 1975). **Other calls** Low piping note uttered during Distraction Display (Buller 1888).

Young CALLS BASED ON SQUEAKING SOUNDS: BEGGING CALL: Consist of a series of squeaks; Begging Calls of young nestlings lack temporal structure; but Begging Calls of older nestlings and fledgelings (for a few days after leaving nest) have developed a regular structure. CALLS BASED ON HARSH SOUNDS: BEGGING CALL: Fledgelings beg with a harsh high-pitched call, with frequency modulation; with age, this call becomes lower in pitch and covers a wider range of frequencies, and becomes indistinguishable from Begging Call of adult (Hay 1975). Also given in submission, and when being chased by parents at the time of rejection (Hay 1975; Flack 1976a). DISTRESS SQUEAL: A distress call, similar to that of adult, was once heard from an older nestling. OTHER CALLS UTTERED BEFORE INDEPENDENCE: In first month after fledging, young utter all calls except Song and vocalizations related to Song. Calls based on *chuck* notes are uttered mainly in aggressive encounters with siblings, and bill-clicks are given. The Downscale Call changes from a juvenile location call to an adult territorial call (Hay 1975). DEVELOPMENT OF SONG: Quiet Subsong occurs before full Song (Hay 1975; Powlesland 1983c). Structure of Song differs from that of adult Song, there being fewer notes per phrase and fewer constraints on the types of notes used. Most juveniles start to sing in autumn when adults undergoing post-breeding moult, though some were heard to sing as early as Oct. in the breeding season in which they were raised. After independence, the more precocious males disperse and establish themselves in subterritories, maintaining exclusive use of small areas of habitat, advertising their presence by loud singing, and commonly responding to the Song of neighbours by counter-singing (see Social Organization: Breeding dispersion, and Social Behaviour: Agonistic behaviour). The singing of one such individual was monitored for 3.5 weeks, during which time the patterns in which notes were used changed and the number of types of note used showed an overall reduction, a large number being removed from the repertoire and a smaller number being introduced, some being copied or modified from neighbours. There is little relationship between the Songs of adult males and those of their offspring (Hay 1975).

BREEDING Well known. Account based on detailed studies of breeding biology of subspecies *longipes* in Pureora Forest Park, NI, over two breeding seasons, 1996–98 (Powlesland *et al.* 2000); of translocated subspecies *longipes* on Tiritiri Matangi I., NI, over seven breeding seasons 1992–99 (Armstrong *et al.* 2000); and of nominate *australis* at Kowhai Bush, Kaikoura, SI, over five breeding seasons, 1971–77 (Flack 1979); and at same site over two seasons, 1977–79 (Powlesland 1980a, 1983b); also from information summarized from NZ

NRS in Heather & Robertson (1997). Breed in pairs in all-purpose territories that are defended throughout year; usually keep same partner from year to year; usually first breed when 1 year old, but sometimes birds on islands do not breed till 2 years old (Wilkinson & Wilkinson 1952; Flack 1979; Heather & Robertson 1997; also see Social Organization).

Season Throughout range, laying recorded early May to late Mar., usually Sept.–Jan. (see references below); laying and breeding appear to start and finish slightly earlier on SI compared with NI, e.g. from detailed studies below, mean dates of first clutches 20 and 26 Sept. in NI and 15 Aug. in SI (see below). (For general timing of breeding, also see Soper [1963] and Heather & Robertson [1997].) NI: In Pureora Forest, lay early Sept. to late Mar.; mean date of laying of first clutches (from completion of clutch), 20 Sept. (8.8. days; 9 Sept.–16 Oct.; 21); and mean date of laying of last clutches, 17 Dec. (18.9 days; 3 Nov.–27 Jan.; 35). On Tiritiri Matangi I., breed early Sept. till late Feb.; mean date of laying of first clutches, 26 Sept. (19.7 days; 15 Aug.–10 Dec.; 97 clutches, 1992–99); mean date of laying of last clutches, 13 Nov. (29.5 days; 1 Sept.–6 Jan.; 97 clutches, 1992–99); last fledgeling still being fed by parents in mid-Mar. Otherwise, breeding recorded Oct.–Dec. on Little Barrier I. (Oliver); and from Sept. till Apr. or so on Kapiti I. (Wilkinson & Wilkinson 1952). SI: At Kowhai Bush, 1971–77, most pairs produce more than three clutches, sometimes up to six, with laying recorded early May to early Jan.; first clutches usually laid Aug., and last clutches in late Dec. (Flack 1979). At Kowhai Bush, 1977–78, laying recorded July to late Dec., and nestlings recorded into Jan. (Gill *et al.* 1983). Also at Kowhai Bush, 1977–79, laying began Aug. and finished Jan., with mean date of laying of first clutches 15 Aug. (23 July–1 Sept.; 40 clutches); as mean length of nest-building and pre-laying periods combined was 11 days in Aug., mean date of start of building was 4 Aug.; last clutches of season laid in early Jan.; fledged young hatched from late clutches were still being fed in Mar. (though most eggs or nestlings from late clutches were eaten by predators, so breeding mostly finished by late Jan.) (Powlesland 1983b). On Chetwode I., eggs said to be laid between Sept. and Nov. (NZRD).

Site Usually in forks of trunk or large branches in trees or shrubs, in forks between branches and trunks of trees, in cavity in tree-trunk left by a fallen limb, in hollows or spouts of trunks or branches of trees (including fallen branches), and on dead stumps (including tree-ferns); less often in crowns of tree-ferns, or attached to trunks of tree-ferns, on epiphytes next to trunk of tree; among dense tangles of vines; exposed roots of large tree; in epiphytes growing on trees; in Bracken; occasionally on ground, at base of tree, among dry Bracken and other ferns or among fronds; and, on Kapiti I., on banks or rock ledges, sheltered from above by rock or bank overhang or vegetation. Also often in, or on top of, old and disused nests of New Zealand Robins, Common Blackbirds *Turdus merula*, Song Thrushes *T. philomelos*, Bellbirds or Tuis *Prosthemadera novaeseelandiae* (Wilkinson 1927; Moncrieff 1932; Wilkinson & Wilkinson 1952; Soper 1963; St Paul 1976; Powlesland 1983b; Heather & Robertson 1997; Oliver; see below). In PUREORA FOREST, five types of sites were distinguished (n=146 nests): on trunks or in fork in trunk (35.6%); in junctions between trunks and branches (34.2%); on epiphytes growing on trunks (15.1%); on central portion of branches (11.0%); or on outer portion of branches (4.1%); two nests (1.4%) were old nests from previous seasons. Nests were evenly distributed throughout various levels of forest; of

164 nests: 30.8% were in shaded canopy, 39.7% in upper understorey, and 29.5% in lower understorey (0.3–2.0 m above ground) (Powlesland *et al.* 2000). Main species of trees in which nests were built, or on which epiphytes that contained nests were growing: Tawa *Beilschmiedia tawa* (24.0%); tree-fern *Dicksonia* and *Cyathea* (19.2%); Mahoe *Melicytus ramiflorus* (9.6%); *Coprosma* and Totara *Podocarpus totara* (4.1% each); Miro *Prumnopitys ferruginea*, Kamahi *Weinmannia racemosa*, Pigeonwood *Hedycarya arborea* and Tanekaha *Phyllocladus trichomanoides* (3.4% each); and dead trunks of unidentified trees (10.3%) (Powlesland *et al.* 2000). On TIRITIRI MATANGI I., of 131 nests: 50% were in forks of branches of live trees or shrubs (13 nests in Manuka *Leptospermum scoparium*, nine in Mapou *Myrsine australis*, eight in Kanuka *Kunzea ericoides*, seven in Pohutukawa *Metrosideros excelsa*, seven in Kohekohe *Dysoxylum spectabile*, six in Ti Kouka *Cordyline australis*, five in Mahoe, four in *Coprosma macrocarpa*, three in Hangehange *Geniostoma rupestre*, two in Karo *Pittosporum crassifolium*, and one in Akepiro *Olearia furfuracea*); 41% were in tree-ferns (including 41 in crowns, seven attached to trunks, three in hollow in top of broken-off trunk of dead fern, one in fork of branching tree-fern, one wedged between trunks of two ferns, and one in cavity in side of dead fern); 3% (four nests) were in cavities in trunks or branches of Pohutukawa (two nests), Mahoe (one), or Kohekohe (one); 2.2% (three) each in hollow in broken-off branches of Crested Wattle *Albizia lophantha* or in branches of dead trees or shrubs; and 0.75% (one) each either suspended among vines or in epiphytes on Kanuka (Armstrong *et al.* 2000). On LITTLE BARRIER I., one nest was in crevice of trunk of Manuka (Parkin & Parkin 1952). At KOWHAI BUSH, nest usually placed on tree-trunks or in forks of branches, in mistletoe *Loranthus micranthus*, in crowns of Kanuka or in disused nests from previous seasons; of 164 nests in two seasons: 34% had been used in previous seasons by Robins, Song Thrushes and Blackbirds, and were merely re-lined, but a nest was re-used for successive clutches in a season only once (Powlesland 1983b). RE-NESTING: At KOWHAI BUSH, proportion of nests re-used per month declined towards end of breeding season, from peak of 54% in Aug. to 17% in Dec. (Powlesland 1983b). In Pureora Forest, mean distance between a failed nest and new one, 60 m (31.4; 12–160; 48); and mean distance between a successful nest (fledging young) and new nest, 44 m (30.3; 5–117; 24) (Powlesland *et al.* 2000). MEASUREMENTS (m): Height of nest: usually 1–4 above ground, but occasionally up to 11 (Wilkinson 1927; Heather & Robertson 1997). In Pureora Forest, 5.3 (3.05; 1.0–10.5; 146). On Tiritiri Matangi I., 3.5 (0.9–10; 131). At Kowhai Bush, 3.7 (0.8–8.7; 164); new nests higher (4.0; n=109) than re-used ones (3.0; n=55) (Powlesland 1983b).

Nest, Materials Nest bulky, with compact cup. Made of twigs, bark, grass, dead leaves, lichen, moss or pieces of ferns, bound together with spider web; lined with scales of tree-ferns, moss, fine grass and, occasionally, feathers or wool (Mathews 1930; Moncrieff 1932; Parkin & Parkin 1952; Wilkinson & Wilkinson 1952; Turbott 1967; Heather & Robertson 1997; Oliver). In Pureora Forest, composition of nests varied little, except for type of coarse material used to form base; bulk of each nest mainly moss, and usually lined with scales from tree-ferns *Dicksonia* or *Cyathea*. Only female builds nest (Wilkinson & Wilkinson 1952; Soper 1963; Flack 1973; Powlesland 1983b; Maloney & McLean 1995; Heather & Robertson 1997; Armstrong *et al.* 2000; Powlesland *et al.* 2000; Oliver). Nest usually built in 1–7 days (Soper 1963;

Heather & Robertson 1997). At Kowhai Bush, female made mean of 22.4 trips/h with material to nest (n=117 h obs.), but rate of visits with material decreased as nest neared completion. Most material collected within 50 m of nest, usually from ground or tree-trunks, but sometimes from old nests of own or other species. Females building nests fed by mate, on average 3.2 times/h (89 h obs.) (Powlesland 1983b). Three stages of building a new nest discernible: (1) Coarse material, such as rootlets, twigs and strips of bark, brought to site and bound together with spider web; (2) Nest lined with finer material, especially moss, but no spider web used; and (3) thin layer of very fine material such as moss, scales from ferns, dry grass, paperbark, skeletons of leaves and occasionally a few feathers added but not pressed into place. New nests took mean of 3.4 days to build (2–6; 27), though construction sometimes longer if female abandons site after building at it for several hours; number of days taken to finish nest decreased during season, e.g. 4.8 days in July, 2.5 days in Dec. Re-lining of old nests took <1 day (Powlesland 1983b). Time between finishing nest and onset of laying averaged 4.2 days (2–8; 44); at this time, female fed by mate on average 1.5 times/h (48.3 h obs.) (Powlesland 1983b). MEASUREMENTS (cm): External width, 14; external depth, 10; internal width, 7.5; internal depth, 5 (Wilkinson & Wilkinson 1952).

Eggs Ovoid; creamy white or greyish cream, with fine light-brown or purplish-brown spots or blotches, often concentrated at large end, forming indistinct band (Wilkinson 1927; Mathews 1930; Wilkinson & Wilkinson 1952; Heather & Robertson 1997; Oliver). At Kowhai Bush, colour ranged from white with no markings to pale brown with evenly distributed brown, purplish-brown or black blotches and spots; most eggs chalky white with brownish markings concentrated at large end (Powlesland 1983b; Powlesland et al. 2000). MEASUREMENTS: In Pureora Forest (subspecies *longipes*): 24.7 (0.6; 24.0–26.2; 17) × 18.4 (0.4; 17.5–19.0). At Kowhai Bush (nominate *australis*): 24.9 (0.1; 21.8–28.2; 363) × 18.6 (0.04; 17.6–20.0) (Powlesland 1983b). Throughout range, 23–25 × 17–19 (Wilkinson 1927; Mathews 1930; Wilkinson & Wilkinson 1952; Heather & Robertson 1997; Oliver). WEIGHT: Mean fresh weight, 4.5 (0.27; 126), representing 12.9% of average body-weight of female (Powlesland 1983b).

Clutch-size Two to four, usually two or three (Mathews 1930; Stead 1941; Wilkinson & Wilkinson 1952; Soper 1963; Oliver); round lower Kowhai R., first clutches usually C/2, later clutches usually C/3 (Flack 1979). In Pureora Forest, mean 2.6 (0.49; 2–3; 78) with mean clutch-size varying over season: 2.18 in Sept. (n=17), 2.24 in Oct. (n=12), 2.93 in Nov. (n=27), 2.76 in Dec. (n=17) and 2.20 in Jan (n=5). On Tiritiri Matangi I., mean 2.34 (0.48; 2–3; 127); clutch-size did not vary between years, and did not vary significantly over season. At Kowhai Bush, mean 2.7 (0.5; 2–4; 150 clutches in

two seasons): C/2 × 48, C/3 × 99, C/4 × 3; mean clutch-size varied over season, from 2.0 in July to 3.0 in Oct. Mean clutch-size for four age-classes of females summarized in Table 3; no significant difference between age-classes for size of first clutch, or for all clutches (first and replacement clutches) (Powlesland 1983b).

Laying Eggs laid at intervals of 24 h; usually within 3 h of sunrise (Parkin & Parkin 1952; Flack 1979; Powlesland 1983b; Powlesland et al. 2000); twice, egg laid several days after previous one (Powlesland 1983b). At Kowhai Bush, pre-laying period (completion of nest to day before first egg laid), 4.2 days (2–8; 44); period varied over season, being longest in July (6.8 days [5–8; 4]) and shortest in Nov. (2.9 days [2–4; 13]). Male regularly fed partner during this period, at 1.5 times/h (48 h obs.), half the rate of that when female building nest (Powlesland 1983b). On Tiritiri Matangi I., mean interval between fledging of one brood and laying of next clutch, 27.3 days (12.6; 15); mean interval between failure of nest and laying of next clutch, 14 days (8.4 days; 3) (Armstrong et al. 2000). Pairs can produce two or three broods in a season; and can make up to six attempts in a season if re-nesting after losses (Wilkinson & Wilkinson 1952; Soper 1963; Flack 1979; Heather & Robertson 1997). At Kowhai Bush, there are usually four peaks of laying in a season, sometimes with a fifth and smaller peak late in season: (1) mean date of laying of first egg of first clutches, 16 Aug.; (2) second peak in Sept., reflecting replacement of failed first attempts; (3) second clutches laid after fledging of first brood, usually in mid-Oct.; (4) a fourth peak in Nov., mainly reflecting replacement of many second clutches and broods destroyed by predators after Sept.; and (5), a fifth peak, if second brood fledged and a third clutch laid in about mid-Dec. (Gill et al. 1983). Also at Kowhai Bush, mean date of start of laying varied with age of females: earliest for 3-year-old females, followed by 2-year-olds, then 1-year-olds and lastly, those at least 4 years old. Though most pairs were capable of raising three broods in a season, many built more than three nests to replace clutches taken by predators. Over two breeding seasons, 40 females built and laid in a mean of 4.1 nests per season: 12 females built three nests each, 14 built four, 11 built five, and 3 built six (Powlesland 1983b). In Pureora Forest, pairs had mean of 3.1 nests/season (0.87; 1–5; 44): one nest 2.4%; two nests 22.0%; three nests 46.3%; four nests 24.4%; five nests 4.8%. On Tiritiri Matangi I, females made mean of 1.92 breeding attempts/year (1.5–2.14; 84): single attempt, 29%; two attempts, 51%; three attempts, 15%; four attempts, 2%; no attempts 3%. At St Arnaud, SI, of nine breeding pairs closely followed in 1998–99 season, after control of predators in area: one pair had two nesting attempts, six pairs had three attempts, and two pairs had four attempts; in total, the nine pairs nested 28 times, a mean of 3.1 nests/pair (Etheridge &

Table 3. Frequency distribution of clutch-size and mean clutch-size for four age-classes of New Zealand Robins for first clutches of a season and for all clutches during a season; data combined for 1977–78 and 1978–79 breeding seasons (Powlesland 1983b).

| AGE | FIRST CLUTCHES | | | | ALL CLUTCHES | | | |
	C/2	C/3	C/4	MEAN	C/2	C/3	C/4	MEAN
1 year	12	3	–	2.2	21	36	1	2.7
2 years	6	1	–	2.1	10	16	–	2.6
3 years	4	2	–	2.3	5	16	1	2.8
≥4 years	8	4	–	2.3	12	31	1	2.7

Powlesland 2001). On Stewart I., rarely breed more often than once a year; if nest lost, replaced in just over 1 week; females usually re-nest while young still dependent, roughly 1–2 weeks after fledging (NZRD).

Incubation By female only, with incubating female fed by mate, throughout day (Wilkinson & Wilkinson 1952; Gill *et al.* 1980; Powlesland 1983b; Armstrong *et al.* 2000; Powlesland *et al.* 2000; Oliver). Incubation usually begins with laying of last egg, though sometimes starts with laying of second egg in clutches of three or four (Flack 1979). At Kowhai Bush (n=236 h obs.), females usually start incubation fully on day of laying last egg but, after Aug., some did so on day of laying penultimate egg of clutches of three and four. Females spent mean of 81.0% of daylight time incubating. During incubation, males made mean of 2.5 feeding visits/h to incubating female (n=236 h obs.), though rate depended on whether male feeding fledged juveniles of earlier brood, when rate of feeding visits to incubating female was 1.1 visits/h (n=58 h obs.), or not, when rate 2.9 visits/h (n=178 h). Incubating females fed at low rates often spent less time incubating (78% of time; n=58 h obs.) than those fed at higher rates (83%; 178 h) (Powlesland 1983b). Female seen to carry eggshells up to 6 m or so from nest (Parkin & Parkin 1952). INCUBATION PERIOD: From 17 to 20 days (Soper 1963; Flack 1979; see below). At Kowhai Bush, mean 17.7 days: 17 days × 10, 18 days × 19, 19 days × 1 (Powlesland 1983b). In Pureora Forest, NI, 18 days × 2, 20 days × 2 (Powlesland *et al.* 2000). Also claimed to be *c.* 14 days on Kapiti I. (Wilkinson & Wilkinson 1952).

Young Altricial, nidicolous. Eggs of clutch usually hatch within a few hours of one another, but can take up to 24–48 h to hatch (Flack 1979; Powlesland 1983b). Nestlings open eyes when *c.* 6 days old (Soper 1963) or 9–10 days old (Flack 1979). Young brooded by female only (Soper 1963; Powlesland 1983b; Powlesland *et al.* 2000). Time spent brooding by female gradually decreases; at 15 days old, nestlings not brooded during day (Soper 1963; Powlesland 1983b). At Kowhai Bush, females brooded for *c.* 80% of daylight hours when nestlings 1–2 days old; time spent brooding gradually decreased as nestlings grew, and nestlings not brooded during day at 15 days old (Powlesland 1983b). Nestlings fed by both parents equally (Fleming 1950; Wilkinson & Wilkinson 1952; Soper 1963; Flack 1973); male usually feeds young directly, though male sometimes passes food to female to feed to nestlings during first 3 days (Powlesland 1983b), up to 5 days (Powlesland *et al.* 2000), or first week (Soper 1963) after hatching. **Growth** No information.

Fledging to independence FLEDGING PERIOD: 19–22 days (Wilkinson & Wilkinson 1952; Powlesland *et al.* 2000; Oliver; see below). At Kowhai Bush, 20.8 days (19–22; 19 broods) (Powlesland 1983b); or 20–22 days, possibly up to 26 days in poor weather conditions (Flack 1979). FLEDGELINGS: At Kowhai Bush, at fledging, tails of young not fully grown and some downy feathers retained on crown; fledgelings flew poorly and perched in same place for several hours but able to fly well 2 weeks after leaving nest, and also able to forage on ground (Powlesland 1983b). PARENTAL CARE: Fledgelings fed by parents, usually for 3–7 weeks after leaving nest. Patterns of care of young and roles of parents appear to depend on size of brood, and thus how many cared for by female, and whether, and how quickly, female attempt to re-nest, and thus timing of hatching of subsequent clutches (Powlesland 1983b; Armstrong *et al.* 2000; see below). After fledging, broods of more than one usually divided, each parent taking charge of one or two young and, if number of juveniles odd, males usually feeding extra young; single fledgelings usually attended and fed by male only (Wilkinson & Wilkinson 1952; Soper 1963; Flack 1976a; Powlesland 1983b; Heather & Robertson 1997; Armstrong *et al.* 2000). When multiple broods raised in one season, male continues to feed young of one brood till next clutch hatches (Flack 1973; Powlesland 1983b). At Kowhai Bush, when only one fledgeling (n=12), male took sole care of it, and female often started to build next nest within 3 days of fledging of young. If more than one fledgeling, brood divided, with male and female each feeding particular juveniles of a brood (n=5 instances); division of brood seemed to happen within first week of leaving nest. Once female started re-nesting, male fed all juveniles. When females cared for two fledgelings, re-nesting could be delayed for up to 35 days of fledging. Number of days parents fed juveniles varied greatly; if parents re-nest, juveniles usually fed till next clutch hatches or soon after hatching: single fledgeling often fed for a few days after subsequent clutch hatched but driven from territory *c.* 24 days after it fledged; if re-nesting failed, fledgelings could be fed for up to 50 days before they were ousted from territory (Powlesland 1983b). On Tiritiri Matangi I., if only one fledgeling, it was usually fed primarily by male; if two fledgelings, each fed by different parent; if three, two were usually fed mainly by male and one by female; brood division broke down as chicks approached independence, when they would beg from and follow both parents. Males usually fed chicks more than females did; females did not feed fledgelings after laying next clutch, but males sometimes fed them till next brood had hatched. The earliest a juvenile was no longer fed by parents was 4.5 weeks after fledging; the latest a juvenile was fed was 7 weeks after fledging (n=34 broods of fledgelings); young disperse 7.5–10 weeks after fledging (Armstrong *et al.* 2000; also see Social Organization: Parental care).

Success Nesting success low, and many nesting attempts appear to fail through predation, particularly by mustelids and rodents (see below). In PUREORA FOREST, in 1996–97 and 1997–98, of 127 eggs not taken by predators, in 49 nesting attempts, 113 (89%) hatched; at least seven of the 14 eggs that did not hatch were infertile, including two (4.1%) complete clutches and one egg that contained a partly developed embryo. Of 46 banded nestlings not taken by predators, in 21 nesting attempts, at least 41 (89.1%) survived at least 1 week after fledging (Powlesland *et al.* 2000). Control of mammalian predators by poisoning at two sites in Pureora Forest (poison laid at Tahae but not Waimanoa 1996–97, poison laid at Waimanoa but not Tahae 1997–98) greatly affected nesting success: in untreated areas (no poison laid, and predators uncontrolled), for both seasons combined, breeding success (proportion of nesting attempts producing at least one fledgeling surviving for at least 1 week) was 22.9%, and mean number of offspring was 1.1 fledgelings/pair (n=37); in areas where poison laid just before breeding started, success was 68.7%, and pairs raised mean of 3.8 fledgelings/pair (n=17) (see Table 4, below) (Powlesland *et al.* 1999, 2000). For translocated population on TIRITIRI MATANGI I., over six seasons, 1992–93 to 1998–99, of 226 eggs that remained in nest long enough to have hatched, 192 (85%) hatched; overall, 51% of nests fledged at least one young, and success did not vary significantly between years; mean number of fledgelings/female/year was 2.48 (2.14–3.00; 89), and did not differ significantly between years. Number of fledgelings/female/year was lowest for females breeding in the year that they were

moved to Tiritiri Matangi (in 1992–93 season, production 0.57 fledglings/female/year for seven females translocated in 1992; and in 1993–94 season, production 1.0 for females translocated in 1993). Of 56 nest failures, ten nests were tipped by emerging fronds in crowns of tree-ferns, seven were probably damaged during strong winds, seven appeared to have been disturbed by animals, 16 nests were found empty, and 16 contained at least one deserted egg (Armstrong et al. 2000). At KAHAROA, NI, of 43 nests with eggs: seven (16.3%) fledged at least one chick; at least 25 (58.1%) failed through predation, mostly by Black Rats (18 nests) and Southern

Boobooks Ninox novaeseelandiae (2 nests); four (9.3%) were deserted; five (11.6%) were destroyed by growth of new fronds of tree-ferns; and two (4.6%) failed for unknown reasons (Brown 1997). At KOWHAI BUSH, of 521 nests 1971–77: 32% produced at least one fledgeling; 55% failed through predation, mainly by Stoats Mustela erminea and Weasels M. nivalis, and less often by Black Rats; and 13% were abandoned or failed for other reasons. Survival of young between fledging and independence usually high, and sometimes reaches 85% (Flack 1979). In another study at KOWHAI BUSH, of 405 eggs laid in two seasons 1977–79, 255 (63%) hatched, 94 (23.2%)

Table 4. Breeding success at Pureora Forest Park, NI, with and without control of mammalian predators by poisoning. Success measured as number of nests that produced at least one fledgeling surviving at least 1 week (Powlesland et al. 1999).

| | 1996–97 SEASON | | 1997–98 SEASON | |
	No Poisoning	Poisoning	No Poisoning	Poisoning
Number of pairs monitored	14	7	23	10
Number of nests monitored	35	18	67	30
Nesting success	4 (11%)	13 (72%)	20 (30%)	20 (67%)
Number of fledgelings	6	26	34	38
Mean no. fledgelings/pair	0.4	3.7	1.5	3.8

Table 5. Breeding success at Kowhai Bush, SI, and causes of failure; figures are percentage of total number of eggs or nestlings. Apparent large difference in proportion of eggs taken by predators from female age-classes not real, because age-classes were unevenly represented in two seasons when levels of predation differed (from Powlesland 1983b).

EGGS	N	SUCCESS % Hatched	CAUSES OF FAILURE Predation	Fell from nest	Abandoned or died in nest	Did not hatch	Not known
Total eggs	405	63.0	23.2	1.2	3.9	6.2	2.2
1977–78	274	55.5	29.5	2.2	3.3	6.6	2.9
1978–79	131	77.4	11.3	0.0	5.2	5.3	0.8
July	8	62.5	0.0	0.0	0.0	25.0	12.5
Aug.	80	73.8	2.5	3.7	7.5	7.5	5.0
Sept.	59	81.4	0.0	0.0	5.1	11.8	1.7
Oct.	91	62.6	22.0	3.3	3.3	6.6	2.2
Nov.	105	56.2	38.1	0.0	1.9	2.9	0.9
Dec.	62	42.2	53.1	0.0	3.1	1.6	0.0
AGE OF BREEDING FEMALE							
1 year old	154	57.2	26.6	3.9	2.6	7.1	2.6
2 years old	68	77.9	8.8	0.0	5.9	5.9	1.5
3 years old[1]	62	40.3	43.6	0.0	4.8	6.5	4.8
4 years old	121	73.6	16.5	0.0	4.1	5.0	0.8

NESTLINGS		% Fledged	Predation	Fell from nest	Abandoned or died in nest		Not known
Total 255	42.0	46.3	3.5	3.9	4.3		
1977–78	152	42.1	48.0	2.0	3.3		4.6
1978–79	103	41.8	43.7	5.8	4.8		3.9
July	5	100.0	0.0	0.0	0.0		0.0
Aug.	59	64.4	11.9	3.4	16.9		3.4
Sept.	48	56.2	35.4	4.2	0.0		4.2
Oct.	57	31.6	54.4	7.0	0.0		7.0
Nov.	26	30.8	61.5	0.0	0.0		7.7
Dec.	27	18.5	77.8	3.7	0.0		0.0
FEMALE AGE							
1 year old	88	33.0	50.0	7.9	2.3		6.8
2 years old	53	43.3	48.1	3.8	1.9		3.8
3 years old[1]	25	60.0	32.0	0.0	8.0		0.0
4 years old	89	44.9	46.1	0.0	5.6		3.4

[1] Not present during 1978–79 season.

taken by predators (88.3% by Stoats and Weasels, and the rest by Black Rats and House Mice *Mus musculus*), 16 (3.9%) were abandoned, six (1.5%) fell from nest, nine (2.2%) failed for unknown reasons and 25 (6.2%) did not hatch; of the 255 nestlings, 107 (42.0%) fledged, 118 (46.3%) taken by predators (94% by mustelids, and rest by rodents), ten (3.9%) died in nest, nine (3.5%) fell from nest and died, and 11 (4.3%) failed for unknown reasons; success and causes of failure summarized in Table 5, showing results for each breeding season, for each month of season, and for different age-classes of female. One-year-old females fledged significantly fewer young than 2-year-olds and those 4 years or older; 3-year-old females fledged the greatest number of young, but not significantly greater than the other age-classes (Powlesland 1983b). At same site, in 1977–78 season (n=30 pairs), mean number of young fledged per pair was 2.1; in 1978–79 (n=15 pairs), mean was 2.9 fledgelings/pair (Powlesland 1983b). Also at KOWHAI BUSH, of 45 nests in 1975–77 for which outcome known, 18 (40%) hatched at least one egg and six (13.3%) fledged at least one young; six nests were abandoned (13.3%); 31 (68.9%) were depredated (19 nests at egg-stage and 12 with young); predation was by mustelids at 25 nests and by rodents at six (Moors 1983). On KAPITI I., in 1925–26 season, only three of ten nests produced any young, with heavy losses to rats and Long-tailed Cuckoos *Eudynamis taitensis* (Wilkinson 1927; Wilkinson & Wilkinson 1952). At St Arnaud, SI, after control of predators in 1998–99 breeding season, of 28 nesting attempts by nine breeding pairs, 25 (89.3%) were successful, raising mean of 5.9 fledgelings/pair/season (4–8; 9 pairs); and three failed (one lost to predators, two abandoned). Three pairs each reared two broods, five pairs each reared three broods, and one pair reared four broods; success rate much greater than that recorded for other mainland population (see above) where there was no control of predators (Etheridge & Powlesland 2001). CUCKOOS: Parasitized by Long-tailed Cuckoo (Beaven 1997; see above).

PLUMAGES Prepared by A.M. Dunn. Fledge in juvenile plumage. Partial post-juvenile (first pre-basic) moult probably begins shortly after fledging, and results in first immature (first basic) plumage, appearance of which varies between subspecies (see below). Probably attain adult plumage in complete first immature post-breeding (second pre-basic) moult at end of first year or early in second year, at least in nominate *australis* (possibly longer in subspecies *longipes*). After attaining adult plumage, a complete post-breeding (pre-basic) moult each cycle produces successive adult plumages without change in appearance. Sexes differ in adult and immature plumages. Three subspecies; nominate *australis* described below, based on examination of skins of 25 adult males, ten adult females, one juvenile, six first immature males and three first immature females (AIM, NMNZ).

Adult male (Definitive basic). HEAD AND NECK: Small patch of feathers in centre of lower forehead, white, forming small white frontal spot that is separated from top of bill by narrow line of grey-black (82) feathers. Size and shape of frontal spot can be changed by raising or drawing back surrounding feathers (Flack 1976a). Rest of forehead, crown, nape, hindneck and sides of neck, grey-black (c82) with slightly darker (ne) fringes to tips of feathers, giving faintly scalloped appearance when plumage fresh; concealed bases to feathers, grey (87) with white shafts. Narrow eye-ring, off-white (ne). Lores, ear-coverts, chin and throat, dark grey (c83) with off-white (ne) shafts to feathers, giving faintly

streaked appearance. UPPERPARTS: All feathers grey-black (c82) with concealed grey (87) bases and concealed white shafts to bases. UNDERPARTS: Most of breast and belly, yellow-white (ne) to cream (c54), separated from dark throat in straight but slightly ragged line. Sides of breast, flanks and, in some, sides of belly, dark grey (c83); extent of dark grey on underparts varies individually. Vent and undertail-coverts, yellow-white (ne) to cream (c54). Thighs, brownish grey (c79). Concealed bases to all feathers of underparts, grey-black (82). TAIL: Black-brown (c119). UPPERWING: All secondary coverts and alula, black-brown (c119). Marginal and median primary coverts, black-brown (c119) with grey (84) fringes at tips. Greater primary coverts mostly black-brown (c119), but inner 3–4 sometimes have narrow white fringes at tips. Tertials, black-brown (c119). Secondaries and inner five primaries, black-brown (c119) with concealed white bar near bases of inner webs, diffuse grey (84) smudge near bases of outer webs, and diffuse grey (84) smudge along outer edges about one-third length from tip; faint grey smudges to outer webs align to form faint ill-defined central wing-bar and trailing wing-bar (see Fig. 1 in Petroicidae account, p. 576). Outer five primaries wholly black-brown (c119). UNDERWING: Secondary coverts, grey (c84) with white suffusion to tips. Marginal and median primary coverts, dark grey (83). Greater primary coverts, white with grey (84) suffusion to tips. Tertials and outer five primaries, black-brown (c119). Secondaries and inner five primaries, black-brown (c119) with white bar near base of inner webs.

Adult female (Definitive basic). Similar to adult male, but slightly paler overall, with smaller pale area on underparts. HEAD AND NECK: White frontal spot similar to that of adult male, but usually slightly smaller. Rest of forehead, crown, nape, hindneck and sides of neck, very similar to adult male, but usually slightly paler, grey-black (c82) to dark grey (c83) with slight brownish (ne) tinge, and white shafts to bases of feathers that are often partly exposed on crown. Narrow eye-ring as adult male. Lores, ear-coverts, chin and throat, paler than adult male, brownish grey (c79) with diffuse off-white (ne) shaft-streaks to feathers giving slightly mottled or streaked appearance. UPPERPARTS: As adult male or slightly paler, grey-black (c82) to dark grey (c83). UNDERPARTS: Centre of breast and belly, off-white (ne) to cream (c54), and pale area usually smaller than in adult male. Sides of breast, flanks and, in some, sides of belly, brownish grey (c79); dark area usually larger than in adult male, but much individual variation. Vent and undertail-coverts, off-white (ne) to cream (c54). Thighs, brownish grey (c80). WING AND TAIL: As adult male or slightly paler and browner; ground-colour, black-brown (119) to dark brown (c121).

Nestling Down, dark grey (83) (photos: Moon 1992; Edwards 1997).

Juvenile Sexes probably similar. Like adult female but usually browner with more fine streaking to top of head and upperparts, and softer, fluffier appearance overall. HEAD AND NECK: White frontal spot very small or obsolete. Rest of, or whole, forehead, crown, nape, hindneck and sides of neck, dark brown (221) with white shaft-streaks to feathers. Lores, ear-coverts and eye-ring, as adult female. Chin and throat, brownish grey (c79) with diffuse, off-white (ne) suffusion to centres of feathers, resulting in rather mottled appearance. All feathers have soft and loose texture, giving slightly fluffy appearance. UPPERPARTS: Mantle, back and scapulars, dark brown (221) with fine white shaft-streaks to feathers. Rump and uppertail-coverts, dark brown (221). UNDERPARTS:

Mostly as adult female, but with less off-white in centre of breast and belly, and with buff (c124) wash to vent and undertail-coverts; sides of belly, flanks and sides of breast, brownish grey (c79). TAIL: As adult female. UPPERWING: Similar to adult female but slightly browner. Ground-colour of coverts, dark brown (c119A). Secondaries and inner primaries have light grey-brown (c45) smudges to outer webs (cf. grey in adult), and off-white (ne) bar to inner webs (cf. clean white in adult). UNDERWING: Mostly as adult female, but with off-white (ne) bar to inner webs of secondaries and inner primaries (cf. clean white in adult).

First immature male (First basic). Like adult male but retain juvenile feathers of wing, and white shafts to feathers of crown to mantle often slightly more exposed, giving more streaked appearance. Retained juvenile remiges, greater coverts and alula appear slightly browner and slightly more worn than new first immature plumage. Usually appear slightly darker than first immature female.

First immature female (First basic). Like adult female, and very difficult to separate. Those examined appear very similar to adult female, but retain juvenile wing, and white shafts to feathers of crown to mantle usually slightly more exposed, giving more streaked appearance. Retained juvenile remiges, greater coverts and alula appeared slightly browner and slightly more worn than new immature plumage.

Aberrant plumage A partly leucistic bird described: back and underparts, white, with patches of white in rest of plumage; remiges and rectrices normal (Oliver).

BARE PARTS Based on photos (Moon 1992; Anon. 1995; Edwards 1997; NZRD; unpubl.: M.J. Carter; B. Chudleigh), museum labels, and published descriptions. Subspecies combined. **Adult male** Bill, black (89); also described as brownish black or blackish brown (Oliver). Gape usually black (89) but buff in some (c124) but black (Oliver). Iris, dark brown (121) or black-brown (119); or black (Oliver). Orbital ring, grey (84). Legs, grey-black (82) or dark brown (c121); described as olive-brown or fuscous (NMNZ). Feet, grey-black (82); or brownish black or pale yellowish-brown (Oliver). Soles, yellow (Oliver); or orange-yellow or straw-yellow with orange tint (NMNZ). **Adult female** Probably much overlap with adult male, but photos showed following differences from adult male: Bill mostly black (89) with light grey-brown (119D) or buff-yellow (c53) base to lower mandible. Gape, light grey-brown (119D) or buff-yellow (c53). Legs, dark brown (21). Feet, dark brown (21). **Nestling** Bill, grey (84) with yellow-white (ne) cutting edges. Gape, puffy and yellow-white (ne). Skin, pink (c3); or flesh-coloured (NZRD). **Juvenile, First immature** No information.

MOULTS Based on examination of 56 adult and 14 juvenile and immature skins (all subspecies) (AIM, NMNZ); unpublished banding study at Dunedin, SI (P. Schweigman); and published information. Subspecies combined. **Adult post-breeding** (Third and subsequent pre-basic). Complete; primaries outward. From skins, moult of primaries probably started in Dec. or Jan. and finished in Mar.; moult recorded: Dec. (0 of 1); Feb. (2 of 2; PMS 31, 36); and Mar. (2 of 8; PMS 44, 46) (with no skins for Jan.); all of 17 in Apr. had finished moult; and none of 28 moulting primaries May–Nov. Timing of moult of tail appeared to be similar to that of moult of primaries; recorded Feb. (n=2) and Mar. (n=1), having replaced just over half of tail. Moult of body appeared to be most active in Feb. (2 of 2) and Mar. (4 of 8) when adults had

heavy moult of feathers in both upperparts and underparts. Three were finishing moult of body in Apr. with slight moult of body in either upperparts or underparts, but not both. From banding study at Dunedin, two males recorded with active moult of tail in Feb. On Little Barrier I., one finishing moult of wing in early Mar. (Gill & Veitch 1990). At Kowhai R., SI, moult began in Dec. and, for most pairs, finished before their last offspring independent (Flack 1973). **Post-juvenile** (First pre-basic). Appears to be partial; those identified as first immature (first basic) had retained juvenile remiges and appeared to have retained greater primary coverts and alula. Timing uncertain. None of the skins examined was in moult. Probably occurs soon after becoming independent from parents (Armstrong et al. 2000). **First immature post-breeding** (Second pre-basic). Few data. Probably occurs in Feb. after first breeding season (Armstrong et al. 2000). From skins, four appeared to be undergoing this moult in Feb.–Apr.

MEASUREMENTS NOMINATE AUSTRALIS, SI: (1–2) Skins (AIM, NMNZ): (1) Adults; (2) Juveniles and first immatures. (3) Adults, skins (Fleming 1950). (4) Dunedin, adults, live (P. Schweigman).

		MALES	FEMALES	
WING	(1)	100.0 (3.69; 92–105; 22)	97.0 (2.78; 94–102; 9)	*
	(2)	98.4 (4.35; 93–104; 7)	95, 96, 102	
	(3)	98.3 (3.16; 93–103; 35)	96 (2.7; 91–100; 19)	**
	(4)	100.6 (2.52; 96–105; 20)	96.0 (2.10; 93–98; 6)	**
TAIL	(1)	72.0 (3.86; 63–80; 22)	69.1 (4.01; 61–75; 9)	ns
	(2)	72.0 (6.32; 65–82; 7)	65, 68, 74	
	(3)	73.1 (3.8; 65–79; 35)	71 (2.5; 67–77; 19)	*
	(4)	76.2 (5.61; 65–86; 17)	75.8 (5.19; 70–85; 6)	ns
BILL S	(1)	21.1 (0.70; 19.8–22.5; 21)	20.3 (0.83; 19.1–21.7; 8)	*
	(2)	20.6 (0.71; 19.6–21.7; 7)	20.8, 21.1, 21.3	
BILL F	(4)	15.5 (1.00; 13.8–17.0; 19)	14.4 (1.08l; 12.8–15.6; 6)	*
THL	(4)	45.3 (0.93; 43.5–47.1; 20)	44.2 (0.55; 43.6–45.0; 6)	*
TARSUS	(1)	37.4 (1.67; 34.9–40.7; 21)	36.2 (1.10; 35.1–38.4; 7)	ns
	(2)	37.2 (2.04; 34.3–39.9; 7)	35.5, 36.3, 38.1	
	(3)	38.6 (1.5; 35–42; 35)	37.4 (1.35; 36–40; 19)	**
	(4)	38.1 (1.01; 36.0–40.1; 20)	36.6 (1.25; 35.3–38.9; 6)	**

(5) Dundedin, SI, adults, unsexed, live (P. Schweigman).

		UNSEXED
WING	(5)	96.5 (2.43; 93–102; 18)
TAIL	(5)	71.3 (6.44; 50–78; 17)
BILL F	(5)	13.8 (1.48; 11.5–16.7; 18)
THL	(5)	43.4 (0.98; 42.3–46.2; 18)
TARSUS	(5)	37.4 (0.74; 36.2–38.5; 17)

SUBSPECIES *LONGIPES*, NI and adjacent islands: (6–7) Skins (AIM, NMNZ): (6) Adults; (7) Juveniles and first immatures. (8) Adults, skins (Fleming 1950). (9) Mamaku Plateau, all ages, live (Armstrong 2001). (10–11) Tiritiri Matangi I., live (Armstrong 2001): (10) Adults; (11) Juveniles.

		MALES	FEMALES	
WING	(6)	93.3 (1.89; 89–95; 10)	91.6 (3.78; 86–96; 5)	ns
	(7)	90	86	
	(8)	90.7 (2.9; 85–95; 15)	89.5 (3.78; 87–95; 4)	ns
TAIL	(6)	66.2 (3.71; 58–69; 10)	63.6 (3.29; 60–69; 5)	ns
	(7)	61	62	
	(8)	64 (2.4; 59–67; 15)	62.2 (3.86; 60–68; 4)	ns
BILL S	(6)	19.8 (0.87; 18.6–20.8; 10)	19.1 (0.33; 18.7–19.5; 4)	ns

		MALES	FEMALES	
	(7)	–	18.5	
THL	(9)	41.9 (0.8; 23)	41.7 (0.5; 7)	ns
	(10)	42.0 (0.8; 11)	41.6 (0.3; 4)	ns
	(11)	41.4 (0.6; 11)	40.5 (0.5; 6)	**
TARSUS	(6)	35.4 (1.73; 31.7–37.7; 9)	34.8 (1.25; 33.7–36.6; 4)	ns
	(7)	–	33.7	
	(8)	36.2 (1.36; 34–38; 15)	36.5 (1.29; 35–38; 4)	ns
	(9)	36.6 (1.0; 23)	35.1 (1.0; 7)	**
	(10)	36.2 (0.9; 17)	35.0 (0.8; 8)	**
	(11)	36.3 (1.1; 16)	34.5 (1.0; 11)	**

(9) NI and adjacent islands, adults, unsexed, skins (AIM).

		UNSEXED
WING	(9)	90.8 (2.72; 87–95; 12)
TAIL	(9)	62.3 (2.74; 59–67; 12)
BILL S	(9)	19.6 (1.07; 18.3–22.0; 9)
TARSUS	(9)	34.3 (2.00; 31.4–38.0; 11)

SUBSPECIES RAKIURA, Stewart I. and outlying islands: (10) Adults, skins (NMNZ). (11) Adults, skins (Fleming 1950).

		MALES	FEMALES	
WING	(10)	95.7 (5.12; 89–101; 4)	88, 95, 98	
	(11)	94.9 (2.98; 90–98; 6)	89.7 (2.5; 87–93; 4)	*
TAIL	(10)	70.0 (4.32; 64–74; 4)	65, 71, 76	
	(11)	71.8 (3.82; 65–75.5; 6)	67.4 (2.69; 64–70; 4)	*
BILL S	(10)	19.2, 20.4, 20.9	19.2, 20.2, 20.6	
TARSUS	(10)	36.2 (1.89; 33.8–38.3; 4)	30.0, 34.7, 38.2	
	(11)	37.1 (1.43; 35–39; 6)	36.2 (1.55; 34–37.5; 4)	ns

WEIGHTS NOMINATE AUSTRALIS, SI: (1–2) From museum labels (NMNZ): (1) Adults; (2) Juveniles and first immatures. (3) Dunedin, adults, live (P. Schweigman). SUBSPECIES LONGIPES, NI and adjacent islands: (4–5) From museum labels (AIM, NMNZ): (4) Adults; (5) Juveniles and first immatures. (6) Mamaku Plateau, all ages, live (Armstrong 2001). (7–8) Tiritiri Matangi I., live (Armstrong 2001): (7) Adults; (8) Juveniles. (9) Pureora Forest Park, adults and immatures, live (R.G. Powlesland).

	MALES	FEMALES	
(1)	37.7 (9.49; 22.3–47.0; 5)	33.0	
(2)	32.8, 35.0	34.0, 40.0	
(3)	37.5 (2.91; 33.4–43.8; 20)	34.4 (2.04; 30.8–36.0; 5)	*
(4)	24.1 (2.42; 21.2–27.7; 6)	20.5, 35.0	
(5)	28.0	28.4	
(6)	28.1 (1.7; 23)	26.6 (1.4; 7)	*
(7)	28.2 (2.4; 10)	31.5 (0.7; 2)	
(8)	29.2 (1.8; 12)	27.1 (1.6; 8)	**
(9)	30.2 (2.14; 26.7–35.0; 29)	28.3 (1.78; 25.9–31.5; 17)	**

Unsexed adult *longipes*: from NI and adjacent islands, 23.7 (5.35; 15.0–30.0; 6) (AIM); and two from Little Barrier I., 29 and 30 g (Gill & Veitch 1990). No data for *rakiura*.

STRUCTURE Wing moderately long and broad with rounded tip. Ten primaries: p6 longest; p5 and p7 sometimes equal; p10 42–49 mm shorter, p9 15–20, p8 4–6, p7 0–2, p5 0–2, p4 3–7, p3 10–14, p2 15–17, p1 17–20. P5–p8 emarginated on outer webs; no emarginations on inner webs. Nine secondaries, including three tertials; tips of longest tertials do not reach tips of secondaries on folded wing. Tail moderately long, with square or slightly rounded tip; 12 rectrices. Bill straight and rather robust; about half length of head. Tarsus long and slender; scaling, holothecal. Tibia fully feathered. Middle toe with claw 25.1 (0.50; 24.7–26.0; 6). Outer toe 71–82% of middle, inner toe 67–76%, hindtoe 82–90%.

SEXING Armstrong (2001) used length of tarsus as an indicator of sex (for all ages combined) with a cut-off of 35.6 mm giving best separation of sexes: 80% of those with Tarsus >35.6 mm male, and 77% of those with Tarsus <35.6 mm female (n=56 males; n=26 females).

GEOGRAPHICAL VARIATION Three subspecies currently recognized (NZCL): *australis*, *longipes* and *rakiura*. Little or no evidence of geographical variation in plumage within each subspecies (Fleming 1950; this study). Recently suggested that *australis* and *longipes* be treated as full species (Holdaway et al. 2001).

NOMINATE AUSTRALIS occurs SI and adjacent islands (excluding Stewart I. and its outliers). Largest subspecies, and significantly larger than *longipes* and *rakiura* (see Measurements and below). Some evidence of clinal variation in size within nominate *australis*, with n. populations having slightly longer wings than s. populations (Fleming 1950). Plumage described fully above.

SUBSPECIES LONGIPES occurs NI and adjacent islands. Smallest subspecies. Significantly smaller than *australis* in Wing (P<0.01), Tail (P<0.01 male, P<0.05 female), Bill S (P<0.01 male, P<0.05 female), Tarsus (P<0.01 male, female ns) and weight (P<0.01 male); possibly slightly smaller than *rakiura*, but sample sizes too small for statistical comparison (see Measurements, Weights). Though samples small, possible clinal variation in size, with n. populations appearing to have slightly shorter wings than s. populations (Fleming 1950). The following plumage descriptions based on examination of skins of 11 adult males, five adult females, three juveniles and one first immature. **Adult male** Much more streaked and mottled than adult male nominate. HEAD AND NECK: White frontal spot similar to that of adult male nominate. Forehead, crown, nape, hindneck and sides of neck, grey-black (82) with off-white shafts and narrow black (89) fringes to feathers, giving streaked and scalloped appearance. Eye-ring, off-white (ne). Lores and ear-coverts, grey-black (82) with white shaft-streaks, giving boldly streaked appearance. Feathers of chin and throat, grey (84) with diffuse grey-black (82) fringes and diffuse white shaft-streaks, resulting in rather mottled appearance. UPPERPARTS: Grey-black (82) with off-white (ne) shafts to feathers, giving finely streaked appearance; pale shafts less noticeable on rump and uppertail-coverts. UNDERPARTS: Feathers of most of breast, grey-black (82), grading to grey (84) in centre of feather and with white shafts, giving rather mottled appearance. Lower breast and belly, white, often with faint yellowish (ne) wash, and mottled with grey (c84) at sides; extent of white varies greatly between individuals. Flanks, dark grey (83). Thighs mostly dark grey (83), but inner thighs, white. Vent and undertail-coverts, off-white (ne) with pale-buff (ne) wash in some. All feathers have concealed grey-black (82) bases. WING AND TAIL: As adult male nominate. **Adult female** Very similar to adult male *longipes*, but usually slightly paler overall and with less white on belly. Ground-colour of feathers of forehead, crown, nape, hindneck, sides of neck, mantle, back and scapulars slightly paler than adult male, dark grey (c83). Eye-ring, off-white (ne). Feathers of chin and throat paler than adult male, light

grey (c85) grading to off-white (ne) in centre of feathers. Feathers of most of breast, dark grey (83), grading to pale grey (c86) in centre of feathers. Centre of lower breast and centre of belly, white. Sides of belly and flanks, grey (84). Rest as adult male or slightly browner. **Juvenile** Browner and more streaked than adult male or female. Similar to juvenile nominate, but pale area of lower breast and belly whiter with dark-brown (c121) mottling to tips of most feathers giving more spotted or mottled appearance, and vent and undertail-coverts washed light grey-brown (c45). **First immature** Sexes similar (Armstrong *et al.* 2000; this study) (cf. in nominate, in which sexes differ). Appearance similar to that of adult female; differences from adult female same as those between adult female and first immature female nominate. Recent evidence (soon to be published) suggests that males of this subspecies probably take longer to attain adult male plumage than those of *australis*. Plumage probably darkens with each successive moult, and some possibly do not attain full adult male plumage till their fourth or fifth year (R.G. Powlesland).

SUBSPECIES *RAKIURA* occurs Stewart I. and adjacent islands. A rather large subspecies, but appearing to be slightly smaller than nominate: significantly smaller than nominate in Bill S (P<0.05 male) but no significant differences in other measurements (but sample sizes of *rakiura* small; see Measurements); possibly slightly larger than *longipes*, but sample sizes too small for statistical comparison. The following plumage descriptions based on examination of skins of four adult males and three adult females (no juveniles or first immatures examined). **Adult male** Very similar to adult male nominate but usually have whiter underparts: centre of breast and belly, usually white but occasionally tinged yellowish (ne). There did not appear to be any significant difference in coloration of upperparts (this study; *contra* Fleming 1950). As in nominate, feathers of upperparts have concealed pale shafts to bases, but these often partly visible in some feathers (this study), resulting in immature-like appearance of many adults, as noted by Fleming (1950). **Adult female** Very similar to adult female nominate but usually have whiter underparts: centre of breast and belly usually white, but occasionally tinged yellowish (ne). As in adult male, pale shafts to base of upperpart feathers often partly exposed on some feathers, resulting in immature-like appearance. **Juveniles, First immatures** No information.

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Scarlet Robin *Petroica multicolor* (page 604)
NOMINATE *MULTICOLOR:* **1** Adult male; **2** Adult female

New Zealand Tomtit *Petroica macrocephala* (page 629)
NOMINATE *MACROCEPHALA:* **3** Adult male; **4** Adult female; **5** Juvenile male; **6** Juvenile female; **7** Adult male
SUBSPECIES *TOITOI:* **8** Adult male
SUBSPECIES *MARRINERI:* **9** Adult female
SUBSPECIES *DANNEFAERDI:* **10** Adult; **11** Juvenile

New Zealand Robin *Petroica australis* (page 706)
NOMINATE *AUSTRALIS:* **12** Adult male; **13** Adult female; **14** Juvenile; **15** Adult male
SUBSPECIES *LONGIPES:* **16** Adult male; **17** Adult female

Black Robin *Petroica traversi* (page 725)
18 Adult