

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

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

The Passeriformes divide into two main groups:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Family 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 Scrub-robin *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), *Plesiodyras* (1, 0), *Gennaeodryas* (1, 0), *Peneothello* (4, 0), *Tregellasia* (2, 2), *Eopsaltria* (5, 4) and *Melanodryas* (2, 2). DAB places *Heteromyias*, *Plesiodyras* 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 (Muscicapidae), whistlers (Pachycephalidae) or monarch flycatchers (Dicuridae) (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

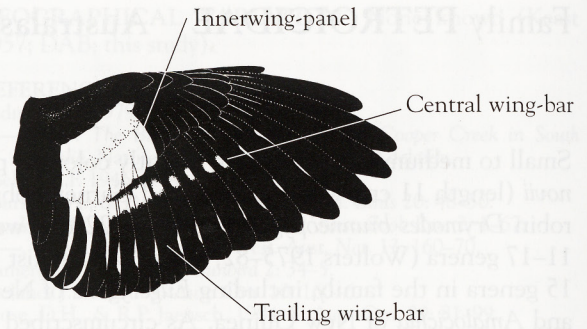
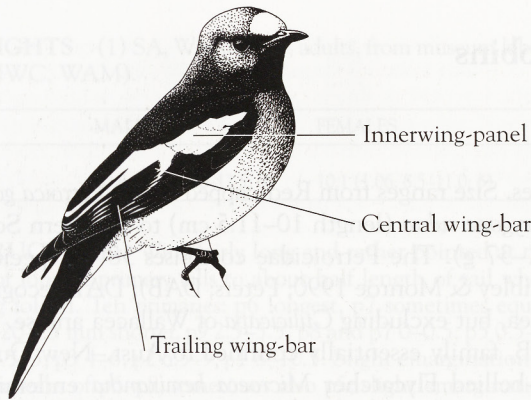


Figure 1(a). Pattern of folded wing of adult male Scarlet Robin (Source: Fig. 1, Rogers 1993)

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 macrocephala **New Zealand Tomtit**

COLOUR PLATE FACING PAGE 609

Parus macrocephalus Gmelin, 1789, *Syst. Nat.* 1(2): 1013 — Queen Charlotte Sound, New Zealand.

The specific name is based on the 'Great-headed Titmouse' of Latham (1783; *Gen. Synop. Birds*, II: 557, pl. lv) (Greek *μακροκέφαλος*, great-headed).

OTHER ENGLISH NAMES Black, North Island, Pied, Southern, White-breasted or Yellow-breasted Tit or Tomtit; Auckland Island, Chatham Island, Snares or South Island Tit; Snares Island Robin; Wheedler; Butcherbird.

POLYTYPIC Nominate *macrocephala*, SI and Stewart I. and its offshore islands, NZ; *toitoti* (Lesson, 1828), NI and larger offshore islands, NZ; *chathamensis* Fleming, 1950, Chatham Is; *dannefaerdi* (Rothschild, 1894), Snares Is; *marrineri* (Mathews and Iredale, 1913), Auckland Is.

FIELD IDENTIFICATION Length c. 13 cm; wingspan not known; weight 11 g. Medium-small Asian robin. Noticeably smaller than New Zealand Robin *Petroica australis*, with larger head, finer bill, more rotund body, proportionally slightly longer tail and shorter and finer legs, giving altogether daintier jizz. Two plumage morphs, with light morph throughout most of range and dark morph restricted to Snares Is. Sexes differ in all plumages of light morph, but alike in dark morph. Light-morph adult males largely black, with pale-yellow to white lower underbody, small white patch on forehead, prominent white wing-bar, and white sides to tail; light-morph adult females largely dark brown, with pale-yellow to white lower underbody, and buff-white wing-bar and sides to

tail. Dark-morph adult male and female entirely black. No seasonal variation. Juveniles closely resemble adults of same sex, but with pale streaking above and on chin and throat, varying dusky mottling on underbody in light morph and paler brownish lower underbody in some dark morphs, and, in all, paler base to bill. Immatures doubtfully separable from adults (see Plumages). Marked geographical variation, most obvious in adult males, which differ mainly in colour of underbody below dark breast; adult females differ mainly in colour of upperparts and colour and pattern of underbody.

LIGHT MORPH: Adult male Head and neck, black, with small but obvious white patch on lower forehead. Rest of upperparts, including wing and tail, black with: short broad

white wing-bar across bases of remiges (petering out on outer primaries), prominent when perched and in flight; and broad white diagonal band across outer rectrices, prominent when tail spread in flight and showing as obvious white edges to base of folded tail when perched. Black chin, throat and upper breast sharply demarcated from pale rest of underbody, colour of which varies geographically: pale yellow, usually with diffuse narrow line of bright yellow or orange bordering black of upper breast, in SI, Stewart I. and Chatham Is (nominate and *chathamensis*); white in NI (*toittoi*) with undertail-coverts, black with white tips; and somewhat intermediate between these on Auckland Is (*marrineri*) with lower breast and belly, yellow-white, grading to white on vent and flanks, with blackish mottling to rear-flanks and black undertail-coverts finely mottled white, and normally lacking brighter orange or reddish band bordering black upper breast. Undertail, when closed, appears mostly white with darker tip. Underwing, dark brown, with white secondary coverts and prominent white wing-bar across bases of remiges, as on upperwing. Bill, black, though some have paler base to lower mandible. Iris, black-brown. Legs, black to grey-black or dark purplish-brown, with contrasting yellow or orange feet. **Adult female** Similar to adult male but browner above and paler on chin and throat. Differences from male: NI, SI, STEWART I. AND CHATHAM IS (nominate, and subspecies *toittoi* and *chathamensis*): Top and sides of head and neck, dark olive-brown, and white patch on lower forehead slightly smaller; also has narrow off-white eye-ring, and fine off-white streaking or mottling on ear-coverts. Upperbody, dark olive-brown, with paler yellow-brown tips to feathers of rump in some birds. Tail and upperwing patterned as male, but ground-colour browner, black-brown; wing-bar duller and narrower buff-white; and sides of tail buff-white. Ground-colour of underparts varies geographically: yellowish white, often with buff wash to breast, in SI, Stewart I. and Chatham Is (*macrocephala* and *chathamensis*), and white in NI (*toittoi*), and otherwise marked with: chin and throat often mottled or variously washed dark grey; sides of breast washed olive-brown; and belly, vent and flanks often have scattered buff or light-brown smudging. Bare parts as male except gape is buff in some. AUCKLAND IS (subspecies *marrineri*): Unlike other light-morph females, very similar to adult male, from which differs by: Upperparts only slightly duller black or black-brown, and uppertail-coverts tipped buff. White wing-bar duller, buff-white. Chin, throat and upper breast, black, slightly darker than upperparts and rest of head, and less sharply demarcated from pale underbody than in male; lower breast, belly, vent and flanks, yellow-white to white, usually lacking dark mottling on rear-flanks. **Juvenile male** Broadly similar to adult male of each subspecies, from which differs by: Upperbody, including top and sides of head and neck, slightly duller and browner, black-brown, finely and faintly streaked off-white, and with slightly smaller white patch on forehead (similar to that of adult female); feathers of rump and uppertail-coverts tipped yellow-brown in some (especially *chathamensis*). Dark chin and throat finely streaked (nominate and *marrineri*) or mottled (in *toittoi* and *chathamensis*) pale; underbody usually paler and whiter; lower breast less sharply demarcated from dark throat and upper breast, and finely peppered or scalloped dusky (most heavily in *macrocephala*; lacking in *chathamensis*); in *chathamensis*, juveniles also lack dusky mottling on flanks of adult. Bill mostly blackish, merging to paler brownish-orange base and tomia; and tops of feet mostly blackish, as tarsi. Recently fledged birds

also have prominent swollen fleshy gape. **Juvenile female** Apparently broadly similar to adult female of respective subspecies (but no information on *marrineri*), from which differs by: Upperbody and top and sides of head and neck clearly streaked off-white, most strongly over top of head and neck (and more strongly than in juvenile male); pale patch on forehead tiny and virtually absent; and with diffuse dusky mottling on chin, throat and breast. Bare parts as juvenile male. **DARK MORPH: Adult** Entirely black, with female slightly less glossy, especially below. **Juvenile** Slightly duller and browner than adult, black-brown, with fine pale streaking on head, neck, upperbody and breast. In some birds, possibly females, lower belly, vent and thighs slightly paler than rest of plumage, light brown.

Similar species Unlikely to be mistaken, but see comments under New Zealand Robin.

Seen singly, in pairs or family groups; sometimes join mixed-species feeding-flocks of other small passerines. Usually tame and confiding, often flying in close to inspect intruder, then flying off; often perch sideways on tree-trunks, usually with head pointing downward; on perch, often cock tail and droop wings. Forage mainly by scanning for insect prey from perch, flying out to catch prey from nearby foliage, tree-trunk, branch or from ground, before returning to nearby or, less often, same perch; also glean insects from foliage, occasionally by hover-gleaning, but only rarely catch them on wing. On some offshore islands, often also forage among leaf-litter on forest floor and occasionally on shoreline and among colonies of penguins and seals. Calls distinctive, including simple musical warbling Song uttered by male from high perch, and simple short, high-pitched single notes in contact (see Voice).

HABITAT Native forests at all altitudes, from lowland podocarp–broadleaf forest to high-altitude beech *Nothofagus* forest, including both mature and regrowth forests. Also in Manuka *Leptospermum scoparium* or Kanuka *Kunzea ericoides* scrub (including regrowth), subalpine scrub, and, on Snares and Auckland Is, in tussock grassland with scattered shrubs; sometimes in plantations of exotic conifers (Riney *et al.* 1959; Challies 1966; St Paul 1976; Dawson *et al.* 1978; Kearton 1979; Elliott & Ogle 1985; Brown 1997; Heather & Robertson 1997; Oliver; see below). Sometimes occur in settled districts (Oliver), but only rarely in suburbia and towns proper (D.J. Onley).

Throughout much of range, commonly in native podocarp–broadleaf forests, mixed beech and podocarp–broadleaf forests, and beech *Nothofagus* forest; examples of these associations given below. (1) **PODOCARP–BROADLEAF FORESTS:** Low closed coastal forest dominated by Kamahi *Weinmannia racemosa*, with emergent Rimu *Dacrydium cupressinum* and Northern Rata *Metrosideros robusta*, abundant epiphytes, a dense subcanopy and shrub layer of Rimu and rata saplings and shrubs (including *Coprosma*, *Carpodetus*, *Geniostoma*, *Macropiper*, *Myrsine* and *Olearia*), and an open or sparse ground-cover (Onley 1980; Moeed & Fitzgerald 1982; Fitzgerald *et al.* 1989; Knegtman & Powlesland 1999); on Little Barrier I., broadleaf forest dominated by Puriri *Vitex lucens* and Pohutukawa *Metrosideros excelsa*, with a dense understorey (Kikkawa 1964a; Gravatt 1971); and on South East I., broadleaf forest dominated by Chatham Island Mahoe *Meliccytus chathamicus* and Chatham Island Matipo *Myrsine chathamica*, with some Chatham Island Ribbonwood *Plagianthus chathamicus* and Ngaio *Myoporum laetum*

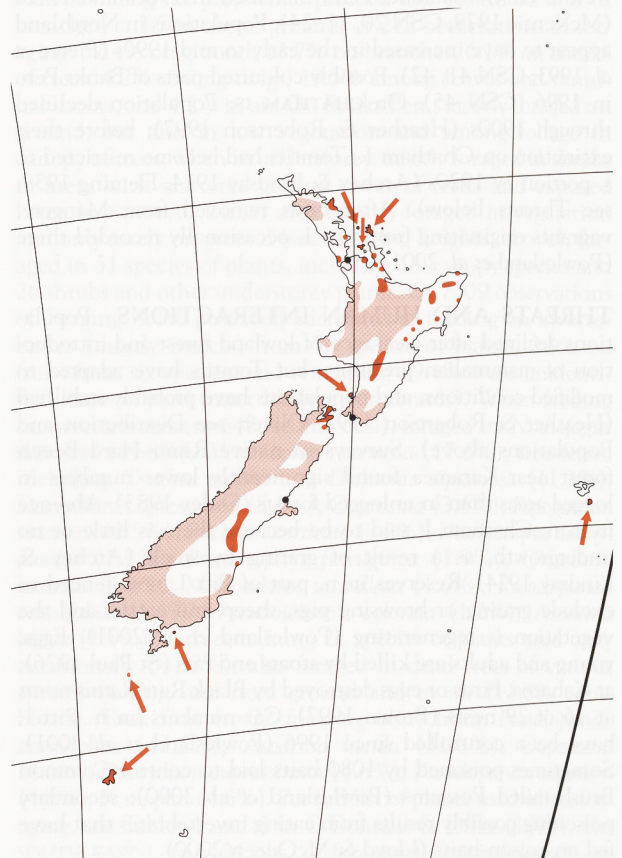
(O'Donnell & Dilks 1993; R.G. Powlesland). (2) **MIXED BEECH AND PODOCARP–BROADLEAF FORESTS:** Forest dominated by Rimu, Kahikatea *Dacrycarpus dacrydioides*, Mountain Totara *Podocarpus cunninghamii*, Miro *Prumnopitys ferruginea*, Kamahi, Southern Rata *Metrosideros umbellata* and Silver Beech *Nothofagus menziesii*, with a dense shrub layer including *Pseudopanax crassifolius*, *P. edgerleyi*, *P. simplex*, *Ascarina lucida* and *Coprosma pseudocuneata* (Guest 1975; Onley 1980; O'Donnell & Dilks 1989, 1994); or tall closed Hard Beech *Nothofagus truncata* forest, sometimes mixed with Rimu, *Podocarpus ferrugineus*, Mountain Beech *Nothofagus solandri*, Rewarewa *Knightia excelsa* and *Elaeocarpus dentatus*, with subcanopy trees, such as Kamahi, often present, and open shrub layer of *Cyathodes fasciculata*, *Cyathea dealbata*, *Hedycarya arborea*, *Brachyglottis repanda*, *Coprosma robusta*, *C. rhamnoides*, *Pseudopanax crassifolium* and *Olearia rani* (Moeed & Fitzgerald 1982). (3) **BEECH FOREST** (Sibson 1958; Wilson *et al.* 1988): e.g. forests dominated by Red Beech *Nothofagus fusca*, Silver Beech and Mountain Beech, and often with diverse and complex understorey (Guest 1975; Onley 1980). Also occur in **REGROWTH FORESTS**, e.g. regrowth podocarp–broadleaf forests, such as broadleaf forest dominated by Kotukutuka *Fuchsia excorticata* and Pepper Tree *Pseudowintera colorata*, with scattered podocarps, such as Hall's Totara *Podocarpus hallii*, and a mid-storey of *Coprosma rotundifolia*, Pate *Schefflera digitata* and regenerating canopy species, with open leaf-litter or ground cover of low ferns (Kearton 1979). In Waitakere Ra., mainly in largely undisturbed habitats but occupy regrowth in unburnt areas, with large Rimu trees (Skinner 1978). However, numbers lower in logged forest compared with unlogged forest (see Threats). **OTHER ASSOCIATIONS:** Occur in **MANUKA AND KANUKA REGROWTH** (Challies 1962; Kikkawa 1964a; CSN 7, 31, 38, 39, 43). Sometimes occur in **SUBALPINE SCRUB** of Leatherwood *Olearia colensoi* or *Senecio claeagnifolius* (Turbott *et al.* 1959; Challies 1966; CSN 21, 22). On Snares Is, mostly inhabit **SHRUB FOREST** of *Olearia lyallii* and *Brachyglottis stewartiae*, though also occur in dense coastal **TUSsock GRASSLAND** surrounding *Olearia* shrub forest (Best 1975; McLean & Miskelly 1988; Oliver). Also forage in tussock grassland with scattered shrubs on Auckland Is, and on Auckland and Snares Is, occasionally recorded foraging on coastal rocks and even onto floating kelp (Heather & Robertson 1997). **MODIFIED HABITATS:** Sometimes recorded in exotic plantations of pines *Pinus* and fir *Pseudotsuga* (Fleming 1950; Gibb 1961; Clout & Gaze 1984; Owen & Sell 1985; CSN). In plantations of exotic conifers in Kaingaroa Forest, NI, recorded densities in: Monterey Pine, 1.16 birds/ha; fir *Pseudotsuga taxifolia*, 0.91 birds/ha; Austrian Pine *P. nigra*, 0.52 birds/ha; and Western Yellow Pine *Pinus ponderosa*, 0.50 birds/ha (Gibb 1961). Sometimes also recorded in open farmland (Penniket 1955; CSN 4) and said to occur in cultivated districts most often after breeding season (Oliver). Sometimes also occur in parks and gardens (McKenzie 1974; CSN; D.J. Onley).

DISTRIBUTION AND POPULATION

Endemic to NZ.
NI Recorded in Northland, from near Hihi S to Tuamoe Ra., and from near Whangaruru S to Bream Head and middle reaches of Wairoa R., round Tangowahine. Recorded on Hen & Chickens Is, and very occasionally S to Wellsford. Widespread on Little Barrier I., and occasionally recorded Great Barrier I. (record at Mt Hobson on Great Barrier I., 6 Jan. 1996, was first record for island since 1973; Bell 1976; CSN 44). Occasionally recorded in Waitakere and Hunua

Ras, and on Coromandel Pen., S to Whangamata. Scattered in Bay of Plenty, away from coast. Most widespread S of 38°S, S to line from near Tutira in n. Hawkes Bay, through Waiouru, to middle reaches of Whanganui R.; recorded E into East Coast, mainly to Urewera NP, though also recorded farther E in Raukumara Ra.; and in W, mainly recorded W to c. 174°30'E, or to line joining Uruti and Patea, though also occur farther W, in Mt Egmont NP and round New Plymouth. In s. Hawkes Bay, occur S along Ruahine Ra. Also recorded at Porangahau (just N of Taumatāwhakatāngihanga-koauauotamateapokaiwhenuakitanatahu) and in Puketoi Ra. Also occur in Wairarapa and Wellington in Tararua and Rimutaka Ras, as well as E of Wainuioru R. and in Aorangi Mts (NZ Atlas; CSN). **SI** In Marlborough, widespread in Marlborough Sounds and in Richmond, St Arnaud and Spenser Ras; also occur in Seaward Kaikoura Ras, S into n. Canterbury, round lower reaches of Hurunui R. and Motunau Beach. Also occur inland in Canterbury, from upper reaches of Okuku and Ashley Rs, along e. slopes of Southern Alps, S to Hunter Hills, W of Timarau. Isolated population on Banks Pen. Recorded at a few sparsely scattered sites from e. Kakanui Mts, S to Otago Pen., but more widespread farther S in s. Otago and throughout most of Southland. Widespread on Stewart I. and associated islets. Widespread from Toes Bay, NE on and W of Southern Alps, through Fiordland, West Coast, w. Otago and w. Canterbury, to Nelson (NZ Atlas; CSN).

Chatham Is Extinct on Chatham I. since c. 1975, but occur on Pitt, Mangere, Little Mangere and South East Is (Freeman 1994; Nilsson *et al.* 1994; Powlesland *et al.* 2001; NZCL).



Snares Is Mostly inhabit main island (Warham 1967; Best 1975; NZCL).

Auckland Is Occur on Auckland, Adams, Ocean, Rose, Ewing and Enderby Is (NZCL).

Breeding Assumed to breed throughout range.

Introductions Entire population (19 birds) removed from Mangere I. and Tapuaenuku (five birds) in 1976 as part of Black Robin *Petroica traversi* Recovery Program. However, eight birds transported back to Mangere I. from South East I. in Jan. 1987, nine in 1988 and 21 in 1989, and now re-established (Butler & Merton 1992; Powlesland *et al.* 2001). In Feb. 1998, 40 birds were transferred from South East I. to Tuku Valley on Chatham I. (Powlesland *et al.* 2001).

Populations In exotic conifer forests in Kaingaroa Forest, NI, recorded at densities of 0.50–1.16 birds/ha (Gibb 1961; see Habitat). On CHATHAM IS: Total population <1000 birds: c. 500 on Pitt I.; 200–300 on South East I.; 70–100 on Mangere; occasional vagrant to Little Mangere; extinct Chatham I. (Powlesland *et al.* 2001). After reintroduction to Mangere I., population in Oct. 1989 was three pairs, which increased to ≥ 13 birds by Dec. 1989 (Butler & Merton 1992).

Change in range, populations Formerly widespread throughout main islands at time of European settlement; populations declined after clearance of habitat and introduction of mammalian predators and birds (Heather & Robertson 1997; Oliver). Noted as 'very common' at Bay of Islands in c. 1840, but not recorded there since 1899 (Oliver). In early 1900s, population on NI considered liable to become extinct (Hutton & Drummond 1904), but has since stabilized (Heather & Robertson 1997). Populations in Hunua Ras, as well as on Coromandel Pen., increased in 1960s and 1970s (McKenzie 1979; CSN 20, 21, 24). Populations in Northland appear to have increased in the early to mid-1990s (Pierce *et al.* 1993; CSN 41, 42). Possibly colonized parts of Banks Pen. in 1996 (CSN 45). On CHATHAM IS: Population declined through 1900s (Heather & Robertson 1997); before their extinction on Chatham I., Tomtits had become restricted to s. portion by 1920s (Archey & Lindsay 1924; Fleming 1939; see Threats below). After birds removed from Mangere, vagrants originating from Pitt I. occasionally recorded there (Powlesland *et al.* 2001).

THREATS AND HUMAN INTERACTIONS Populations declined after clearance of lowland forest and introduction of mammalian predators, but Tomtits have adapted to modified conditions, and populations have probably stabilized (Heather & Robertson 1997; Oliver; see Distribution and Populations above). Surveys in native Rimu–Hard Beech forest near Karamea found significantly lower numbers in logged areas than in unlogged forests (Onley 1983). Absence from n. Chatham I. said to be because there is little or no undergrowth, as a result of grazing by stock (Archey & Lindsay 1924). Reserves in n. part of Pitt I. now fenced to exclude grazing or browsing pigs, sheep and cattle, and the vegetation is regenerating (Powlesland *et al.* 2001). Eggs, young and adults are killed by stoats and rats (St Paul 1976); at Kaharoa, birds or eggs destroyed by Black Rats *Rattus rattus* at 16 of 29 nests (Brown 1997). Cat numbers on n. Pitt I. have been controlled since 1996 (Powlesland *et al.* 2001). Sometimes poisoned by 1080 baits laid to control Common Brush-tailed Possums (Powlesland *et al.* 2000); secondary poisoning possibly results from eating invertebrates that have fed on poison baits (Lloyd & McQueen 2000).

MOVEMENTS Not well known. Described as resident (see below) and sedentary (Fleming 1950), though some seasonal movements described (see below). Said to undertake few small-scale and no large-scale seasonal movements (Fleming 1950). However, also said to be good dispersers (Flack 1976).

Considered sedentary, resident or present throughout year at many sites. On NI: at Hihi Bush, Mangonui (CSN 41); Waitakere Ra., Auckland (Skinner 1978); Matakana (one pair; CSN 34); Kapiti I. (Wilkinson 1927; Moncrieff 1929; Wilkinson & Wilkinson 1952); Moutoukai, Clevedon (CSN 1); Minginui (St Paul 1976); and Maunga–Haumia, East Coast (McLean 1911); and on SI: on Banks Pen., where territorial throughout year, but with some local movements (Kearton 1979); parts of Dunedin (Moncrieff 1929); between Pt Elizabeth and Mahinapua (CSN 42); and in forests near Reefton (Dawson *et al.* 1978).

Some seasonal movements apparent, either local or altitudinal movements (though some apparent movements may be a result of being less conspicuous during winter, e.g. Dawson *et al.* 1978). NI: Appear to move from forest or other dense habitats to more open areas in spring in East Coast (McLean 1907, 1911) and Mt Egmont NP (Moncrieff 1929). However, in Taumaranui, occur in open country during autumn to spring (Moncrieff 1929). Around Minginui, part of population moves from higher altitudes in autumn–winter to Minginui; in spring, return to upland breeding areas (St Paul 1976). Regularly recorded on mainland adjacent to Kapiti I., Oct.–Feb. (Moncrieff 1929). In Taranaki, occur during spring to autumn (Moncrieff 1929). SI: Autumn–winter visitor to various towns, including Hororata, Dunedin and Greymouth, returning to forest to breed (Moncrieff 1929; Kikkawa 1966; CSN 19). In w. Paparoas, West Coast, some move into coastal forest in autumn–winter from nearby forests (Onley 1980). In forests near Reefton, recorded more often during summer than at other times of year (Dawson *et al.* 1978). Higher numbers at Central Ohikanui in June, suggest possible movement there in winter (Wilson *et al.* 1988).

Banding Of 104 banded to 1974, 30 recoveries (28.8%) (Robertson 1975). Of 803 banded on Snares Is, 1950–96, eight recoveries, 1988–93 (Cossee 1989, 1991, 1993, 1995, 1997, 1998a,b; Cossee & Wakelin 1991). Of 33 banded on Banks Pen., SI, 1977–79, six (18.2%) retrapped; some juveniles dispersed from natal territory 5–6 weeks after becoming independent (Kearton 1979).

FOOD Invertebrates, mostly insects, and, occasionally, fruit. **Behaviour** Largely arboreal. Forage at all levels of vegetation: in canopy, subcanopy, shrub layer and on ground (see Foraging Heights below). Catch prey mainly by sallying, mostly sally-pouncing from perches onto ground, or sally-striking at foliage, branches and tree-trunks; occasionally sally-hover and, very occasionally, sally-strike in air; also sometimes glean (see Foraging Methods below). **DETAILED STUDIES:** SUBSPECIES *TOITOI* (NI): In exotic conifer plantations in Kaingaroa Forest, 1958–59 (Gibb 1961); and on Little Barrier I., Nov. 1967–Oct. 1968 (Gravatt 1969, 1971). NOMINATE *MACROCEPHALA* (SI): In Mt Fitzgerald Scenic Reserve, Banks Pen., 1977–79 (Kearton 1979); in Windbag Valley area, South Westland, Oct. 1983–Dec. 1985 (O'Donnell & Dilks 1994); and in *Nothofagus* forest, nw. Fiordland, 6 Jan.–12 Feb. 1976 (Dodgshun 1976). SUBSPECIES *CHATHAMENSIS*, on South East I., Chatham Is, 23 Mar.–6 Apr. 1990 (O'Donnell & Dilks 1993), and 29 Mar.–7 Apr. 1992

(McLean *et al.* 1994). SUBSPECIES *DANNEFAERDI*, on Snares Is, Nov. 1974–Mar. 1975 (Best 1975) and 3–21 Mar. 1994 (McLean *et al.* 1994). SIZE OF FORAGING GROUPS: Forage singly or in twos; not seen foraging in flocks (Kearton 1979); also see Social Organization. In Arthurs Pass NP, observed foraging in mixed-species feeding flocks, mainly with Yellowheads *Mohoua ochrocephala* and Yellow-fronted Parakeets *Cyanoramphus auriceps*; sometimes with Grey Warblers *Gerygone igata*, Grey Fantails *Rhipidura fuliginosa* and Brown Creepers *Fimschia novaeseelandiae*; such flocks often encountered from mid-Jan. to late Feb. (Read & McClelland 1984; Read 1987). On Snares Is, loosely associated with Snares Penguins *Eudyptes robustus*, foraging in Penguin colonies, which provide ideal conditions for flies (McLean 1991). Territorial for most of year; both sexes defend feeding territories against conspecifics and other small insectivorous birds (Bissett 1978b; Skinner 1978; Kearton 1979; Heather & Robertson 1997; see Social Organization). FORAGING HEIGHTS: Forage at all levels of vegetation: in canopy, sub-canopy, shrub layer and on ground. However, relative frequency of use of various levels of vegetation varies from study to study; populations in native vegetation on main islands appear to forage mainly in vegetation, mostly in understorey, and rarely on ground (Riney *et al.* 1959; Gibb 1961; Dodgshun 1976; Skinner 1978; Kearton 1979; O'Donnell & Dilks 1994; Oliver) while populations on islands and in atypical habitats appear to forage mostly on ground, and rarely at any height in trees or in air (McLean 1911; Fleming 1950; Gibb 1961; Soper 1963; Warham 1967; Gravatt 1969, 1971; Best 1975; St Paul 1976; Skinner 1978; Kearton 1979; McLean *et al.* 1994; Oliver); also see Foraging sites below. In Kaingaroa Forest, mainly foraged on or near ground, and less often in trees; of 187 observations of foraging (figures approximate, read from graph): c. 61% on or near ground; c. 11% 1.1–5 m above ground, c. 18% 5.1–10 m, c. 6% 10–15 m, c. 3% 15.1–20 m, and c. 1% 20.1–25 m. On Little Barrier I., mostly foraged on ground, including among litter and grass, and on logs and bare ground; of 191 observations of foraging: 58.1% on ground, 11.5% in lower understorey, 6.3% in mid-storey, 16.8% in upper understorey, 6.3% in sub-canopy, and 1.0% in canopy; actual heights at which foraging was recorded were: 58.5% on ground, 9.8% 0.1–1.5 m above ground, 6.2% 1.6–3.0 m, 3.1% 3.1–4.5 m, 7.3% 4.5–6 m, 5.7% 6.1–7.5 m, 5.7% 7.6–9.0 m, 2.1% 9.1–10.5 m, and 1.5% >10.5 m. On Chicken I., usually foraged in tree-tops (Chambers *et al.* 1955). On Banks Pen., foraged at all heights of forest, from among litter on ground to canopy, but most commonly recorded foraging on ground and in lower understorey (0–4 m); when foraging on ground, moved from one low (within 15 cm of ground) vantage point to another. In Windbag Valley area, mainly foraged in understorey of forest; of 7109 foraging observations: 3% on ground, 61% in lower understorey, 21% in upper understorey, 10% in shaded canopy (within canopy), 4% in unshaded canopy (on top of canopy), and 1% in emergent foliage. In nw. Fiordland, foraged evenly at all heights from canopy to understorey, but not on ground; of 120 observations of foraging: 21% in lower understorey, 21% in middle understorey, 18% in upper understorey, 24% in subcanopy, and 16% in canopy. In podocarp-*rimu* forests in Fyffe–Palmer Scenic Reserve, Kaikoura, birds remained high in trees and did not forage on ground (Kearton 1979). On South East I., mostly foraged in lower understorey of forest, within 2 m of ground; of 104 observations of foraging: 6.7% on ground, 72.1% in lower understorey, 19.2% in

upper understorey, and 2% in canopy; actual heights at which foraging recorded: 6.7% on ground, 48.1% up to 1 m above ground, 31.7% 1–2 m, 9.6% 2–3 m, 1.9% 3–4 m, and 1.9% 4–5 (O'Donnell & Dilks 1993). Also on South East I., of 60 observations of foraging: 57% on ground; 10% above ground, at 0.1–10% of height of canopy (actual height of canopy not stated), 19% within 10–40%, and 10% above 60% (McLean *et al.* 1994). On Snares Is, foraged mostly on or near ground; of 537 observations of foraging: 60% <2 m above ground, 27% 2.1–4.0 m, 10% 4.1–6 m, and 3% >6 m (Best 1975). Also on Snares Is, of 97 observations of foraging: 51% on ground, 19% above ground at 0.1–10% of height of canopy (actual height of canopy not stated), 7% within 10–20%, 10% within 20–40%, 7% within 40–60%, and 6% above 60% (McLean *et al.* 1994).

FORAGING SITES: Forage at all levels in vegetation, from foliage, twigs, bark of branches and trunks of trees, and on ground, among leaf-litter and grasses; also occasionally aerially. As with foraging height, relative frequency of use of sites varies from study to study, with populations in native habitats on main islands appearing to forage mainly in vegetation and rarely on ground, while those on islands and in atypical habitats appear to forage mostly on ground, e.g. one seen taking worm from lawn (CSN 41) (see references under Foraging heights above). In KAINGAROA FOREST, mainly foraged on or near ground, and less often in trees; of 187 observations of foraging (figures approximate, estimated from graph): c. 60% on ground, c. 10% on trunks of pine trees, c. 7% from branches and pine-cones, c. 13% among live pine-needles, c. 3% among dead pine-needles, and c. 7% in air. On LITTLE BARRIER I., mostly foraged on ground among leaf-litter, though often seen scanning for prey while perched low on trunks and in branches, c. 1.5 m above ground; of 212 observations of foraging: 52.4% on ground, 13.7% on branches, 6.1% on trunks of trees, 4.2% among twigs, 19.3% among leaves and terminal shoots, and 4.2% in air. On Banks Pen., mostly foraged on ground, but also in low vegetation and among foliage in canopy of trees; when in understorey, mostly foraged in shrubs in areas with scattered ground cover of ferns and exposed litter. In WINDBAG VALLEY area, mostly foraged in vegetation and only rarely on ground (see Foraging heights, above); foraged in 51 species of plants, including 13 canopy species and 26 shrubs and other understorey plants. Of 7109 observations of foraging: 9.1% positively identified as feeding on invertebrates (mostly insects) from 36 species of plants, 0.3% on fruits from six species, and remaining 89.1% were unidentified items of food (most likely invertebrates). When feeding on invertebrates (n=647 feeding obs.), foraged in: *Nothofagus menziesii* (19.8%); *Weinmannia racemosa* (17.6%); tree-ferns, including *Cyathea smithii* and *Dicksonia squarrosa* (11.3%); *Dacrydium cupressinum* (5.1%); *Coprosma* (3.6%); *Ripogonum scandens* (2.5%); *Fuchsia exorticata* (2.2%); *Dacrycarpus dacrydioides* (1.9%); *Prumnopitys ferruginea* (1.9%); *Griselinia littoralis* (1.6%); *Metrosideros umbellata* (1.6%); *Pseudopanax crassifolius* (1.4%); *Pseudowintera colorata* (1.2%); *Ascarina lucida* (1.1%); with remaining 21 species of plants used only occasionally (<1.0%); also foraged in dead trees of various species (4.4%); and from ground and in air (11.8% combined). Took fruit (n=22 foraging obs.) from: *Pseudopanax crassifolius* (45.5%); *Ascarina lucida* (31.8%); *Coprosma* (4.6%); *Dacrydium cupressinum* (4.6%); *Pseudopanax edgerleyi* (4.6%); *P. simplex* (4.6%). For full list of plants used when foraging, see Tables 1 and 6 in O'Donnell & Dilks (1994). On SOUTH EAST I. (n=104 obs. of foraging), foraged mostly on

trunks of trees (27.9% from live trees; 10.6% from dead trees); also foraged on branches (5.8%, 9.6%), twigs (18.3%, 7.7%), foliage (1.0%, 0%), live vines (13.5%), and in litter on ground (5.8%). Of these observations, plants in which foraging observed were: Chatham Island Mahoe *Melycitus chathamicus* (32.7%), Chatham Island Matipo *Myrsine chathamica* (13.5%), *Muehlenbeckia australis* (11.5%), Chatham Island Ribbonwood *Plagianthus chathamicus* (7.7%), Ngaio *Myoporum laetum* (4.8%), Chatham Island Akeake *Olearia traversii* (1.9%) Hoho *Pseudopanax chathamicus* (1.9%), Supplejack *Ripogonum scandens* (1.9%) with rest in standing dead trees (9.6%), wind-thrown trees (8.7%), and in leaf-litter on ground (5.8%) (O'Donnell & Dilks 1993). Also on SOUTH EAST I., mostly searched for prey by scanning from elevated perch (see Foraging methods below), mostly trunks and branches of trees (48%) and small branches and twigs (49%) with rest on ground (3%). Most attacks were by pouncing onto ground from perch; of 60 observations of substrate from which prey taken: 48% from ground among litter; 17% from bare ground; 10% from bark of branches and trunks of trees; 13% among foliage; and 7% in air (McLean *et al.* 1994). On SNARES IS, foraged on ground and in vegetation; of 537 observations of foraging: 15% on ground (10% on bare peat, 5% in litter layer), 20% on tree-trunks, 42% on branches, 20% among twigs, 3% in forks of branches and trunks, and <1% among foliage (Best 1975). Also on SNARES IS, mostly searched for prey by scanning from elevated perch (see Foraging methods below), mostly trunks and branches of trees (45%) and small branches and twigs (46%) with some on ground (8%); of 99 observations of substrate from which prey taken: 7% from ground litter, 42% from bare ground, 44% from bark of branches and trunks of trees, 2% among foliage, 2% from dead wood, and 2% in air (McLean *et al.* 1994).

FORAGING METHODS: Search mainly by perch-hunting, and attack mainly by sallying and occasionally by gleaning. **SEARCH BEHAVIOUR:** Usually scan for prey on ground from elevated perch (McLean 1911; Oliver 1922; Fleming 1950; Merton 1966; O'Donnell & Dilks 1993). In KAINGAROA FOREST, perched on vantage points c. 3 m above ground, and scanned ground below; not seen to turn over leaf-litter on ground. On Banks Pen., used perch-hunting to search for and locate most prey. Bird would fly to perch and scan area in front of it, usually staying still and not moving head; if no prey sighted, bird would fly to another perch and scan again; bird continued searching in this way till prey sighted. Areas scanned included twigs, branches, tree-trunks, leaves and litter on ground. Scanned from vantage points of all angles, with vertical branches and trunks used as often as horizontal ones; also scanned from stumps, fallen branches, shrubs, vines, stems of dead thistles, grass, rocks and fences. At edge of forest and in open paddocks, used any suitable raised perch. Period spent scanning from vantage point varied from 5 s to 70 s, with 5–10 s being modal period. When changing position, flew to new perch, often within 30 cm of previous one; if scanning from fence, moved 20–30 m along fence. When in dense foliage, searched by moving rapidly through foliage, stopping for 2–3 s to look for prey; this method used by females during incubation. In WINDBAG VALLEY, much of time spent foraging was occupied by searching for prey by scanning from perches, with birds stooping on a perch, looking for prey, and then flying to another perch if no prey sighted; of 7109 observations of foraging behaviour, c. 90% were of birds scanning for prey. On SOUTH EAST I., searched for prey from

vantage perches; when searching, made 15.0 ± 12.69 moves between perches per min, covering a distance of 3.0 ± 2.25 m in 15.7 ± 14.48 s (McLean *et al.* 1994). On SNARES IS, behaviour similar to that on South East I.; made 15.2 ± 14.85 moves between perches per min, covering 6.3 ± 7.89 m in 22.8 ± 19.38 s (McLean *et al.* 1994). **ATTACK:** Catch prey mainly by sallying, mostly sally-pouncing from perches onto ground, or sally-striking at hard substrates such as foliage, branches and tree-trunks; occasionally sally-hover at foliage or tree-trunks and, very occasionally, sally-strike in air; also glean prey from foliage, bark of branches or tree-trunks, or on ground (McLean 1911; Moncrieff 1929; Fleming 1950; Merton 1966; Turbott 1967; Warham 1967; Gravatt 1971; Oliver; CSN 24; see below). On Banks Pen., most prey caught by sallying, usually by sally-pouncing onto prey on ground, landing briefly to pick up prey, and returning to another perch; only rarely returned to same perch; also observed catching prey by sally-hovering, and sally-striking in air and from vegetation. In open paddocks, prey usually spotted and attacked from up to 10 m away; in forest, distances of attack varied from 5 cm to 10 cm. In WINDBAG VALLEY, attacked mostly by sallying; of 7109 observations of foraging: c. 85% were of scanning and sally-pouncing onto prey on ground, or sally-striking prey on vegetation; also obtained prey by gleaning (c. 10%), by sally-striking in air (c. 3%), and snatching prey from tips of foliage by sally-hovering (c. 1%). On SOUTH EAST I., attacked prey mainly by sallying; of 60 observations of foraging: 93% by sallying, including sally-pouncing and sally-striking on hard substrates; 5% sally-striking in air; and 2% by gleaning (O'Donnell & Dilks 1993). On SNARES IS, foraged mainly by sallying; of 99 observations of foraging: 84% by sallying, including sally-pouncing and sally-striking on hard substrates; 4% sally-striking in air; and 12% by gleaning (McLean *et al.* 1994) *contra* claim that, on Snares Is, foraged by gleaning more often than by sallying (Best 1975). Feed in penguin colonies on insect larvae that breed prolifically in soil; also forage among sea-lions (Oliver). **FOOD HANDLING:** Small prey usually eaten where caught; large prey carried back to perch, bashed on branch or the like, then eaten. Very large or long prey, such as earthworms, usually cut into pieces before being eaten, or before being carried back to feed young or female (Kearton 1979). Large insects usually broken up before being eaten (Notman & Yeates 1992). **DRINKING:** One bird dropped from branch into small pool to drink three times in 5 min (CSN 32).

Detailed studies Diet at ORONGORONGO VALLEY, NI (from faecal samples; Moeed & Fitzgerald 1982) summarized in Table 1.

Other records **Plants** Fruit¹⁵. **GYMNOSPERMS:** Podocarpaceae: *Dacrydium cupressinum* fru.¹² **DICOTYLEDONS:** Araliaceae: *Pseudopanax crassifolius* fru.¹²; *P. edgerleyi* fru.¹²; *P. simplex* fru.¹²; Chloranthaceae: *Ascarina lucida* fru.¹²; Cunoniaceae: *Weinmannia racemosa* fru.²¹; Rubiaceae: *Coprosma* fru.^{6,11}; *C. pseudocuneata* fru.¹² **Animals** **ANNELIDS:** Oligochaetes^{1,10,11,16,20}, **SPIDERS**^{11,16,18}. **DIPLOPODS**¹⁶. **INSECTS:** Ads^{2,3,6,7,8,10}, larv.^{1,4,7,8,10}; Coleoptera^{8,11,15}: Scarabaeidae: *Odontria* larv.¹; Diptera^{8,13,16}: Calliphoridae^{5,11}; *Xenocalliphora eudypsis*¹⁴; Muscidae¹¹; Tachinidae¹¹; Tipulidae¹¹; Erioptera¹⁴; Leptotarsus¹⁴; Hemiptera: Aphididae⁸; Hymenoptera: Apidae¹¹; Formicidae¹⁰; Lepidoptera: ads^{4,11,13,16}; larv.^{4,8,9,11,13,16}; Hepialidae: *Charagia*¹⁶; *Hepialus virescens*³; Orthoptera: crickets¹⁹; Anastomatidae and Rhophado-phoridae¹⁵. **Other matter** Bread crumbs^{2,17}.

REFERENCES: ¹ Smith 1893; ² Hutton & Drummond 1904; ³ McLean 1911; ⁴ Stead 1948; ⁵ Parkin 1951; ⁶ Riney *et al.* 1959; ⁷ Merton 1966; ⁸ Turbott 1967; ⁹ McKenzie 1974; ¹⁰ St Paul 1976; ¹¹ Kearton 1979; ¹² O'Donnell & Dilks 1989; ¹³ Miskelly 1990; ¹⁴ McLean 1991; ¹⁵ Heather & Robertson 1997; ¹⁶ Oliver; CSN 17 1, 18 6, 19 9, 20 41.

Young Both parents feed nestlings and fledgelings. One adult feeding young would catch an insect and, before offering each insect to young, would fly down to creek and dunk prey in water (Heinekamp 1970). **NESTLINGS:** Male does most of feeding of young throughout nestling period (see below). In first week, male brings most food for young, and female spends most time brooding; thereafter, female feeds nestlings more, but male does most feeding of young (Stead 1948; Anglesey 1957; Kearton 1979). On Banks Pen., both sexes fed nestlings, though rate of feeding by male was higher

Table 1. Seasonal distribution of food items identified from faecal samples of adults, Oct. 1973–Aug. 1976 (from Moeed & Fitzgerald 1982). Figures are number of faecal samples containing item. Plant material consists of fruit or seeds.

Food items	Spring	Summer	Autumn	Winter	Total
	Sept. –Nov.	Dec. –Feb.	Mar. –May	June –Aug.	
Animals					
SPIDERS	4	6	24	16	50
Opiliones	2	–	3	–	5
MITES	–	–	1	–	1
PSEUDOSCORPIONS	1	–	6	–	7
DIPLOPODS	–	2	–	1	3
AMPHIPODS	1	–	8	8	17
ISOPODS	–	–	–	1	1
INSECTS					
COLEOPTERA					
Adults	5	8	28	14	55
Larvae	–	2	1	2	5
Curculionidae	3	5	20	6	34
<i>Apion metrosideros</i>	–	–	2	–	2
Elateridae	–	–	2	1	3
Staphylinidae	–	–	2	–	2
DIPTERA	2	5	7	10	24
EPHEMEROPTERA					
HEMIPTERA	3	1	10	5	19
Cicadellidae	2	–	9	–	11
HYMENOPTERA					
Formicidae	1	–	5	3	9
LEPIDOPTERA					
Adults	3	5	17	7	32
Larvae	4	6	20	14	44
PLECOPTERA					
ORTHOPTERA	–	–	–	1	1
Stenopelmatidae	3	3	13	11	30
Plants					
Unidentified	–	–	–	2	2
DICOTYLEDONS					
Cornaceae					
<i>Griselinia lucida</i>	–	–	3	5	8
Epacridaceae					
<i>Cyathodes fasciculata</i>	–	–	1	–	1
Loganiaceae					
<i>Geniostoma ligustrifolium</i>	–	–	–	1	1
Rubiaceae					
<i>Coprosma</i>	–	–	1	–	1
No. of faecal samples	5	8	29	17	59

than that by female for nearly all of nestling period. At one nest with five nestlings: on Day 1 (day of hatching) male made 2.8 feeds/h and female 0.8 feeds/h; on Day 6, male made 6.5 feeds/h and female 1.1 feeds/h; on Days 10 and 11, both parents increased frequency of feeding, but male continued to feed at higher rate: on Day 10 male made 8.6 feeds/h and female 4.8 feeds/h, and on Day 11 male made 7.1 feeds/h and female 6.7 feeds/h; rates of feeding from Days 12 to 16 similar to those on Days 10 and 11; on Day 16, male and female fed nestlings at equal rate (8.8 feeds/h); on Day 18, just before fledging, male did almost all the feeding, at a rate similar to that of Day 1, with male making 11.2 feeds/h and female 1.6 feeds/h. On Stewart I., three nestlings were fed four times in 10 min (CSN 19). Female fed nestlings at highest rate near dusk (Kearton 1979). **FLEDGELINGS:** Young fed for several weeks, up to 35 days, after fledging, by both parents, though male will take over feeding of fledgelings if female re-nests (see Breeding: Fledging to independence). On Banks Pen., fledgelings fed by parents for c. 19 days, with males continuing to do most feeding of young; fledgelings first seen trying to catch prey on Days 8–9 after fledging (Day 1 = day of fledging), and searching for prey on ground on Days 10–12, but with little or no success; fledgelings searched actively and regularly caught prey on Days 15–16 (Kearton 1979; see Breeding: Fledging to independence). Young independent of parents between 19 and 35 days after fledging (see Social Organization).

Detailed studies In ORONGORONGO VALLEY, NI (items identified from 71 faecal samples and eight pellets from young in two broods, 1974–75 breeding season; Moeed & Fitzgerald 1982): **CRUSTACEANS:** Amphipods 32% freq. in faecal samples, 62% freq. in pellets. **DIPLOPODS** 13, 25. **SPIDERS** 85, 100. **INSECTS:** Coleoptera: Ads 85, 100, larv. 9, –; Curculionidae 25, 12; Diptera 45, 62; Hemiptera: Cicadellidae 35, 50; Hymenoptera 44, 37; Lepidoptera: ads 80, 87, larv. 52, 75; Neuroptera 34, 50; Plecoptera 15, 25; Orthoptera: Stenopelmatidae 8, 25.

Other records **SPIDERS**^{1,2}. **INSECTS**^{1,3}: Coleoptera: Scarabaeidae: *Megadromus antarctica*²; *Odontria*²; *Pyronota*²; Curculionidae²; Diptera: Tipulidae^{2,3}; Lepidoptera: larv.^{1,2}

REFERENCES: ¹ Guthrie-Smith 1914; ² Kearton 1979; ³ CSN 1.

SOCIAL ORGANIZATION Well known. Detailed study on breeding biology on Banks Pen., SI, 1977–79 (subspecies *macrocephala*; Kearton 1979); some information also from study of singing and social behaviour in Hunua Ras, NI, 1976–78 (subspecies *toitoti*; Bissett 1978a) and from Snares Is (subspecies *dannefaerdi*; Best 1975; McLean & Miskelly 1988; McLean 1991). Usually seen singly or in twos, which are probably pairs; and sometimes in small groups, in autumn and winter (McLean 1911; CSN); on Chatham Is, family parties evident by late Dec. (Fleming 1939). Sometimes join mixed-species feeding flocks of other small passerines (see Food).

Bonds Breed in monogamous pairs, which usually maintained for successive years; can breed when 1 year old (Wilkinson 1930; Wilkinson & Wilkinson 1952; Kearton 1979; McLean 1991; Heather & Robertson 1997). Said that pairing usually begins July and, once, occurred as early as 21 May (McLean 1911), but these observations probably refer to an increase in territorial defence leading up to the breeding season rather than to pair-formation. Both members of pair defend territory, most intensely during breeding season (Fleming 1950; Bissett 1978a; Kearton 1979; see Territories,

and Social Behaviour). **Parental care** Incubation usually by female alone, though, rarely, male assists; only female broods nestlings, almost constantly for first few days after hatching but for only short periods later on (see Breeding). Both sexes feed nestlings and fledgelings, and remove faecal sacs from nest; occasionally male gives food to female to feed to young (Wilkinson 1930; Stead 1948; Fleming 1950; Kearton 1979; Oliver). For additional information on rates of feeding of young and roles of parents, see Food (Young) and Breeding (Young, Fledging to independence). **DEPENDENCE AND DISPERSAL OF YOUNG:** Juveniles fed for several weeks after fledging, from 19 to 35 days (see Breeding: Fledging to independence). On Banks Pen., some young leave natal territory 5–6 weeks after becoming independent, but others continue to move about within natal territory, or set up a subterritory within the natal territory (Kearton 1979). On Auckland Is, adult male drove off male fledgeling but continued to feed female fledgelings (Fleming 1950). Said that young of second brood driven off territory when adults moulting in Jan. (NZRD).

Breeding dispersion Territorial throughout year (see below). **NI:** Estimated 0.44–1.08 pairs/ha in pine forest at Kaingaroa (Gibb 1961; McLean & Miskelly 1988); <0.25 pairs/ha on Kapiti I. (Wilkinson & Wilkinson 1952; Kikkawa 1960; McLean & Miskelly 1988); 0.33–0.40 pairs/ha on Hen I. (Turbott 1940); 0.39–0.63 pairs/ha on Little Barrier I. (Kikkawa 1964b; McLean & Miskelly 1988). On NI, non-neighbouring territories at least 200 m apart (Bissett 1978a). Near Moumoukai, Nov. 1972, one bird singing every 185 m or so (CSN 20). **SI AND STEWART I.:** Estimated 0.53 pairs/ha (0.14–0.88) at 14 sites on SI and Stewart I. (Kikkawa 1966; McLean & Miskelly 1988); on Banks Pen., estimated six pairs nesting within 8 ha, equivalent to c. 0.8 pairs/ha (Kearton 1979); 0.42 pairs/ha on Ulva I. (Kikkawa 1966; McLean & Miskelly 1988); and 5 pairs/ha on Little Solander I. (McLean & Miskelly 1988). On **SNARES IS,** at least 26 nests in 9.6 ha, equivalent to c. 2.7 pairs/ha (McLean & Miskelly 1988). **Territories** Adult pairs defend all-purpose territories, usually throughout year, though intensity of defence varies with stage of breeding cycle, and some territories apparently not defended for parts of year (Stead 1948; Fleming 1950; Bissett 1978a; Skinner 1978; Kearton 1979; see below). Both sexes defend foraging and nesting area against conspecifics; each defending against others of their own sex (Bissett 1978a,b). Advertising of ownership of territory and defence of territory strongest in breeding season (Bissett 1978a,b; Kearton 1979) and marked by July–Aug. (Fleming 1950; Kearton 1979); advertisement and defence declines after breeding, particularly during post-breeding moult (Bissett 1978a; Kearton 1979). On Banks Pen., SI, during post-breeding moult, in Feb.–Apr., adults withdrew to small part of breeding territories, and males did not react to playback of Song. On Banks Pen., males sometimes move into another territory deliberately, e.g. to bathe. Soon after independence, some juvenile males and females set up small subterritories of ≤ 0.1 ha on edge of adults' territory. When adults moulting and defence of territory weak, juveniles move through territories unchallenged. Some unpaired birds lived as floaters, inhabiting and moving about quietly in territories held by other Tomtits (Kearton 1979). On Snares Is, a male held different foraging territory to his mate: he fed almost exclusively in a colony of Snares Penguins, but female rarely fed there (McLean 1991). Philopatric to nest-site, returning in successive seasons (Wilkinson 1927; Bissett 1978a; Kearton 1979). **SIZE OF**

TERRITORIES: In NI (subspecies *toitoti*), 1.5 ha (Bissett 1978a); 1.2–2.5 ha, depending on habitat (Skinner 1978); on Kapiti I., c. 4 ha (Wilkinson 1930). On Banks Pen., SI, 0.49–2.57 ha ($n=15$), though nesting successful only in territories ≥ 1 ha in area. Several of these territories contracted after start of breeding season, in early Sept.; and territories often expanded in non-breeding season to include open areas at edge of breeding territory (Kearton 1979). On Snares I., mean size of territories estimated at 0.22 ha (Kearton 1979).

Roosting No information.

SOCIAL BEHAVIOUR Well known. Detailed studies on breeding biology on Banks Pen., SI, 1977–79 (nominate *macrocephala*; Kearton 1979); and on aspects of singing and social behaviour in Hunua Ras, NI, 1976–78 (subspecies *toitoti*; Bissett 1978a); some information also from Snares Is (subspecies *dannefaerdi*; Best 1975; McLean & Miskelly 1988; McLean 1991). Usually tame and confiding, often flying in close to inspect intruder (Oliver 1922; Wilkinson 1927; Warham 1967), especially males (McLean 1911; Wilkinson 1930); females said to have retiring disposition (Stidolph 1922), but tolerant of human observers near nests (McLean & Miskelly 1988). Active and restless; flight often short and darting (Oliver 1922; St Paul 1976; Oliver). Often perch sideways on tree-trunks (McLean 1911; Bissett 1978a). On open perch, cock tail and droop wings (McLean 1911); flick tail up at an angle (cf. New Zealand Robin) (Stead 1948). Both sexes respond to imitations or playback of vocalizations (see Voice): fly rapidly at source with feathers of crown raised and adopting Aggressive Posture; juvenile males also respond by giving loud calls (Bissett 1978a; Kearton 1979). During nest-building, male once sat in nest apparently recently discarded by female (Wilkinson 1930). **NORMAL POSTURE:** Perch at angle of 45°, with plumage sleeked and frontal spot visible as slit of colour above bill (Bissett 1978a; Kearton 1979; see Fig. 1a). **ALERT POSTURE:** Often given by male when observing a disturbance from vantage point 5–10 m above ground; or by a male trespassing in another male's territory. Thought to be submissive behaviour. Similar to Aggressive Posture (see below) but legs held straight, neck stretched upward, head cocked and raised, with feathers of head sleeked, and frontal spot almost invisible (Bissett 1978a; Kearton 1979). **Displays HORIZONTAL WING-DISPLAY:** Bird holds wings horizontal for a few seconds, with wings either still or quivering, and usually calling at same time; display can be repeated several times. Display appears to be a reaction to novel stimuli (Kearton 1979). **VERTICAL WING-DISPLAY:** Bird lowers wings, which are held still or quivered, for 2–3 s, and does not call; observed only between birds of opposite sex, either adult or juvenile (Kearton 1979). **COMFORT BEHAVIOUR:** A male observed bathing: dipped head into water, crouched down and fluttered wings; fledgelings also bathed in

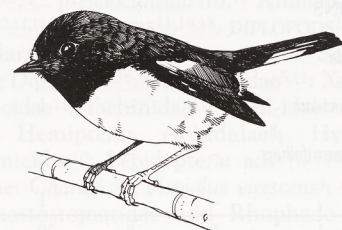


Figure 1a. Normal posture

shallow stream (Kearton 1979). Once, male preened between bouts of Subsong; and once preened during aggressive encounter (Bissett 1978a). A female at nest stood up, peered into nest, then resettled (Kearton 1979).

Agonistic behaviour Aggression between males occurs throughout year (Fleming 1950), but most aggressive behaviour occurs during breeding season, particularly at start of season (including courtship phase) with territorial behaviour conspicuous by July–Aug., and decreasing in intensity at time of post-breeding moult at end of breeding (see also Voice for annual patterns of use of Song). On Banks Pen., aggression between males was less common after breeding, Feb.–June (Kearton 1979). On Snares I., little territorial fighting occurred when nesting or young fledging (Best 1975). Birds react more aggressively to birds that are not neighbours (Bissett 1978a). Males advertise ownership of territory by singing loudly throughout territory, often from exposed perches in canopy. Males also commonly perform **CIRCUIT SINGING**, moving progressively along boundary of territory, singing in short bouts from high, exposed perches; rarely give more than ten Songs before shifting perch. Aggressive behaviours include Aggressive Posture, Frontal Spot Display, Territorial Boundary Display, chases, fights, and Counter-singing by males. Most aggression associated with intrusions by birds into territory of another, or interactions at territorial boundaries. Both members of pair defend territory against conspecifics (Fleming 1950; Hay 1975; Bissett 1978a,b; Kearton 1979; also see Social Organization [Territories] and Voice); each defend against others of their own sex (Bissett 1978a,b). Each sex reacts more aggressively towards its own sex or reflection in mirror, especially when mate is present, adopting Aggressive Posture, including Frontal Spot Display (Bissett 1978a). **COUNTER-SINGING AND COUNTER-CALLING**: When a male trespasses on another's territory, the two males exchange loud call-notes (Kearton 1979). Counter-calling also accompanied some aggressive displays (see below). Counter-singing occurred throughout the day and was probably used to protect territorial boundaries. Counter-singing could be elicited by playback of a stranger's Song, and was often followed Territorial Boundary Display or chases (Bissett 1978a). **TERRITORIAL BOUNDARY DISPLAY**: Defend established territories mainly by singing. When patrolling territorial boundaries, two males can follow each other for up to 30 m along boundary, usually flying only 1–3 m at a time, then stopping to face each other, giving aggressive Chuck or Chip calls while perched sideways (see Fig. 1b) with wings and tail fanned, and feathers of head and frontal spot raised (Bissett 1978a). **AGGRESSIVE POSTURE**: If trespassing bird does not leave after exchange of calls, the two birds approach to within c. 30 cm, at any level above ground, then face each other in an aggressive posture for 15–30 s, after which intruder usually retreats (Kearton 1979). Given by aggressor during most aggressive encounters between conspecifics, particularly between those of same sex; can also be directed at mirror reflections or models. Bird stands with legs bent and raises feathers of crown, enlarges and displays frontal spot, adopts an upright stance, and stares and points bill at intruder or object of aggression (see Fig. 1c). If further antagonized by intruder, bird fluffs feathers of breast, lowers and slightly spreads wings to reveal more white, and constantly flicks wings and tail (Bissett 1978a; Kearton 1979). **FRONTAL SPOT DISPLAY**: Given as part of Aggressive Posture, but also sometimes in response to novel or mildly alarming stimuli (Kearton 1979). Raise feathers of forehead and display frontal



Figure 1b. Territorial boundary display

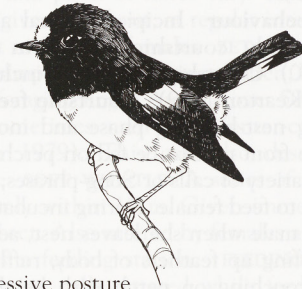


Figure 1c. Aggressive posture

spot towards intruder (Fleming 1950), though this not observed in melanistic subspecies *dannefaerdi* of Snares Is (Best 1975). **OTHER THREATENING DISPLAYS**: Rarely, while defending territory, male also holds wings horizontally to display wing-bar, slowly raises and lowers wings (to c. 40° above horizontal) several times, while constantly counter-calling and fluffing up feathers of body (Kearton 1979). Display consisting of fluttering of wings and accompanied by darting flights with arched wings, possibly describes same display (Fleming 1950). Adversaries sometimes fan wings and tail (Warham 1967; Bissett 1978a). Once, similar display occurred between adult male and female, though function unknown (Kearton 1979). **Chases** If intruder does not retreat after territorial owner adopts Aggressive Posture, it is chased by owner of territory (Kearton 1979). Accompanied by peevish chattering and bill-clicking; most occur between males at start of breeding season; usually begin in air and end on ground (McLean 1911; Bissett 1978a; Kearton 1979). Chases are usually initiated by aggressive calls and are similar to Territorial Boundary Display (Bissett 1978a; see below). Chases occur between sexes (Kearton 1979) and can include bill-clicking. Adult males chase young males more often than they chase young females (Kearton 1979). Chases also occur between siblings (see Relations within family group). **Fights** Chases or Territorial Boundary Display sometimes develop into physical interactions. Once, on Banks Pen., chasing birds seen to fall to ground with claws locked together, then flutter about for 15 s before resuming chase; both birds puffed feathers of body and crown throughout encounter; and once, during breeding season, a male briefly grappled twice with mate after chasing her (Kearton 1979). Physical contact also recorded between two males on boundary patrol (Bissett 1978a). Bill-clicking can be given during fights (Bissett 1978a; Kearton 1979). **Submissive behaviour** One juvenile male gave submissive call when pecked by adult male while on ground (Bissett 1978a). **Alarm and Distress** Bill-clicking can be given when distressed (Bissett 1978a; Kearton 1979).

When Swamp Harrier *Circus approximans* nearby, both sexes uttered loud alarm call and continued to call till after Harrier out of sight (Kearton 1979). Alternatively, silent when low-flying predator flies over, or, sometimes, give sibilant high-pitched whistle (Bissett 1978a). **INTERSPECIFIC AGGRESSION:** Rarely aggressive towards other species, though both sexes sometimes chase Silvereyes *Zosterops lateralis* and Grey Warblers, especially near Tomtit nest or young (Bissett 1978a; Kearton 1979); male once attacked a Southern Boobook *Ninox novaeseelandiae* for 20 min (McLean 1911). Female gives Chip calls in response to Silvereyes uttering vocalizations similar to Tomtit Subsong (Bissett 1978a). Often chased by other species including Common Blackbird *Turdus merula*, Bellbird *Anthornis melanura* and Dunnock *Prunella modularis* (Kearton 1979).

Sexual behaviour Incipient sexual activity, probably referring to early courtship, noted in autumn–winter (Fleming 1950). Courtship sometimes includes non-aggressive chasing (Kearton 1979). **Courtship feeding** Male feeds female during nest-building phase and incubation, usually calling female from nest to be fed on perch up to 6 m from nest using a variety of calls or Song-phrases; male sometimes comes to nest to feed female. During incubation, female begs for food from male when she leaves nest, adopting **BEGGING POSTURE**, fluffing up feathers of body, ruffling or fluttering wings, and crouching on perch with head thrust forward; though sometimes feeds herself and exercises early in incubation (Wilkinson 1927; Wilkinson 1930; Turbott 1947; Stead 1948; Parkin & Parkin 1951; Wilkinson & Wilkinson 1952; Chambers *et al.* 1955; Anglesey 1957; Soper 1963; Turbott 1967; Best 1975; St Paul 1976; Kearton 1979; McLean & Miskelly 1988; Knegtman & Powlesland 1999; Powlesland *et al.* 2001; Oliver; CSN 1, 6). Begging Posture appears to be a submissive posture (Kearton 1979; see Relations within family group below). Male helps select nest-site by entering hole in tree and calling to female as invitation to inspect site. During nest-building, members of pair maintain contact by single soft call-notes, and answer each other till they come together (Wilkinson 1930). **BUTTERFLY FLIGHT:** Male chases female, with male holding wings somewhat awkwardly, high and forward, and accompanied by bill-snapping (Fleming 1950). **WING-FLASH DISPLAY:** On Little Barrier I., a pair faced each other and alternately flicked their wings towards each other, flicking both wings together (Orenstein 1979). Similar behaviour also seen on Banks Pen., but wings extended very slowly; directed towards female by male on vertical tree-trunk, possibly as part of courtship (Kearton 1979).

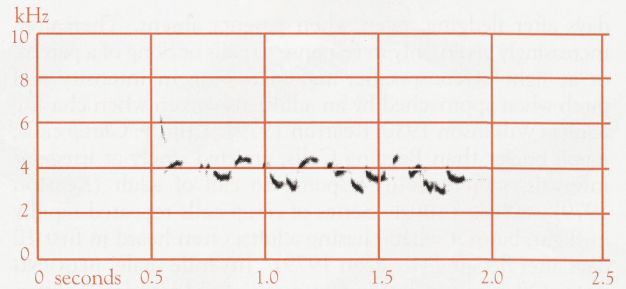
Relations within family group Both sexes feed nestlings and fledgelings; male will sometimes give food to female to feed nestlings and will feed fledgelings solely if female re-nests (see Breeding, Food). When observer present, male appeared more cautious than female when approaching nest with food (Wilkinson 1930). During incubation, male stands guard at nest when female leaves nest, usually to wash or preen (St Paul 1976). Female vocalizes quietly when close to, or attending, young (Wilkinson 1930). After young fledge, brood sometimes divided, with female feeding female offspring and male feeding males. Parents also encourage recent fledgelings to move high into trees (Wilkinson 1930). If fledgeling becomes separated from parents, parents call persistently to call brood together (Kearton 1979). When some of young in brood are independent, they are chased away from nest by adults if others in same brood are still being fed; adult male chases away young of both sexes, adult female chases only

female young (Fleming 1950; Kearton 1979). Juveniles often chase each other, with much bill-clicking, and occasionally uttering staccato Chuck call; chases sometimes end in birds tumbling about grasping each other's claws. Chases and grappling between siblings nearly always initiated by juvenile males; juvenile females usually chase each other for only a few metres (Kearton 1979). **BEGGING POSTURE:** Juveniles beg with same posture used by adult females when begging for food (Stead 1948; McLean & Miskelly 1988). Posture apparently submissive; nearly independent juveniles that do not beg when meeting an adult male are often chased. Female fledgelings sometimes beg for food from newly independent males if closely approached by male, but female usually chased away by male or stopped begging after a few seconds (Kearton 1979). When close to fledging, nestlings peck at their siblings in nest (Best 1975). **Anti-predator responses of young** Newly fledged young perch in a group near tops of trees where twigs and foliage dense (Best 1975; Kearton 1979); said to be encouraged to do so by parents (Wilkinson 1930). **Parental anti-predator strategies** Female crouches low in nest when incubating, so that only top of head, including bill and eye, and tail visible (Wilkinson 1930; Kearton 1979). Give distress calls when Long-tailed Cuckoo *Eudynamis taitensis* near nest (Beaven 1997). Do not defend nest against predation by Black Rat *Rattus rattus* (Brown 1997). In response to observer at nest with young, female flew very close to observer, making snapping noises with bill, raising feathers of head and ruffling wings, and sometimes alighting on head or shoulder of observer (Wilkinson 1930). **DISTRACTION DISPLAYS:** When threatened or alarmed near nest with young, parents fly and perch low to distract threat (Anglesey 1957); also feign injury to lead threat away from nest (Oliver); or perform distraction displays. **FULL DISPLAY:** Bird raises wings, which are spread and quivered, and fans tail; accompanied by jerky, puppet-like movements on ground (Buller 1888; Soper 1976; Kearton 1979). **PARTIAL DISPLAY:** On two occasions when intruder approached fledgelings too closely, male raised one wing vertically and quivered it, then did same with other wing; repeated 3–4 times (Kearton 1979).

VOICE Well known; detailed studies in Hunua Ras, near Auckland, NI (Bissett 1978a), which includes sonagrams, and is the source of unreferenced statements in this account; and on Banks Pen., SI (Kearton 1979), which also includes sonagrams. There are further observations in Hay (1975), which includes sonagrams. Vocalizations rendered in musical notation in McLean (1911) and in Andersen (1909, 1911, 1913, 1915, 1918, 1923, 1926). Males sing loud stereotyped Songs, audible to 200 m on still days, sometimes singing for several hours at a time (Hay 1975; Bissett 1978a). In Kaingaroa Forest, NI, in late Oct., one male sang mean of 8.3 Songs/min from 09:00 to 10:00, and sang in all but seven of the 60-min period (Gibb 1961). When singing, bill is opened only fractionally, and whole body appears to be involved in production of sound. Most calls are common to both sexes, and are given throughout year. Buzz and Churr share a mixture of Song and call characteristics, and are more complex than other calls. **ANNUAL PATTERN:** Levels of singing and of counter-singing are highest in July (before first brood in Aug.) and in Oct. (before second brood in Nov.); there is a deep decline during post-breeding moult. **DIURNAL PATTERN:** Vocalizations are distributed reasonably uniformly throughout daylight hours, but with much higher levels around dawn and dusk. Singing occurs most often between 11:00 and

15:00, and, in breeding season, level of counter-singing increased slightly in late afternoon. Vocal activity, notably singing and counter-singing, reduced on windy days. **COUNTER-SINGING:** Only males participate in counter-singing, which increases during courtship and breeding. Birds sometimes counter-call with Zet and Chuck calls. **INDIVIDUAL DIFFERENCES:** Each male had a characteristic Song (or, in some cases, two Songs) which was stabilized over course of breeding season and which did not vary significantly through study period. Apart from those individuals that had two Songs, variation within Songs of an individual was much less than variation between individuals. Similarity between Songs of males decreased as distance between them increased (Hay 1975; Bissett 1978a). Another study found that where regular boundary patrolling occurred, males answered each other with similar Songs, but where resident birds had few interactions with their neighbours, their Songs were often more different (Kearton 1979). **REGIONAL VARIATION:** Songs from neighbouring populations usually more similar in structure of notes and in pattern of frequencies than are Songs of birds from widely separated populations. Songs of populations from small islands often more varied than in other populations, with a greater number of notes and a smaller range of frequencies, and with a greater proportion of birds singing more than one Song. A significant difference is apparent between Songs of birds on Chatham Is and those of NI and SI, which do not differ significantly; in Chatham Is populations, main call outside Song-period is a 'downscale' call, similar to that of the Black Robin; both sexes give this call, but only the males perform full Song (Hay 1975). **RESPONSE TO PLAYBACK:** Both sexes respond to playback of vocalizations or imitations of calls; also respond to squeaking and to sound of cork rubbed on glass (McLean 1911; Bissett 1978a; Skinner 1978; Kearton 1979). Intensity of reaction to playback of Song often mirrors the level of singing activity (see Annual pattern, above). In playback trials, males respond more strongly to Songs of non-neighbours than to those of neighbours, and to Songs of their own locality than to those from other areas. **NON-VOCAL SOUNDS:** Bill-clicking, consisting of repeated snapping together of mandibles, occurs in highly aggressive situations, e.g. during chases or fights, when swooping at observer or when very distressed; individual bill-clicks are heard when birds unsuccessfully snap at prey items (McLean 1911; Wilkinson 1930; Fleming 1950; Bissett 1978a; Kearton 1979).

Adult male SONG: Highly stereotyped musical warble, lasting up to 2.4 s (Hay 1975; Bissett 1978a; Kearton 1979). Intervals between notes very short, so that individual notes are rarely distinguishable to human ear (Hay 1975). Harmonics occur very occasionally. Described as a cheery, vigorous *ti-oly-oly-ho* and as *yodi-yodi-yodi* (Reischek 1887; Wilkinson 1930; Fleming 1950). Sonagram A shows a song which could be rendered *tih-oly-oly-oly* or *tih-yodi-yodi-yodi* (T. Howard). When singing, give mean of 9.7 Songs/min. Usually the only differences in Songs within a bout is when the final section of a Song is truncated (Hay 1975). In each of two studies, c. 10% of males of population sang two different Songs, which were randomly interchanged in a single bout of Song (Bissett 1978a; Kearton 1979). Males without mates sang for longer periods and with greater intensity than males with mates (Hay 1975; Bissett 1978a). Circuit-singing along territorial boundaries common, birds seldom uttering more than ten Songs from one perch before moving on (Hay 1975; Bissett 1978a; see Social Behaviour). **Adult female**



A L.B. McPherson; Banks Pen., SI, Aug. 1984; P106

SUBSONG: Soft and rambling, lasting only a few seconds; length, number and pitch of notes vary. Often only six or seven Subsongs given in a bout, at regular intervals. Audible to 20 m. **Adult males and females ZET:** From one to five, most often one, simple *zet* notes, uttered often, but at irregular intervals, when foraging singly. Audible over 50 m. Probably a contact call. Sometimes used for counter-calling (Bissett 1978a; Kearton 1979). This call also described as *tick* (Kearton 1979). **SOFT WHISTLE:** A series of closely spaced notes, audible only within 10 m. Given immediately before capture of an insect. Also uttered by females at a rich source of food, such as a feeding station. **FEEDING CALL:** High-pitched and varying calls, uttered while feeding juveniles. **CHURR:** A throaty rattle, comprising a series of notes, first decreasing, then at a constant pitch. Given during aggressive encounters, or directed towards persistent intruders. **BUZZ:** Shorter than Churr, with closely spaced notes. Often accompanied by bill clicks. Given rarely, before a fight or when patrolling territorial boundary. **SEET:** From two to seven, most often three, loud *seet* notes, uttered when disturbed. Sometimes used in counter-calling. **CHUCK:** A single sharp, penetrating call. Audible to 10 m. Given in highly aggressive situations, such as boundary disputes, when given by opponents in rapid alternation. **CHIP:** Short repeated *chip* notes, given in mildly aggressive situations. Possibly given only by females. **PREDATOR ALARM CALL:** Loud alarm calls (once, c. 80 consecutive calls) given when a predator, such as a Swamp Harrier or Australian Magpie *Gymnorhina tibicen*, is nearby; also given in response to presence of New Zealand Pigeon *Hemiphaga novaeseelandiae* (Kearton 1979). On Chatham Is, utter a sibilant high-pitched whistle in response to aerial predators (Hay 1975). **DISTRESS CALL:** A harsh grating squeal, consisting of a series of closely spaced notes; uttered when handled (Bissett 1978a; Kearton 1979). An undescribed distress call given when a Long-tailed Cuckoo took a nestling (Beaven 1997). **PRE-SONG CHATTER:** A varying sequence of rambling notes and soft warbles interwoven with calls, including Seet calls and calls similar to Churrs, but with notes of higher pitch. Commonly given in the few minutes preceding male Song or female Subsong. **Other calls** Brief low-pitched single notes, varying in structure, usually uttered in bouts of two or three; associated with Subsong, Pre-Song Chatter and aggressive vocalizations. Brief soft twitter when male fed female (Kearton 1979). Harsh hissing accompanies Distraction Display (Soper 1976).

Nestling BEGGING CALLS: Barely audible at hatching, but become louder as nestlings grow; uttered when adult arrives at nest; in the few days before fledging, given as soon as an adult calls or sings near nest, and continues for a few seconds after adult leaves nest (Kearton 1979). **Fledgeling BEGGING CALL:** Given almost continuously for the first few

days after fledging, even when parents absent. Thereafter, increasingly given only in response to calls or Song of a parent, or at sight of conspecific, and increasing in intensity and pitch when approached by an adult; also given when chasing adults (Wilkinson 1930; Kearton 1979). **CHRUP**: *Chrup* calls, much briefer than Begging Calls, emitted singly at irregular intervals, sometimes in response to call of adult (Kearton 1979). **FLYING CHRUP**: Series of *chrup* calls repeated rapidly in flight, but not when chasing adults; often heard in first 10 days after fledging (Kearton 1979). **Juvenile male BEGGING CALL**: Often given during first week of independence, often interspersed with juvenile Song and Subsong (Kearton 1979). **SUBMISSIVE CALL**: On Chatham Is, an undescribed submissive call was given by a juvenile male being pecked by an adult male (Hay 1975, which includes sonagram of call). **DEVELOPMENT OF SONG**: Subsong is longer, softer, and more varying than Song, covers a greater range of frequencies, and contains some interspersed call-notes; often given for up to several hours at a time. Subsong develops into full Song largely by elimination of call-notes and extreme frequencies (Bissett 1978a). Another study found that shortly after juveniles moult, Subsong develops into a form resembling Song of adult males, but with some plasticity, e.g. after moulting, one banded bird sang a random repertoire of four or five phrases, but, by the following breeding season, retained as Song only the phrase sung most often in Subsong (Kearton 1979).

BREEDING Well known. Detailed studies of **NOMINATE MACROCEPHALA** at Mt Fitzgerald Scenic Reserve, Banks Pen., SI, 1977–79 (Kearton 1979); **SUBSPECIES TOITOI** in Pureora Forest Park, NI, 1997–98 (Knegtman & Powlesland 1999); **SUBSPECIES DANNEFAERDI** on Snares Is, summer 1987, with some observations over previous five summers (McLean & Miskelly 1988); and **SUBSPECIES CHATHAMENSIS** on South East I., Chatham Is, 1981–89 (Powlesland *et al.* 2001). Also observations in NI and SI (Mathews 1930) and on Kapiti I. (Wilkinson 1927; Wilkinson & Wilkinson 1952); and on Snares Is (Stead 1948). Some information extracted from NZ NRS (Kearton 1979; Heather & Robertson 1997; Knegtman & Powlesland 1999). Monogamous (see Social Organization). Multi-brooded. On Snares Is, sometimes breed very close to colonies of endemic Snares Penguins, with success related to closeness to colony (McLean 1991; see below).

Season Throughout range, breeding recorded Sept.–Feb., mainly Oct.–Dec.; laying recorded Sept. to early Jan. in main islands and to mid-Dec. on Chatham Is (see below). **SUBSPECIES TOITOI**: Breed Sept.–Feb., with laying from late Sept. till late Dec. or early Jan. (Gibb 1961); laying of one clutch began mid-Sept.; fledgelings from mid-Nov. (Knegtman & Powlesland 1999); on Kapiti I., breeding from late Aug. to Feb. (Wilkinson & Wilkinson 1952). **NOMINATE MACROCEPHALA**: Breed Sept. till late Dec. (Soper 1963); at Mt Fitzgerald, laying occurs late Sept. to early Oct.; young hatch mid- to late Oct. (Kearton 1979). **SUBSPECIES CHATHAMENSIS**: Lay mid-Oct. to mid-Dec. (McLean & Miskelly 1988). On South East I., 1981–89, first clutches laid late Sept. and first half of Oct., and last clutches late Nov. to early Dec., with a few late nesting attempts completed late Jan. (Powlesland *et al.* 2001). **SUBSPECIES DANNEFAERDI**: Breed early Oct. to mid-Dec., mostly in Nov. and sometimes finishing late Jan. (McLean & Miskelly 1988; CSN 24). On Snares Is, season apparently affected by meteorological variation caused by El Niño: in 1982–83 season, affected by strong El Niño, single nest recorded, with young fledging in

Jan.; after-effects of El Niño subsided in subsequent years, 11–37 nests recorded per season, and mean date of fledging was 4 Dec. (1–6 Dec.) (Miskelly 1990; McLean & Miskelly 1988).

Site Nest usually sheltered from several sides and sometimes from above. In hole or hollow in tree, in hollow log, in tangle of vines, under head of cabbage tree, among loose bark on trunk of tree or tree-fern, or in dead hanging fronds of tree-ferns; less often on sheltered cleft or ledge in bank or cliff, or among foliage of shrub or low tree; once in 'pig-rootings' and once in cup-shaped hollow on perpendicular face of lichen-covered boulder (Wilkinson 1924; Mathews 1930; Stead 1948; Weeks 1949; Fleming 1950; Wilkinson & Wilkinson 1952; Chambers *et al.* 1955; Soper 1963; Hadden 1988; Nilsson *et al.* 1994; Heather & Robertson 1997; Powlesland *et al.* 2001; Oliver; CSN 4, 6, 24). Sometimes build inside huts or beneath overhangs of artificial structures, such as under eaves or verandahs of huts or houses, or on arch of bridge (Mathews 1930; Stead 1948; Anglesey 1957; CSN 1, 3, 6). Occasionally nest in nest-boxes (Gibb 1961; NZ NRS). Said to nest in trees during wet seasons and on stumps or banks in dry seasons (St Paul 1976). Of 32 nests in NZ NRS from 1923 to 1991 from NI: nine in tree-ferns; seven in nest-boxes; five in forks in trees; three on 'ledges in trees'; two in hollows in trees; two in holes (in ground, rocks or bank); and singles in foliage of tree, on ledge (in rock, ground or bank), in a building, and among fallen twigs (Knegtman & Powlesland 1999). In Pureora Forest Park, of 11 nests, seven built against trunks of tree-ferns or among dead hanging fronds of tree-ferns; two in hollows in trees; one on 'ledge in tree'; and one in disused nest of New Zealand Robin in fork in tree. On Kapiti I., most nests built in hollow spouts of Mahoe *Meliccytus ramiflorus*, with singles on top of dead tree-fern *Cyathea* and on ground beside rock (Wilkinson 1927). On Banks Pen., of 16 nests, six were in hole or cavity in trunk or main branch of tree; three in tangle of bush lawyer *Rubus cissoide* just under canopy of tree and where leaves of vine formed continuous cover round and over nest; three on trunk of tree-fern; two on ledge at rotted-out end of trunk or branch of tree; singles in fork between trunk and main branch, and among foliage of pepper tree *Pseudowintera colorata* (Kearton 1979). Of 42 nests in NZ NRS, from records up to 1979 (all subspecies): 16 in hollows in trees; eight on 'ledges in trees'; seven in holes in rocks or on ground; three in forks in trees; two in bush lawyer; two among roots of upturned trees; two in buildings; one in other trees; and one among peeling bark

Plate 19

(P. Slater)

Scarlet Robin *Petroica multicolor* (page 604)

SUBSPECIES BOODANG: 1 Adult male; 2 Adult female;
3 Juvenile; 4 Immature male; 5 Immature female; 6 Adult
male; 7 Adult female

SUBSPECIES CAMPBELLI: 8 Adult female

Red-capped Robin *Petroica goodenovii* (page 649)

9 Adult male; 10 Adult female (typical plumage); 11 Adult
female (reddish variant); 12 Juvenile; 13 Immature male;
14 Immature female; 15 Adult female

Flame Robin *Petroica phoenicea* (page 666)

16 Adult male; 17 Adult female; 18 Juvenile; 19 Immature
male; 20 Adult male; 21 Adult female

(2.4%) (Kearton 1979). On South East I., Chatham Grp, of 378 nests located over eight seasons, 1981–89: 43.4% of nests in tangles of Pohuehue vines *Muehlenbeckia australis*; 16.2% in hollow branches or cavities on trunks; 11.7% on a branch, trunk or stump covered by vines; 6.3% on stumps; 0.5% on branches; 0.5% in shrubs; 0.5% in nest-boxes; with site not stated for remaining 20.9% (Powlesland *et al.* 2001). On Snares Is (n=49 nests), most nests within forest (34 in pure *Olearia* forest; ten in mixed *Olearia*–*Brachyglottis* or *Hebe* forest; and one in stand of *Brachyglottis*) with remaining four on cliffs or exposed ridges. Of these 49 nests: 38 in stumps, trunks or among roots of logs of *Olearia*; four in trunk or among roots of *Brachyglottis*; three in ferns *Polystichum vestitum*; three on ledges of bank; and one under grass tussock (McLean & Miskelly 1988). **RE-NESTING:** On Banks Pen., SI, if first clutch of season abandoned, re-nest at new site, usually within 10 m of first nest (n=6 instances of re-nestings), and 1–2 days after first nest abandoned (Kearton 1979). On Snares Is, usually select new nest-site for repeated nesting, but sometimes re-use same nests in consecutive seasons (McLean & Miskelly 1988). **MEASUREMENTS (m):** Height of nest, 1–18.2, mostly 1–4 (Wilkinson 1927; Mathews 1930; Stead 1948; Soper 1963; St Paul 1976; Heather & Robertson 1997; Oliver; NZ NRS; see below). At Pureora Forest Park, 3.4 (0.82; 1.9–4.5; 11) with nine nests in upper understorey and two in lower understorey. On South East I., Chatham Grp, 2.7 (1.52; 0.5–8.0; 370 nests, 1981–89) with 88.6% <4.1 m above ground; mean height varied significantly between seasons (Powlesland *et al.* 2001). On Snares Is, 0.64 (0.57; 0–3.5; 49) with 82% ≤1 above ground, 16% 1–2, and only one (2%) >2; height of canopy above nests, 4.4 (1.4; 4–7; 46) (McLean & Miskelly 1988). From NZ NRS, for records up to 1979 (all subspecies), height of nest, 5.08 (0–18.2; 35) (Kearton 1979); for records from 1923 to 1991, from NI: 2.8 (1.66; 0.7–8.0; 34) (Knegtmans & Powlesland 1999). On Banks Pen., 4.06 (1.84; 1.75–8; 16). Height of nest-tree, at Pureora Forest Park, 5.2 (1.23; 3.0–7.5; 11).

Nest, Materials Nest bulky, conical to round, with a deep cup. Made of moss, leaves, rootlets, grass or bark; bound tightly with spider web; and lined with scales of tree-ferns, fine grass and feathers or wool (Wilkinson 1927; Mathews 1930; Wilkinson & Wilkinson 1952; Soper 1963; Turbott 1967; Powlesland *et al.* 2001; Oliver; CSN 1; see below). Some nests made entirely of moss and lined with bark of Ribbonwood *Hoheria populnea* (Turbott 1967). On Banks Pen., nest usually consists of a basal platform and a cup, which is placed in or on platform; some nests, such as those built in hollows, have either very small or no basal platform, while others have a thick basal platform (to provide support for nests built on sides of tree-trunks or in tangle of vines). Material used in base includes dead leaves, twigs, scraps of

bark, rotten wood, pieces of moss and lichen, dead fern-fronds, and roots of ground ferns; these sometimes mixed with spider web. Cup made of tightly compressed moss, especially *Weymouthia mollis* (which was used almost exclusively in some nests), mixed with scales of tree-fern. Outside of cup often decorated with coarse material, such as liverworts, pieces of bark, moss and petioles from bush lawyer vine; in some nests, rim of cup covered with spider web. Inside of cup lined with feathers (Kearton 1979). On South East I., nests varied little in composition, except in the coarse materials used to form base; while the bulk of each nest consisted of mosses and lace-like dried inner bark from dead Chatham Island Ribbonwood *Plagianthus chathamicus* trees, other material included leaves, lichens, twigs and spider web; lining was mosses or feathers (predominantly of seabirds and Red-crowned Parakeets *Cyanoramphus novaeseelandiae*) or both (Powlesland *et al.* 2001). **CONSTRUCTION OF NEST:** Female builds nest, though male sometimes brings material to female (McLean 1911; Wilkinson 1930; Stead 1948; Bissett 1978a; Kearton 1979; Powlesland *et al.* 2001; Oliver). On Banks Pen., basal platform built first, then cup added; material gathered within 20 m of nest, mostly from litter layer, but also up to c. 5 m above ground in knotholes and round bases of fern-fronds; scales of tree-ferns collected from trunks of ferns, especially bases of dead fronds. Do not build continuously throughout day but build in stints of several hours at a time, e.g. once recorded building continuously for 2.5 h. While building, sometimes make up to eight trips per minute to nest. Males fed females while they built (Kearton 1979). On Snares Is, when building, female first laid down dry moss, mixed with fern scales and a few bits of grass, in a small circle; this gradually built up, and bound with rootlets, fibres and spider web; centre of nest composed mainly of fern scales, and lined with fern scales and a few feathers (Stead 1948). Building takes 3–5 days (Stead 1948; Anglesey 1957; Heather & Robertson 1997; Oliver). On South East I., construction took 3.4 days (1.31; 2–8; 23) (Powlesland *et al.* 2001). **MEASUREMENTS (cm):** External diameter, 10.2; external depth, c. 7.6; and internal depth, 3.8; diameter of another nest, 5.7 (Turbott 1967). On Snares Is, internal diameter, 6.5; internal depth, 4.0 (Stead 1948).

Eggs Ovoid. Creamy white, with small yellowish-purple or light-brown and grey spots all over, forming dense band at large end (Mathews 1930; Stead 1948; Fleming 1950; Wilkinson & Wilkinson 1952; Heather & Robertson 1997; Oliver). On South East I. (78 eggs collected 1981–87), most eggs ovoid but a few almost spherical; eggs mainly white, with brown and grey spots and blotches concentrated at larger end, though on three eggs markings were concentrated at narrower end and five eggs had fine brown-grey spots distributed evenly over entire shell (Powlesland *et al.* 2001). **MEASUREMENTS: NOMINATE MACROCEPHALA:** 18.2 (0.7; 17.5–19.6; 8) × 14.9 (0.5; 14.5–15.8) (Kearton 1979); 17.9 (0.31; 17.6–18.2; 3) × 14.5 (0.31; 14.4–14.8) (Oliver); also given as 19 × 15 (Mathews 1930). **SUBSPECIES TOITOI:** 17.7 (0.58; 17–18; 3) × 14.7 (1.15; 14–16) (Oliver); also given as 22 × 20 (Mathews 1930) and about 18 × 15 (Fleming 1950). **SUBSPECIES CHATHAMENSIS:** On South East I., 19.1 (0.62; 17.4–20.3; 99) × 15.0 (0.31; 14.2–15.6) (Powlesland *et al.* 2001). **SUBSPECIES DANNEFAERDI:** 20.0 (1.50; 18.5–21.5; 3) × 15.2 (0.76; 14.5–16.0) (Oliver); also given as 23 × 16.5 (Fleming 1950). **SUBSPECIES MARRINERI:** 23 × 16.5 (Fleming 1950). **WEIGHT:** On South East I., mean fresh weight estimated to be 2.35 g (Powlesland *et al.* 2001).

Plate 20

(P. Slater)

Rose Robin *Petroica rosea* (page 684)

1 Adult male; 2 Adult female; 3 Juvenile; 4 Immature male; 5 Immature female; 6 Adult male

Pink Robin *Petroica rodinogaster* (page 696)

NOMINATE RODINOGASTER: 7 Adult male; 8 Adult female; 9 Juvenile; 10 Immature male; 11 Immature female; 12 Adult male

Clutch-size From two to six, usually three or four. On NI and SI, clutch usually three or four, but up to six; on Chatham Is, clutches of 1–4 recorded, with most being C/3; and on Snares Is, only C/2 and C/3 recorded, with most C/3 (Mathews 1930; Wilkinson 1930; Stead 1941; Fleming 1950; Wilkinson & Wilkinson 1952; Turbott 1967; Kearton 1979; Hadden 1988; McLean & Miskelly 1988; Nilsson *et al.* 1994; Heather & Robertson 1997; Knegtman & Powlesland 1999; Oliver; see data below). **SUBSPECIES TOITOI** (NI): From NZ NRS, 4.0 (0.84; 3–6; 15): C/3 × 4, C/4 × 8, C/5 × 2, C/6 × 1 (Kearton 1979). At Kaharoa, 4.0 (0.38; 3–4; 13) (Brown 1994); in nest-boxes in Kaingaroa Forest, 4.0 (0.82; 2–4; 6): C/2 × 1, C/3 × 2, C/4 × 3 (Gibb 1961); in Pureora Forest Park, 4.1 (0.94; 3–6; 11): C/3 × 3, C/4 × 5, C/5 × 2, C/6 × 1 (Knegtmans & Powlesland 1999). **NOMINATE MACROCEPHALA** (SI and Stewart I.): From NZ NRS, 4.0 (0.64; 3–5; 18): C/3 × 3, C/4 × 11, C/5 × 4 (Kearton 1979). On Banks Pen., usually 3–5, rarely six (Kearton 1979). **SUBSPECIES CHATHAMENSIS** (On South East I., mean clutch-size over all seasons 3.13 (0.51; 2–4; 284 clutches, 1981–89): C2 × 20, C/3 × 207, C/4 × 57; while clutch-size appeared to vary over a breeding season, differences were not significant (Powlesland *et al.* 2001). On Chatham Is, 3.3 (0.4; 3–4; 24) (McLean & Miskelly 1988). **SUBSPECIES DANNEFAERDI**: On Snares Is, 2.83 (0.37; 2–3; 30): C/2 × 5, C/3 × 25 (McLean & Miskelly 1988). Pairs breeding near penguin colonies laid larger clutches than pairs breeding away from colonies: of 27 pairs, 23 with nests within 36±5.4 m of penguin colony laid clutches of three, while four pairs that nested within 41±21 m of colony laid only clutches of two (McLean 1991); further information needed.

Laying Eggs usually laid at intervals of 24 h, soon after sunrise (Anglesey 1957; Kearton 1979; Heather & Robertson 1997; Knegtman & Powlesland 1999; Powlesland *et al.* 2001; Oliver). However, on South East I., of 221 eggs, most (96%) laid at daily intervals with rest laid during second day; and on Snares Is, said to lay at intervals of 48 h (Stead 1948). Laying sometimes begins immediately after nest finished (Anglesey 1957); or up to 15 days after completion of nest. On Banks Pen., time between completion of first nest and laying first egg was 6–11 days; and time between completion of subsequent nests and laying was 1–4 days (Kearton 1979). On South East I., time between completion of nest and laying 5.9 days (2.81; 2–15; 88), longer in Oct. (7.1 days [3.13; 2–15; 45]) than in Nov. (4.6 days [1.72; 1–11; 43]); time between failure of a nest (by desertion or destruction) and re-nesting, 1.75 days (1.00; 1–5; 36) (Powlesland *et al.* 2001). On Snares Is, eggs laid 3 days after nest finished (Stead 1948). Multi-brooded. Pairs often raise two or three broods per season; but if nests fail, will lay up to six times in a season (Gibb 1961; Soper 1963; Turbott 1967; Kearton 1979; Heather & Robertson 1997). However, on Snares Is, probably only lay one clutch in a season (McLean & Miskelly 1988).

Incubation Usually only by female (Wilkinson 1930; Anglesey 1957; Best 1975; Kearton 1979; Powlesland *et al.* 2001); though once male reported sitting, in stints lasting 15–30 min (Oliver), but this unusual (Fleming 1950). Begins with completion of clutch (Anglesey 1957); on South East I., usually starts on day last egg laid (82.4%, n=85), occasionally on day penultimate egg laid (9.4%), or day after clutch completed (8.2%) (Powlesland *et al.* 2001). Female fed by male regularly throughout day during incubation, usually off nest (see Social Behaviour). After being fed by male, female returns to nest indirectly (Parkin & Parkin 1951; St Paul

1976). On Banks Pen., incubation usually started with laying of last egg in clutch; time spent incubating depended on how often incubating female was fed by male; at two nests, female spent 72.5% of 8.6 h observation time incubating; mean stint of incubation was c. 16 min (0.5–49 min) (Kearton 1979). **INCUBATION PERIOD**: Usually 15–17 days (Wilkinson & Wilkinson 1952; Anglesey 1957; Heather & Robertson 1997; Oliver). For one nest on South East I., period for one nest was 17 days (Powlesland *et al.* 2001). Period possibly 18–20 days for subspecies *dannefaerdi* and 17–18 days for *chathamensis* (Heather & Robertson 1997).

Young Altricial, nidicolous. Almost naked till Day 3, but covered with down by Day 5; eyes begin to open about Day 7; and feathers of wing and tail fully formed by Day 10, when feathers of head and body developing. By Day 15, nestlings almost fully feathered and readily sexed by differences in colour of plumage (Powlesland *et al.* 2001). **BROODING**: Only female broods (Wilkinson & Wilkinson 1952; Kearton 1979; Heather & Robertson 1997; Knegtman & Powlesland 1999; Powlesland *et al.* 2001). On Banks Pen., SI, at one nest: on first day after hatching (n=146 min obs.), female spent 66% of time brooding, in stints of 2–50 min; on Day 6 (n=158 min obs.), female spent 40% of time brooding, in stints of 4–11 min; on Day 10, brooding stopped (Kearton 1979). Female warms chicks if away from nest for 10 min or so (Anglesey 1957). **FEEDING OF YOUNG**: Nestlings fed by both parents, usually directly (Wilkinson 1930; Wilkinson & Wilkinson 1952; Anglesey 1957; Soper 1963; Kearton 1979; Heather & Robertson 1997; Knegtman & Powlesland 1999; Powlesland *et al.* 2001), though sometimes male passes food to female to feed nestlings (Wilkinson & Wilkinson 1952; Soper 1963). For further information on rates of feeding of young and role of each parent, see Food. **OTHER BEHAVIOUR**: Faecal sacs removed by both parents (Anglesey 1957; Kearton 1979); eaten till Day 5, but removed and dropped within 20 m of nest thereafter (Kearton 1979); at 18 days, nestlings void faeces over edge of nest (Anglesey 1957).

Fledging to independence **FLEDGING PERIOD**: NI: 17–20 days (Heather & Robertson 1997); on Kapiti I., 17–18 days (Wilkinson & Wilkinson 1952). SI: 20 days (Anglesey 1957). On Snares Is, 17–22 days. On South East I., 18.8 days (17–21; 6 broods, 1981–82) (Powlesland *et al.* 2001); on Chatham Is, 16–19 days (Heather & Robertson 1997). **FEEDING OF FLEDGELINGS**: Fed by both parents for c. 10 days, though male takes sole care of fledgelings if female re-nests; male continues to feed fledgelings for another 1–2 weeks (Wilkinson & Wilkinson 1952); for 1–3 days if female re-nests, longer if no re-nesting, with fledgelings being fed for up to 19 days (Kearton 1979). On Snares Is, where re-nesting after success not recorded, fledgelings fed by both sexes for up to 5 weeks (McLean & Miskelly 1988); for 3–4 weeks after leaving nest (Best 1975). Female can re-nest as soon as 1 day after young fledge (see above). In Eglinton Valley, SI, young fed for 3–4 weeks or so after fledging (Soper 1963). For further details of feeding of young, see Food (Young). On Banks Pen., fledgelings stayed high in vegetation, usually beneath canopy (5–10 m high). When feeding young, parents often fed an individual four or five times in succession before feeding others; sometimes, one parent fed particular chicks only. Fledgelings start to follow parents about Days 4–7. Usually first start searching for food as they move through vegetation about Day 8, though one fledgeling seen trying to catch prey on Day 5; by Day 10 seen foraging on ground for first time; by Day 15, fledgelings regularly caught own food. By Day 18,

young moved independently of parents, and by Day 20, were almost fully independent (Kearton 1979). Fledgelings can remain in natal territory for 5–6 weeks after becoming independent (see Social Organization).

Success On South East I., of 97 eggs in 34 clutches 1981–89, 81 (83.5%) hatched; one clutch of three infertile but reasons for failure of other 13 eggs not known. In 1981–82, all of 23 chicks in 11 nests fledged; and 14 (93.3%) of 15 nesting attempts produced at least one fledgeling (Powlesland *et al.* 2001). At Kaharoa, NI, of 29 nests with eggs, two (6.9%) successful, at least 22 (75.8%) failed through predation, three (10.4%) were deserted, and two (6.9%) failed for unknown reasons; predators mainly Black Rats *Rattus rattus* (Brown 1997). At Pureora Forest Park, of 15 nesting attempts, 11 (73.3%) were successful, and four failed, either through desertion or predation (Knegtmans & Powlesland 1999). On Kapiti I., of eight nests 1925–26, only one produced young; eggs were destroyed either by rats or by Long-tailed Cuckoos (Wilkinson 1927). From NZ NRS, for records between 1923 and 1991 from NI, of 11 nests, five (45.5%) were successful, four failed at egg-stage (one deserted in wet weather, one abandoned after nest tipped over; and two depredated, one by a rat), and two failed at nestling stage (one depredated by rat and other either abandoned or depredated) (Knegtmans & Powlesland 1999). Four young hatched and fledged from a clutch of five (Anglesey 1957). **PREDATION:** Eggs and young known to be taken by rats, including Black Rats (see above). At Pureora Forest Park, nesting success possibly influenced by control of predators; in 1997–98 breeding season, of six nests in area without predator control and five in treated areas: in area without predator control, four nests successful, one failed through predation and one abandoned; in area where predators controlled, four (80%) nests successful, and one (20%) failed through predation (Knegtmans & Powlesland 1999; Powlesland *et al.* 2000). At Te Urewera NP, Long-tailed Cuckoo was seen to take nestling from nest (Beaven 1997). On Snares Is, nesting success high, with most nests fledging at least one young (McLean & Miskelly 1988). **CUCKOOS:** Parasitized by Long-tailed Cuckoo (Cunningham 1949; Beaven 1997; HANZAB 4). **PREDATORS OF ADULTS:** A bird found dead, hanging from a twig, caught by its leg by a 16 mm long gordian worm (Nematomorpha, a parasite of invertebrates) (Notman & Yeates 1992).

PLUMAGES Prepared by A.M. Dunn. Acquire down by Day 5 after hatching (see Breeding); fledge in juvenile plumage. Undergo partial post-juvenile (first pre-basic) moult to adult-like first immature (first basic) plumage, probably beginning 2–3 months after fledging. Attain adult plumage in complete first immature post-breeding (second pre-basic) moult, probably at end of first year or early in second. Thereafter, a complete post-breeding (pre-basic) moult each cycle produces successive adult plumages without change in appearance. Five subspecies. Sexes differ at all ages in most subspecies; sexes alike in *dannefaerdi*. Nominate *macrocephala* described below, based on examination of skins of 25 adult males, nine adult females, seven juvenile males and four juvenile females; no first immatures identified from available specimens.

Adult male (Definitive basic). **HEAD AND NECK:** Centre of lower forehead, white, forming small white frontal spot. Feathers of rest of head, black (89) with concealed grey (84) bases. No feathered eye-ring. **UPPERPARTS:** Black (89)

with concealed grey (84) bases to feathers and off-white (ne) shafts to concealed basal halves of feathers. **UNDERPARTS:** Upper breast, black (89), rather sharply demarcated from pale-yellow (c157) lower breast, belly, flanks and vent. Feathers immediately below line of demarcation between upper and lower breast usually washed with orange (17). Axillaries, white. Thighs, black (89). Undertail-coverts mostly pale yellow (c157), but some feathers have black (89) centres. All feathers of underparts have concealed dark-grey (83) bases and off-white (ne) shafts to bases. **TAIL:** T1–t3, black (89); rarely, t3 has small white spot near tip of inner web. T4 mostly black (89) with broad white tip to inner web and fine white edge c. 1 cm long in middle of outer web; white tip triangular, and extends farther down shaft than at edge of feather. T5 and t6, black (89) with broad diagonal white band extending from near tip on inner webs to middle of feather on outer webs. See Figure 2 for illustration of tail-patterns. **UPPERWING:** Most coverts and alula, black (89); inner greater secondary coverts often have white spot at tips, and marginal primary coverts beside alula often have whitish (ne) suffusion. Tertiaries, black (c89) with white edges to basal halves of outer webs on larger one or two. Secondaries, black-brown (c119) grading to black (89) on outer edges, with white bar near bases of feathers; white bar broad on s6 (15–20 mm wide) and narrows to s1 (c. 5 mm wide). Primaries mostly black-brown (c119), grading to black (89) on outer edges; p1–p5 have narrow white bar about one-third from base that peters out on inner web of p5. White bars across bases of secondaries and inner primaries align to form central wing-bar on spread wing (see Fig. 1 in Petroicidae account, p. 576). **UNDERWING:** Secondary coverts, white. Marginal and median primary coverts, black (89) with narrow white tips. Greater primary coverts mostly dark grey (83); outer 2–3 coverts have white fringe to tips. Remiges patterned as upperwing, but ground-colour dark grey-brown (ne).

Adult female (Definitive basic). Much browner than adult males, with paler underparts. **HEAD AND NECK:** Small patch of feathers in centre of lower forehead and feathers at sides of forehead (above anterior lores), white with black tips; those in centre of lower forehead form small off-white frontal spot, much smaller than that of adult male. Rest of forehead, crown, nape, hindneck and sides of neck, olive-brown (c29) with concealed grey (84) bases to feathers. Lores

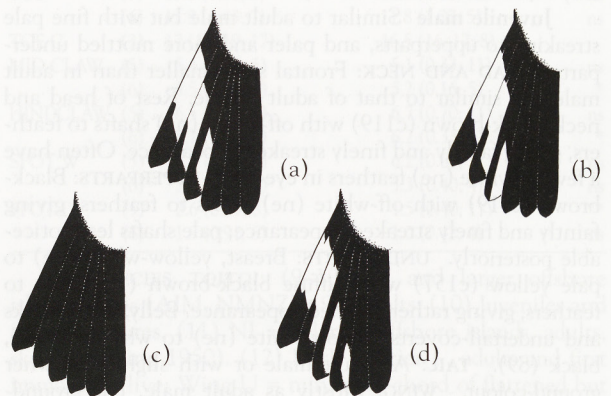


Figure 2. Variation in pattern of undertail between subspecies: (a) *P.m. chathamensis* (b) *P.m. toitoi* and *P.m. macrocephala* (c) *P.m. dannefaerdi* (d) *P.m. marrineri*

and ear-coverts, olive-brown (c29) with off-white (ne) shaft-streaks to feathers, giving rather mottled appearance. Narrow eye-ring, off-white (ne). Feathers of chin and throat, yellowish white (ne) with dark-grey (83) bases to feathers; dark bases can show through feathers, resulting in greyish appearance. **UPPERPARTS:** Mantle, scapulars, back and rump, olive-brown (c29); some feathers of rump can have yellow-brown (c24) tips. Uppertail-coverts, dark olive-brown (129). **UNDERPARTS:** Breast mostly yellow-white (ne), grading to olive-brown (c29) at sides, and sometimes washed with buff (c124). Belly, vent and flanks, yellow-white (ne), often with scattered buff (124) or light-brown (223D) smudges. Axillaries, white. Thighs, brownish grey (c79). Undertail-coverts, yellow-brown (c123C). **TAIL:** Patterned as adult male but ground-colour black-brown (119). **UPPERWING:** Most coverts and alula, dark brown (121); inner greater secondary coverts often have off-white (ne) or buff (c124) spot at tips, and marginal primary coverts beside alula often have white (ne) suffusion. Tertiaries, black-brown (c119) with off-white (ne) or buff-white (ne) edges to basal halves of outer webs on larger two. Secondaries, dark brown (121), grading to black-brown (c119) on outer edges, with off-white (ne) or buff-white (ne) bar near bases of feathers, broad on s6 (15–20 mm wide) and narrowing to s1 (c. 5 mm wide), and suffused with orange-buff (c118) near margins; some have faint, narrow, elongated light-brown (223D) spots on edge of outer webs, about one-third length from tips. Primaries mostly dark brown (121), grading to black-brown (119) on outer edges; p1–p5 have narrow off-white (ne) or buff-white (ne) bar suffused with orange-buff (c118) about one-third from base, which peters out on inner web of p5. Bases of secondaries and inner primaries align to form narrow off-white (ne) or buff-white (ne) central wing-bar; some have faint light-brown spots on distal edges of secondaries that align to form very faint trailing wing-bar on spread wing (see see Fig. 1 in Petroicidae account, p. 576). **UNDERWING:** Secondary coverts, white. Marginal and median primary coverts, brownish grey (79) with fine off-white (ne) fringes to tips. Greater primary coverts, white. Remiges patterned as on upperwing but ground-colour brown-grey (ne), and central wing-bar, white.

Nestling No information for nominate *macrocephala*. Nestlings of *dannefaerdi* hatch mostly naked with 'fluff' on head (McLean & Miskelly 1988). Nestlings of *chathamensis* mostly naked at hatching (Day 1), but covered with down by Day 5 (Powlesland *et al.* 2001).

Juvenile male Similar to adult male but with fine pale streaking to upperparts, and paler and more mottled underparts. **HEAD AND NECK:** Frontal spot smaller than in adult male and similar to that of adult female. Rest of head and neck, black-brown (c119) with off-white (ne) shafts to feathers, giving faintly and finely streaked appearance. Often have a few off-white (ne) feathers in eye-ring. **UPPERPARTS:** Black-brown (c119) with off-white (ne) shafts to feathers, giving faintly and finely streaked appearance; pale shafts less noticeable posteriorly. **UNDERPARTS:** Breast, yellow-white (ne) to pale yellow (c157) with diffuse black-brown (119) tips to feathers, giving rather mottled appearance. Belly, vent, flanks and undertail-coverts, yellow-white (ne) to white. Thighs, black (89). **TAIL:** As adult male or with slightly browner ground-colour. **WING:** Mostly as adult male, but ground-colour slightly browner.

Juvenile female Similar to adult female, but with fine pale streaking to upperparts, and more mottled appearance to underparts. **HEAD AND NECK:** Frontal spot very small or

absent. Forehead, crown, nape, hindneck, sides of neck, lores and ear-coverts, dark brown (c121) with off-white (ne) shaft-streaks to feathers, giving streaked appearance. Streaks more noticeable than in juvenile male. Narrow eye-ring, off-white (ne). Chin and throat, off-white (ne) with diffuse brown (c28) edges to feathers, giving rather mottled appearance. **UPPERPARTS:** Mantle, back, scapulars and rump, dark brown (c121) with narrow off-white (ne) shaft-streaks, which are narrower and less distinct posteriorly. Uppertail-coverts as in adult female. **UNDERPARTS:** Breast, off-white (ne) with diffuse dark-brown (c121) tips to feathers, giving rather mottled appearance. In some, breast has hint of yellowish (ne) suffusion, but much paler than in adult female. Belly, vent and flanks, off-white (ne), often with cream (c92) suffusion, but appears paler than in adult female. Thighs and undertail-coverts as adult female. **WING AND TAIL:** As adult female.

First immature male (First basic). Many or most probably not separable from adult male, but breast can appear paler than that of adult male, and do not have orange on breast seen in many adult males (Kearton 1979). Some possibly separable from adult on wear of primaries, since these retained from juvenile and would be older than those of adult at same time of year, but this should be used with caution because rate of wear of primaries can differ between locations; further study needed.

First immature female (First basic). Most probably not separable from adult female. As with first immature male, some possibly separable on wear of primaries, but caution needed. In study of live birds, white frontal spot was covered with brown-tipped feathers after completion of post-juvenile moult, but gradually attained size and appearance of that of adult female over several months (Kearton 1979).

Aberrant plumages Albinism and part-albinism have been observed (Fleming 1950; Oliver). In 1979, one 'albino' *toitoti* was observed at Matawai, NI (CSN 26). One specimen of *toitoti* had completely white plumage (NMNZ 12216).

BARE PARTS Based on photos (Munn 1984; Moon 1992; NZRD; unpubl.: M.J. Carter; B. Chudleigh) and published information as cited. Subspecies alike and combined below. **Adult male** Bill, black (89); or brownish black with purplish-horn base (Fleming 1950), or brownish black, often with yellow base to lower mandible (Oliver). Gape, black (89). Inside of mouth, and tongue, deep orange (Fleming 1950). Iris, black-brown (119); or dark brown (Fleming 1950; Oliver), or black (Oliver). Orbital ring, black (89). Legs, black (89) or grey-black (82); or dark purplish-brown with distal anterior streak of orange (Fleming 1950). Feet, grey (84), light brown (c239), yellow-brown (c123B) or pink-brown (219C or 221C); or bright orange with purplish brown on phalangeal scutes (Fleming 1950), brownish with brownish-yellow toes, or dark brown (Oliver). Soles, buff (123D); or orange-yellow or yellow (Oliver). Claws, black (Oliver). **Adult female** Bill as adult male; or black (89) with pink-brown (c219D) base to lower mandible. Gape, orange-buff (153). Iris as adult male. Orbital ring, dark grey (83). Legs, dark grey (c83). Feet, yellow-brown (c123C), dark grey (c83), light brown (239) or pink-brown (219C). Soles, orange-buff (c153). **Nestling** Rather advanced feathered nestling: Bill, pale grey (86), grading to white on cutting edges. Gape, white or yellow-white (ne). Inside of mouth, orange (17). No other information. **Juvenile** No photos. Museum labels (AIM) describe: iris, black; feet less yellow than adult; and soles, bright orange. No other information. **First immature** Probably as adult.

MOULTS Based on examination of skins of 79 adults and 20 juveniles and immatures (AIM, NMNZ); data from banding study in West Coast, SI (D.J. Onley); and published information as cited. Subspecies combined for analysis. **Adult post-breeding** (Third and subsequent pre-basic). Complete; primaries outward. Begins after breeding finished, often well into Feb. (Kearton 1979; Oliver). From skins (this study), moult of primaries started in Jan. and finished in Mar.: Jan. (2 of 5, PMS 8, 18); Feb. (2 of 2, PMS 36, 37); Mar. (2 of 8, PMS 42, 45); all in Apr. had finished (n=4); none moulting primaries May–Dec. (n=53). Only two were recorded with active moult of tail; one in Jan. was replacing t4–t6, and one in Apr. was replacing t1–t3. Active moult of body was recorded in Jan. (n=2), Feb. (n=2), Mar. (n=4) and Apr. (n=1). Moult of body appeared most active late Jan. to early Mar.; those in late Mar. and Apr. showed only slight moult of body. In West Coast, moult of primaries started about Jan. and finished about Mar.; moult recorded Jan. (3 of 5; PMS 3, 11, 20), and Mar. (1 of 2; PMS 46); none of one in Feb. was in moult; all were finished by Apr. (n=10), and none was moulting primaries in May (n=4) or July (n=3). Moult of secondaries appeared to start a little later than primaries, but probably finished at about same time. Active moult of tail only recorded from one in Jan.; and active moult of body only recorded from one in Mar. (D.J. Onley). From live birds on Banks Pen., SI, earliest observed moult was a female in Jan.; one adult female in Feb. was replacing p2–p4 but did not appear to have started moult of body or tail; and one male in Mar. had heavy moult of body and was replacing p7, but had not moulted any of tail (Kearton 1979). From skins (Fleming 1950): In NI and SI, both sexes had finished moulting by May; and none was moulting May–Dec.; and on Stewart I. in Mar., adult males had finished moult of primaries, but still had active moult of body. On Chatham Is, in Dec., one adult female was moulting p7–p9 and tail, but no adult males were moulting. On Auckland Is, Mar.–Apr., both sexes were finishing moult, and all had finished by May (Fleming 1950). On Little Barrier I., active moult of tail observed Feb. (Gill & Veitch 1990). **Post-juvenile** (First pre-basic). Usually partial (Kearton 1979), possibly sometimes complete (see below). Replace most plumage of body, and secondary and most primary wing-coverts but usually retain remiges and rectrices and, probably, greater primary coverts and alula. However, in at least some, rectrices, tertials and some or all primaries can be replaced (Fleming 1950; D.J. Onley). On Banks Pen., moult started during latter part of breeding season, probably 7–9 weeks after fledging; earliest active moult noted mid-Jan., last in full juvenile plumage seen in Mar., and usually have first immature appearance before early Apr. (Kearton 1979). From skins (this study), active moult of body recorded Feb. (n=5) and Mar. (n=2), and birds in juvenile plumage only recorded Nov.–Mar. In West Coast, SI, juveniles caught Dec.–Mar. (n=27); and active moult of body recorded Jan. (1 of 4), Feb. (1 of 7), and Mar. (1 of 1); two were recorded with active moult of tail in Feb., one of which was also moulting tertials and primaries (PMS 15) (D.J. Onley). In Jan., one female from Enderby I. was moulting primaries and body (Fleming 1950). On Banks Pen., feathers of breast and belly replaced before those of head (Kearton 1979). **First immature post-breeding** (Second pre-basic). As adult post breeding.

Stewart I. and offshore islands, adults, skins (Fleming 1950). (5–6) Mt Fitzgerald Scenic Reserve, Banks Pen., SI, live; Whiskers = length of longest vibrissa (riactal bristles); Mid-claw = length of claw on middle toe; Hind-claw = length of claw on hindtoe; Spot W = widest diameter of frontal spot; Spot D = depth of frontal spot from top of bill to top of spot (Kearton 1979): (5) Adults; (6) Juveniles. (7–8) West Coast, SI, live (D.J. Onley): (7) Adults; (8) Juveniles.

		MALES	FEMALES	
WING	(1)	73.1 (1.60; 70–76; 22)	70.7 (2.55; 68–76; 9)	**
	(2)	72.8 (1.68; 71–76; 7)	69.5 (0.58; 69–70; 4)	**
	(3)	73.5 (71–77; 14)	74 (72–76; 6)	
	(4)	72.5 (1.54; 70–75; 26)	69.9 (1.98; 67–72; 12)	**
	(5)	73.4 (2.91; 8)	71.2 (2.32; 12)	*
	(6)	74.4 (0.79; 7)	69.8 (1.63; 5)	**
	(7)	72.8 (1.31; 71–75; 14)	70.8 (1.25; 68–72; 11)	**
	(8)	73.0 (1.26; 71–75; 11)	70.1 (1.44; 68–73; 16)	**
TAIL	(1)	52.3 (2.43; 51–61; 22)	54.2 (2.77; 48–58; 9)	*
	(2)	56.7 (2.69; 54–62; 7)	54.2 (1.50; 53–56; 4)	ns
	(3)	54.4 (52–57; 14)	56 (55–57; 6)	
	(4)	55.7 (2.12; 52–59; 26)	53.4 (1.85; 51–57; 12)	**
	(5)	50.0 (2.32; 8)	46.7 (4.02; 12)	**
	(6)	50.6 (1.45; 7)	45.9 (2.46; 5)	**
BILL S	(1)	13.7 (0.40; 13.0–14.6; 19)	13.4 (0.53; 12.5–13.9; 8)	ns
	(2)	13.4 (0.96; 11.3–14.1; 7)	13.2 (0.15; 13.1–13.4; 4)	ns
BILL F	(3)	10.2 (10–11; 14)	9.8 (9.5–10)	
	(5)	10.3 (0.45; 8)	9.8 (0.62; 12)	*
	(6)	9.67 (0.45; 7)	10.3 (0.96; 5)	ns
	(7)	9.0, 10.0	9.4 (0.54; 8.7–10.0; 4)	ns
BILL W	(8)	8.2, 9.1, 9.2	8.4, 9.3, 9.8	
	(5)	4.4 (0.39; 8)	4.1 (0.28; 12)	*
	(6)	4.3 (0.18; 7)	4.5 (0.31; 5)	ns
BILL D	(5)	3.2 (0.17; 8)	3.2 (0.24; 12)	ns
	(6)	3.4 (0.24; 7)	3.1 (0.13; 5)	*
THL	(7)	31.4 (0.44; 30.7–32.0; 14)	31.1 (0.61; 29.8–32.0; 11)	ns
	(8)	31.0 (0.46; 30.3–31.7; 11)	30.6 (0.36; 30.0–31.2; 16)	*
WHISKERS	(5)	10.6 (0.48; 3)	9.35 (0.54; 8)	**
	(6)	8.6 (1.35; 7)	9.5 (1.23; 5)	ns
TARSUS	(1)	22.5 (0.73; 20.9–23.8; 22)	22.7 (1.05; 21.5–25.2; 9)	ns
	(2)	22.1 (1.39; 20.0–23.8; 7)	22.3 (0.68; 21.6–23.1; 4)	ns
	(3)	20.9 (20–22; 14)	23.7 (22.5–25; 6)	
	(4)	23.1 (1.40; 20–25; 26)	22.3 (1.53; 20–24.2; 12)	ns
	(5)	25.3 (1.41; 8)	25.2 (1.23; 11)	ns
	(6)	25.2 (1.56; 7)	25.2 (1.30; 5)	ns
	(7)	22.6 (0.53; 21.7–23.4; 12)	22.4 (0.62; 21.2–23.4; 11)	ns
	(8)	22.7 (0.47; 21.7–23.3; 10)	22.6 (0.69; 21.4–23.9; 16)	ns
TOE	(5)	13.0 (1.31; 8)	12.6 (1.16; 11)	ns
	(6)	12.9 (1.43; 7)	11.8 (1.07; 5)	ns
TOE C	(3)	17 (16–19; 17)	16.5 (16–17; 8)	
	(5)	5.4 (0.56; 5)	5.1 (0.33; 11)	ns
MID-CLAW	(6)	5.5 (0.34; 7)	5.2 (0.16; 5)	*
	(5)	6.5 (0.54; 8)	6.7 (0.70; 11)	ns
HINDCLAW	(6)	6.7 (0.40; 7)	6.2 (0.33; 5)	*
	(5)	6.7 (0.68; 8)	6.2 (0.63; 11)	ns
SPOT W	(6)	5.3 (0.42; 7)	5.3 (0.40; 4)	ns
	(5)	2.6 (0.59; 8)	1.5 (0.40; 11)	**
SPOT D	(6)	1.9 (0.91; 6)	1.0 (0.42; 4)	ns

SUBSPECIES TOITOI: (9–10) NI and larger offshore islands, skins (AIM, NMNZ): (9) Adults; (10) Juveniles and first immatures. (11) NI and larger offshore islands, adults, skins (Fleming 1950). (12) Little Barrier I., adults and first immatures, live; Wing U = minimum chord of flattened but unstraightened wing; Bill N = length of bill from anterior edge of nostril to tip; Tarsus B = length of tarsus from ankle notch to edge of bent-over foot (Gill & Veitch 1990). (13) Orongorongo Valley, NI, adults, live (Robertson *et al.* 1983).

MEASUREMENTS NOMINATE MACROCEPHALA: (1–2) SI, skins (AIM, NMNZ): (1) Adults; (2) Juveniles and first immatures. (3) SI, adults, skins (Fleming 1939). (4) SI,

	MALES	FEMALES	
WING	(9) 69.4 (1.91; 66–73; 34)	67.0 (1.16; 65–70; 21)	**
	(10) 69, 70, 73	67	
	(11) 69.2 (2.12; 65–73; 38)	66.8 (1.4; 65–69; 10)	**
WING U	(12) 66.1 (1.77; 63–69; 7)	63.8 (0.84; 63–65; 5)	*
	(13) 69.3 (2.02; 65–73; 53)	65.6 (2.00; 61–70; 33)	**
TAIL	(9) 51.2 (2.00; 47–55; 33)	49.6 (1.79; 46–53; 20)	**
	(10) 51, 53, 56	52	
	(11) 52.1 (1.86; 47–55; 38)	51.1 (1.74; 47–53; 10)	ns
	(12) 50.4 (2.44; 47–54; 7)	48, 49, 49	
	(13) 51.4 (1.93; 46–54; 30)	50.0 (1.55; 46–54; 25)	**
BILL S	(9) 13.4 (0.41; 12.4–14.3; 34)	13.1 (0.37; 12.6–13.7; 20)	*
	(10) 12.8, 12.9, 13.4	13.6	
BILL N	(12) 7.1 (0.21; 6.9–7.5; 7)	7.0, 7.2, 7.4	
BILL F	(13) 9.3 (0.82; 8–12; 31)	9.1 (0.75; 7–10.5; 25)	ns
TARSUS	(9) 21.0 (0.60; 19.4–22.3; 33)	20.9 (0.65; 19.6–21.8; 20)	ns
	(10) 20.4, 23.1	20.3	
	(11) 21.8 (1.75; 20–23; 38)	21.6 (1.25; 21–22; 10)	ns
	(13) 21.5 (0.52; 21–22; 16)	21.1 (0.70; 20–22; 17)	*
TARSUS B	(12) 21.7 (0.45; 21.0–22.4; 7)	21.8 (0.59; 20.9–22.4; 5)	ns
TOEC	(13) 17.5 (1.36; 15–20; 31)	17.0 (1.15; 15–19; 25)	ns

SUBSPECIES CHATHAMENSIS, Chatham Is: (14–15) skins (AIM, NMNZ): (14) Adults; (15) Juveniles. (16) Adults, skins (Fleming 1939). (17) Adults, skins (Fleming 1950).

	MALES	FEMALES	
WING	(14) 74.8 (2.09; 70–77; 13)	73.4 (2.88; 69–78; 9)	ns
	(15) 70, 72	–	
	(16) 77 (74–85; 13)	74 (72–76; 6)	
	(17) 76.1 (1.08; 74–78; 12)	73.3 (1.59; 71–76; 15)	**
TAIL	(14) 55.6 (2.44; 50–59; 14)	54.8 (1.56; 52–57; 9)	ns
	(15) 52, 57	–	
	(16) 56 (53–60; 13)	56 (55–57; 6)	
	(17) 57.3 (1.72; 54–60; 12)	56.5 (1.57; 54–60; 15)	ns
BILL S	(14) 14.2 (0.56; 13.3–15.1; 13)	13.4 (0.79; 12.3–14.8; 9)	*
	(15) 13.7, 13.9	–	
BILL F	(16) 10.8 (10–12; 13)	9.8 (9.5–10; 6)	
TARSUS	(14) 24.5 (1.14; 21.4–25.6; 14)	24.5 (0.65; 23.7–25.5; 9)	ns
	(15) 23.3, 24.5	–	
	(16) 25.5 (23–28; 13)	23.7 (22.5–25; 6)	
	(17) 25.8 (1.07; 23–27; 12)	25.3 (0.76; 24–26; 15)	ns
TOEC	(16) 18.5 (17–22; 13)	17.7 (16–19; 6)	

SUBSPECIES DANNEFAERDI: (18–19) Snares Is, skins (AIM, NMNZ): (18) Adults; (19) Juveniles and first immatures.

	MALES	FEMALES	
WING	(18) 81.3 (1.89; 79–84; 7)	79.4 (2.07; 76–81; 5)	ns
	(19) 76	75	
TAIL	(18) 62.4 (2.82; 59–67; 7)	64.2 (0.84; 63–65; 5)	ns
	(19) 60	60	
BILL S	(18) 15.5 (0.49; 14.6–16.2; 7)	15.8 (0.46; 15.3–16.4; 5)	ns
	(19) 16.0	14.6	
TARSUS	(18) 24.9 (0.64; 23.9–26.0; 7)	25.1 (0.49; 24.5–25.7; 5)	ns
	(19) 24.2, 24.3	24.1, 25.4	

Snares Is, unsexed: (20) Adults, skins (AIM, NMNZ). (21) Adults, skins (Fleming 1950).

	UNSEXED	
WING	(20) 79.5 (2.79; 76–84; 13)	
	(21) 78.9 (2.15; 76–82; 18)	
TAIL	(20) 60.5 (2.44; 57–65; 13)	

	(21) 61.6 (2.59; 58–66; 18)	
BILL S	(20) 15.6 (0.62; 14.8–16.6; 9)	
TARSUS	(20) 24.7 (0.57; 23.9–26.0; 12)	
	(21) 25.5 (1.87; 25–26; 18)	

SUBSPECIES MARRINERI: Auckland Is: (22–23) Skins (AIM, NMNZ): (22) Adults; (23) Juveniles and immatures. (24) Adults, skins (Fleming 1950).

	MALES	FEMALES	
WING	(22) 79.4 (1.24; 78–82; 9)	76.4 (0.89; 75–77; 5)	**
	(23) 77, 77, 81	–	
	(24) 77.7 (1.72; 75–81; 9)	76 (1.15; 74–77; 7)	*
TAIL	(22) 61.4 (2.35; 59–67; 9)	58.6 (2.30; 56–61; 5)	*
	(23) 56, 59, 61	–	
	(24) 61.8 (1.32; 60–64; 9)	59.7 (1.11; 58–61; 7)	**
BILL S	(22) 14.2 (0.52; 13.4–14.9; 8)	14.0 (0.58; 13.0–14.4; 5)	ns
	(23) 14.0, 14.1	–	
TARSUS	(22) 24.2 (0.62; 22.9–25.0; 8)	23.8 (0.56; 23.1–24.3; 5)	ns
	(23) 24.1 (0.58; 23.5–24.6; 4)	–	
	(24) 25.6 (0.69; 24.5–26.5; 9)	25 (0.81; 24–26; 25)	*

WEIGHTS NOMINATE MACROCEPHALA: (1) SI, adults, from museum labels (NMNZ). (2–3) Mt Fitzgerald Scenic Reserve, Banks Pen., SI, live (Kearton 1979): (2) Adults; (3) Juveniles. (4–5) West Coast, SI, live (D.J. Onley): (4) Adults; (5) Juveniles. **SUBSPECIES TOITOI**: (6) NI and larger offshore islands, adults, from museum labels (AIM, NMNZ). (7) Little Barrier I., adults and first immatures, live (Gill & Veitch 1990). (8) Orongorongo Valley, NI, adults, live (Robertson *et al.* 1983). (9) **SUBSPECIES DANNEFAERDI**, Snares Is, adults, from museum labels (NMNZ). (10) **SUBSPECIES MARRINERI**, Auckland Is, adults, from museum labels (NMNZ).

	MALES	FEMALES	
(1)	12.1 (1.20; 10.0–14.5; 12)	11.0, 11.0, 12.0	
(2)	11.2 (0.71; 8)	11.1 (0.59; 12)	ns
(3)	11.9 (2.19; 7)	11.8 (0.45; 5)	ns
(4)	12.0 (0.57; 11.2–13.2; 14)	11.6 (0.38; 11.0–12.0; 11)	*
(5)	11.9 (0.64; 10.7–12.8; 11)	11.1 (0.54; 10.2–12.2; 15)	**
(6)	8.6 (1.61; 6.0–11.0; 8)	9.0	
(7)	9.8 (0.45; 9.3–10.6; 7)	9.3, 9.7, 9.9	
(8)	10.8 (0.95; 9–14; 51)	10.6 (0.91; 9–13.2; 33)	ns
(9)	16.4, 17.7	–	
(10)	–	14.2	

No weights for *chathamensis*. Unsexed adult *toitoi* from Orongorongo Valley, NI, weighed 10.7 g (n=59) (Moed & Fitzgerald 1982).

STRUCTURE Wing moderately long and broad, with rounded tip. Ten primaries: p6 longest, p7 usually equal; p10 30–36 mm shorter, p9 10–14, p8 2–4, p7 0–1, p5 1–2, p4 7–8, p3 10–13, p2 12–16, p1 15–19. P5–p8 slightly emarginated on outer webs; no emarginations on inner webs. Nine secondaries, including three tertials; tips of longest tertials fall short of tips of secondaries on folded wing. Tail moderately long with slightly rounded tip; 12 rectrices. Bill rather short and straight; less than half length of head. Tarsus long and slender; scaling holothecal. Tibia fully feathered. Middle toe with claw 16.4 (1.19; 15.3–18.6; 6). Outer toe 81–89% of middle, inner 71–77%, hindtoe 85–99%.

GEOGRAPHICAL VARIATION Five subspecies recognized (NZCL): *macrocephala*, *toitoi*, *chathamensis*, *dannefaerdi* and *marrineri*. There does not appear to be any geographical variation within each of the subspecies. Recently suggested that three of these (*macrocephala*, *toitoi* and *dannefaeri*) warrant treatment as full species (Holdaway *et al.* 2001). Differences between subspecies characterized as follows.

NOMINATE MACROCEPHALA: Described fully above. Occurs SI and adjacent islands, including Stewart I. Rather small, but not smallest.

SUBSPECIES TOITOI: Occurs NI and adjacent islands. Smallest subspecies; significantly smaller than nominate *macrocephala* in Wing ($P < 0.01$), Tail ($P < 0.01$), Tarsus ($P < 0.01$) and weight ($P < 0.01$ male) (see Measurements, Weights). The following descriptions based on examination of skins of 36 adult males, 21 adult females, one juvenile male and two juvenile females. **Adult male** Very similar to adult male nominate, but lack yellow on underparts. Lower breast, belly, flanks and vent, white; undertail-coverts, black (89) with broad white fringes at tips. Rest as adult male nominate. **Adult female** Very similar to adult female nominate, but lack yellow on underparts. Chin and throat, white with dark-grey (83) bases to feathers. Breast, white, grading to grey-brown (c19) at sides. Belly, vent and flanks, white, often with scattered buff (124) or light-brown (223D) smudges. Undertail-coverts, buff (c124). Rest as adult female nominate. **Juvenile male** Very similar to juvenile male nominate, but lack yellow on underparts. Breast, white with diffuse black-brown (119) tips to feathers. Belly, vent, flanks and undertail-coverts, white. Rest as juvenile male nominate. **Juvenile female** As juvenile female nominate but never with yellowish suffusion to breast.

SUBSPECIES CHATHAMENSIS: Occurs Chatham Is. Intermediate in size, with rather long tarsus and rather short tail; significantly larger than nominate *macrocephala* in Wing ($P < 0.05$) and Tarsus ($P < 0.01$) for both sexes, and males had significantly longer Bill S ($P < 0.01$) (see Measurements). The following descriptions based on examination of skins of 14 adult males, nine adult females and two juvenile males. **Adult male** Similar to adult male nominate but differ slightly in underparts and pattern to tail. Line of demarcation between black of upper breast and pale lower breast higher than in nominate: only upper edge of breast is black; mid- and lower breast and belly, yellow-white (ne), grading to white on vent and flanks; overall paler than in nominate. Some feathers immediately below line of demarcation on breast washed with orange (17) or, in some, pink-red (c10). Undertail-coverts, black (89) with narrow white fringe to tips. Tail similar to nominate but white on t4 does not extend to tip of inner web (see Fig. 2). Rest as adult male nominate. **Adult female** Similar to adult female nominate but with slightly larger frontal spot, and slightly different upperparts, underparts and pattern of tail. Head and neck mostly as adult female nominate but have black (89) line above large frontal spot, and in some, feathers of lores, ear-coverts and sides of throat, suffused with black (89), giving dark-faced appearance; in one skin, most of chin and throat was suffused with black (89). Upperparts slightly warmer in tone than in nominate, dark brown (c121A). Breast, belly, flanks and vent, off-white (ne) to cream (c92); lack buff or light-brown smudging. Undertail-coverts, light brown (c223D). Tail similar to that of nominate, but white on t4 does not extend to tip of inner web (see Fig. 2). Rest as adult female *macrocephala*. **Juvenile male** Two specimens labelled

as males had similar appearance to adult female, but with off-white shafts to feathers of top of head and upperparts. Pale shafts not as obvious as in juvenile nominate. Fleming (1950) described juvenile males slightly differently: Small white frontal spot. Top of head and upperparts, dull brownish-black with light-brown shafts, most conspicuous on crown and scapulars, and faint ochraceous-buff tips to feathers, most conspicuous on rump and uppertail-coverts. Throat, grey-brown, mottled with white. Breast, belly, flanks, vent and undertail-coverts, white. Wing and tail as adult male. **Juvenile female** No specimens. The following based on description from Fleming (1950). Similar to adult female, but differing by: Upperparts slightly paler, with light ochraceous-buff shafts to feathers. Central wing-bar slightly more buff. Throat, white peppered with brown. Breast, belly, flanks and vent, white with light-buff wash, and greyish-brown flecking to breast and flanks. Thighs and undertail-coverts, pinkish buff.

SUBSPECIES MARRINERI: Occurs on Auckland Is. Rather large subspecies; significantly larger than nominate *macrocephala* in Wing ($P < 0.01$) and Tail ($P < 0.01$) for both sexes, and Bill S ($P < 0.05$) and Tarsus ($P < 0.01$) for males. The following descriptions based on examination of skins of nine adult males, five adult females and three juvenile males; no juvenile females examined. **Adult male** Similar to adult male nominate but differs slightly in underparts and pattern of tail. Lower breast and belly, yellow-white (ne) grading to off-white (ne) on flanks and vent; much paler than in nominate. Feathers of lower flanks also have narrow black (89) fringes to tips, giving slightly mottled appearance. Undertail-coverts, black (89) with narrow white fringe to tips. Pattern of tail varies; often have large oblique white spot near tip of t3 (see Fig. 2), but sometimes have tail as in nominate, and sometimes as in *chathamensis*. Rest as adult male nominate. **Adult female** Degree of sexual dimorphism much less marked than in nominate. Some very difficult to separate from adult male, but usually have slightly browner upperparts and paler, less yellow, underparts, and often lack narrow black fringes to tips of feathers on lower flanks. Demarcation between dark upper breast and pale lower breast usually also smudgy and less sharply defined, and some have greyish (ne) suffusion to throat and upper breast. Tail as adult male. **Juvenile male** As juvenile male nominate but usually have finer black (89) fringes to tips of feathers of breast, and tail as adult male *marrineri*. **Juvenile female** None examined. Probably similar to juvenile male.

SUBSPECIES DANNEFAERDI: Occurs on Snares Is. Largest subspecies; significantly larger than nominate *macrocephala* in Wing ($P < 0.01$), Tail ($P < 0.01$), Bill S ($P < 0.01$) and Tarsus ($P < 0.01$) for both sexes (see Measurements). The following descriptions based on examination of skins of seven adult males, five adult females, 13 unsexed adults, two juvenile males and two juvenile females. This subspecies is melanistic and lacks sexual dimorphism. **Adult** Wholly black (89) with concealed grey-black (82) bases and concealed pale-grey (86) shafts to bases of feathers of head, neck, upperparts and underparts. Remiges fade to black-brown (c119) with wear. **Juvenile** As adult but slightly browner and with fine pale streaking. Feathers of head and neck, upperparts and underparts, black-brown (119) with off-white (ne) shafts to feathers, giving finely streaked appearance; feathers of lower belly, vent and thighs often also have diffuse light-brown (c223D) tips, resulting in slightly paler lower underbody. Tail as adult. Wing, black-brown (c119).

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Volume 6, Plate 18

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