Order PASSERIFORMES

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

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

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

The Passeriformes divide into two main groups:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Arrangement of genera and species within families also follows Christidis & Boles (1994), which was in turn largely based on Schodde (1975) unless there were specific reasons for change. Lastly, with few exceptions, which are discussed in individual species accounts, 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 widepread, and of two distinct types: (1) lateral posture, in which sunning bird squats or sits down, usually on ground, and leans to one side exposing the flank or the 'sun-wing', which has been lowered and partly unfolded, and the fanned tail, which has been brought round to the same side; and (2) spread-eagle posture, in which bird squats or lies flat with both wings open and tail fanned (details in Campbell & Lack 1985; Simmons 1986).

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

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

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

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

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

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Family MELIPHAGIDAE   honeyeaters and Australian chats

Mostly green through olive to brown in colour, though some are black, black-and-white, or red-and-black. Range in size from tiny to medium-large (total length 9–48 cm). In total, *c*. 182 species in *c*. 42 genera (Sibley & Ahlquist 1990; Sibley & Monroe 1990). Endemic to the sw. Pacific: primarily an A'asian family, with centre of diversity in Aust. and New Guinea, but spreading as far E as Hawaii, and W through Wallacea, with a single species occurring in Bali. Largest passerine family in Aust., with 73 species in 23 genera, including elevation of Western Wattlebird *Anthochaera lunulata* to species status (Christidis & Boles 1994; DAB); three species occur in NZ, all in monospecific genera (NZCL).

Sibley & Ahlquist (1985) showed unequivocally that the Meliphagidae belong to the corvoid adaptive radiation in Aust. The family is closely related to the Pardalotidae, Maluridae and Petroicidae. Other nectar-feeding passerines, such as the sunbirds and flowerpeckers (Nectariniidae) and Hawaiian honeycreepers (Drepanidini) are not closely related to honeyeaters.

Evidence from studies of egg-white proteins (Sibley 1976) and molecular and biochemical studies (Sibley & Ahlquist 1985, 1990; Christidis & Schodde 1991; Christidis *et al*. 1993) confirmed that the Aust. chats (*Epthianura* and *Ashbyia*, formerly Epthianuridae) are honeyeaters, as suggested by Parker (1973) on the basis of morphology, noticeably their brush-tongues. *Cleptornis* (Bonin Island 'Honeyeater') is a white-eye (Zosteropidae) (Sibley & Ahlquist 1990) and *Promerops* (Cape Sugar Bird) is not a honeyeater. Furthermore, Christidis *et al*. (1993) established that *Oedistoma* and *Toxorhamphus* of New Guinea are flowerpeckers, whereas *Timeliopsis* is a honeyeater. A few genera whose DNA has not been examined are perhaps questionably honeyeaters, such as *Notiomystis* (Stitchbird *N. cincta*) in NZ and the Hawaiian genera (*Moho* and *Chaetoptila*).

Most remarkably, Macgregor's 'Bird of Paradise' *Macgregoria pulchra* was found to be a honeyeater on the ground of base sequence of mitochondrial DNA (Cracraft & Feinstein 2000). It is close to the New Guinea genus *Melipotes*, with which it shares a number of morphological characters, including a large yellow facial patch or wattle.

The relationships of genera within the Meliphagidae are poorly understood, though some are closely related, e.g. *Lichenostomus* and *Meliphaga* (DAB, which see for further suggested relationships). A few genera are rich in species: *Lichenostomus* has 20 species, mostly in Aust.; and the similar *Meliphaga*, whose centre is New Guinea, has 13 species. *Myzomela* contains many sibling species or several superspecies and is geographically the most widespread genus, occurring from Sulawesi in the W to Micronesia in the N and Fiji in the E. *Melidectes* is a species-rich genus in New Guinea, with strong differentiation of some subspecies on isolated mountain ranges and hybridization between other taxa (Mayr & Gilliard 1952). *Philemon* and *Lichmera* have radiated in Wallacea (Coates *et al*. 1997), though both occur in Aust. and New Caledonia.

There are also several monospecific genera. In some cases their relationships appear obvious and the species have at times been placed in other genera, e.g. *Acanthagenys* in *Anthochaera*. In other cases their relationships are unclear, e.g. *Stresemannia*, *Guadalcanaria*, *Plectrorhyncha* and *Prosthemadera*.

Most honeyeaters are slim-bodied, though a few are solid-looking (e.g. *Meliphaga*) or even dumpy (*Notiomystis*). Almost all species have slightly to markedly decurved bills, short in some genera (*Pycnopygia*, *Melipotes*, *Conopophila*), longer in others (*Myzomela*, *Phylidonyris*) and long in *Acanthorhynchus* and *Melilestes*. *Plectrorhyncha* has a straight dagger-shaped bill. One key characteristic of honeyeaters is the brush-tongue. Salomonsen (1964) describes it as 'prolonged and protrusible; the basal part is curled on either side, forming two long grooves; the distal part is deeply cleft into four parts, which on their edges are delicately frayed and together form the "brush" which licks up nectar.' The length of the brush and number of bristles vary among species. When feeding, the tongue is rapidly extruded and withdrawn, and nectar and other liquids are drawn into the brush by capillary action (Paton & Ford 1977). As the bill closes with the tongue withdrawn, a process inside the upper mandible apparently compresses the brush, forcing any liquid into the groove down the throat. Honeyeaters are also characterized by: Temporal fossa usually small and flanked by zygomatic process that is often slenderly prolonged and longer than postorbital. Nares fully perforate. Palate slender and attenuately streamlined with characteristic structure (see DAB). Nasal bars thickened with one or two distinctive foramina. Ectethmoid plate broadly winged and thickened. Wing with ten primaries and ten secondaries; p10 often reduced, and outermost secondary vestigial. Tail with 12 rectrices. Head of humerus with basically single deep trabeculated fossa; sometimes (e.g. *Conopophila*) develop depression in same position as second fossa of other bird families. Feet stong with scutellate, bilaminiplantar tarsi. The Aust. chats (Epthianurinae) differ from the honeyeaters

(Melaphaginae) by: smaller ectethmoid foramen; slender stems to palatines; nasal bars narrow and imperforate; ectethmoids rather thin; and maxillo-palatine processes flimsy and terete.

Many honeyeaters are greenish, olive or brown, often with some yellow, frequently as plumes or patches on sides of face (particularly on ear-coverts) or sides of neck (e.g. *Lichenostomus*, *Meliphaga*, *Lichmera*). In *Melithreptus*, the head is black or dark brown with a characteristic transverse white stripe across the nape in most species. Many species have an olive or yellow wash or edges to varying number of primaries or secondaries or both, and similar wash or edges to tail-feathers, and which form conspicuous olive to yellow panels on folded wings and tails and which are a strong feature in some *Phylidonyris* and *Grantiella*. Members of a few genera are heavily streaked (*Anthochaera*) or scaly (some *Xanthotis* and *Melidectes*). The large *Gymnomyza* of the Pacific Islands are sooty or greenish black. *Moho* is also black, but with brilliant yellow plumes, which were made into headdresses for Hawaiian royalty (Lepson 1998). Feathers are sometimes long and filamentous, giving a bearded effect (New Holland Honeyeater *Phylidonyris novaehollandiae*, some *Melidectes*). Modification of feathers has been taken to extremes in the Tui *Prosthemadera novaeseelandiae*, which has glossy black plumage with curled white feathers on either side of the breast.

The sexes tend to be monochromatic, though some are strikingly dichromatic. Males of many of the *Myzomela* (and occasionally females) show some brilliant red, whereas females are dull. Spinebills *Acanthorhynchus* and chats *Epthianura* are also sexually dimorphic. Probably males of all species are larger than females, though differences are often slight, with a few exceptions (e.g. Crescent Honeyeater *Phylidonyris pyrrhoptera*, Oahu Oo *Moho apicalis*).

Almost all honeyeaters display coloured bare skin. This may be modest, as in the swollen or extended gape-stripes or lines, eye-rings or eye-patches (e.g. in *Melithreptus*, *Lichenostomus* and *Lichmera*). Large colourful bare facial patches are shown in *Manorina* (yellow), *Melipotes* (yellow to red), *Melidectes* (blue to green) and *Entomyzon* (blue). The friarbirds *Philemon* have mostly bare black heads, often with a prominent knob or casque at the base of the bill. Two species of *Anthochaera* have red or yellow wattles hanging from the sides of their necks. The most adorned species are found in *Melidectes*, which may have bare facial skin and up to three wattles, of contrasting colours. Bills (*Manorina*, *Acanthagenys*) and legs may also be colourful. In a few species the iris is coloured or contrasts with the pupil. The function of most of these characters has not been studied, but they are presumably involved in communication, as the colour or its intensity may change with age (e.g. from green to blue in *Entomyzon*), breeding condition or even with level of excitement (e.g. *Melipotes*).

Adults of most species undergo a single complete post-breeding (pre-basic) moult annually, usually after completion of breeding, and typically from about Oct. to Mar. Some species have two moults annually: e.g. adult Banded Honeyeaters *Certhionyx pectoralis* known to have partial pre-breeding (pre-alternate) and complete post-breeding (pre-basic) moults each cycle, producing alternating breeding and non-breeding plumages. Primaries moult outward (ascendantly, from p1 to p10). Rectrices are moulted centrifugally (from the centre outward).

Nestling honeyeaters hatch blind and naked or almost so, but soon develop light down, with quills appearing after a few days and feathers erupting by about Day 7. Young fledge in complete or almost complete juvenile plumage. In most species the juvenile plumage is like that of the adult, though it is softer (particularly on upperbody and underbody) or duller or both. A few species (e.g. Tawny-crowned Honeyeater *Phylidonyris melanops*) have distinctive juvenile plumages, whereas in the sexually dimorphic species (e.g. Pied Honeyeater *Certhionyx variegatus*), juveniles resemble adult females. Sequence of moults and plumages before attaining adult plumage poorly known in many species. Most species typically undergo a partial post-juvenile (first pre-basic) moult soon after fledging, resulting in a first immature plumage that is often little different from adult plumage, and frequently distinguished only by retained juvenile remiges, rectrices or some wing-coverts; first immatures often not distinguishable in the field. Adult plumage then usually attained in complete first immature (second pre-basic) moult when *c*. 1 year old and that occurs slightly later than adult pre-basic moult.

Bare parts may also differ between juveniles, immatures and adults, with conspicuous yellow or cream, and swollen and fleshy, gapes being common in young birds.

Honeyeaters occupy virtually every habitat in the A'asian region. Several species are characteristic of mangroves (e.g. Mangrove *Lichenostomus fasciogularis* and Red-headed *Myzomela erythrocephala* Honeyeaters). Coconut trees lining beaches may be occupied by White-tufted Honeyeater *Lichmera squamata* in Wallacea (Coates *et al.* 1997). Rainforests in New Guinea and sclerophyll forests, woodlands and heaths in Aust. may have ten or more resident species or regular visitors. In New Guinea, *Melidectes* ventures above the tree-line into subalpine shrubs as far as 4500 m asl (Beehler *et al.* 1986), though no honeyeaters appear to be found regularly in the alpine zones of Aust. or NZ, and altitudinal migration from high country of se. Aust. reported for a number of species (e.g. White-eared Honeyeater *Lichenostomus leucotis*). Semi-arid woodland and shrubland may also be rich in species, with parts of central Aust. regionally abundant as many different habitats are juxtaposed. The chats are particularly prevalent in shrub-steppe, with *Ashbyia* found in desolate gibber plains. No honeyeaters are found regularly in grasslands.

Honeyeaters have been especially successful in colonizing artificial habitats, such as parks and gardens in towns and cities. The White-plumed Honeyeater *Lichenostomus penicillatus* has become a common urban bird in se. Aust., and the larger honeyeaters (wattlebirds *Anthochaera*, Blue-faced Honeyeater *Entomyzon cyanotis*) also do well in

streets planted with native trees and shrubs. Noisy Miner *Manorina melanocephala* have spread through degraded woodland in agricultural regions.

Although most honeyeaters are arboreal, the chats forage and nest on or near the ground. A variety of honeyeaters occupy shrubs, such as Singing Honeyeater *Lichenostomus virescens*, *Acanthagenys* in inland Aust. and *Phylidonyris* in heathland. The genus *Lichenostomus* is especially associated with *Eucalyptus*, as trees or in mallee form.

Almost all honeyeaters are to some degree mobile (Keast 1968). Although many are basically sedentary or resident (many *Meliphaga*, *Lichenostomus*, *Manorina*) they still show local movement, as well as displaying fluctuations in abundance, which indicate movement on some scale. There is probably a tendency for movements to be greater and more erratic in arid than wetter habitats. To some degree this may reflect the fact that most Australians live near the coast. They see irruptions of species such as Crimson Chats *Epthianura tricolor* and Black Honeyeaters *Certhionyx niger* coastward from the inland, whereas incursions of coastal species towards the centre would be overlooked. For instance, the forest-dwelling Scarlet Honeyeater *Myzomela sanguinolenta* may move just as much as Black Honeyeaters. A few species are regular migrants, the best known being Yellow-faced *Lichenostomus chrysops* and White-naped *Melithreptus lunatus* Honeyeaters, which migrate from se. to central-e. Aust. However, even these species may be seen year-round at many localities and resident and migratory sub-populations probably intermingle.

Much movement is associated with flowering patterns of major food plants, such as eucalypts, coastal banksias or arid-zone emu-bush *Eremophila*. In some areas or regions, flowering is a regular event and movements to exploit these events result in regular seasonal movements, for instance the movement in winter to the N of the Great Divide in Vic. to feed on nectar of ironbarks (McGoldrick & Mac Nally 1998). In other cases flowering is irregular, which may lead to erratic influxes of honeyeaters. More curious are cases of intensive flowering that are virtually ignored by honeyeaters. We have barely begun to understand the complex movements of species such as Regent Honeyeaters *Xanthomyza phrygia*. Yellow-faced Honeyeaters show the fixed orientation tendency, NE in early autumn and NW in late autumn and southerly in spring, that is found in true migrants (Munro *et al.* 1993). Curiously, Regent Honeyeaters also show some innate directional tendency to orientate. Many honeyeaters migrate at level of tree-tops during the day, when they may be very conspicuous. Perhaps this behaviour involves an element of searching for resources, as well as a programmed migratory tendency.

Probably all honeyeaters consume some nectar: some depend on it as their main source of energy, others take it when it is abundant locally. Likewise, probably all take some arthropods, often small flying insects captured in the air by sallying, but also insects and spiders gleaned from foliage. A few species, notably Strong-billed Honeyeater *Melithreptus validirostris* and White-eared Honeyeater, probe into and beneath bark for insects and other foods. The former has evolved a strong bill to forage in this way in Tas., a region without treecreepers *Climacteris*. Whereas many species occasionally take fruit, this is a major food source in rainforests (especially for *Meliphaga* in New Guinea), and for a few species (Singing Honeyeater *Lichenostomus virescens* and Spiny-cheeked Honeyeater *Acanthagenys rufogularis*) in arid shrublands. The NZ species also consume fruit (Craig *et al.* 1981; see species accounts). Painted Honeyeater *Grantiella picta* is highly specialized to feed on mistletoe berries. A food source neglected by many observers until quite recently consists of other carbohydrate foods, including: manna, an exudate from eucalypt foliage; lerp, the sugary coating over the nymphs of some psyllids; and honeydew, excretions produced by psyllid and coccid hemipterans (Paton 1980). Sometimes sap from injuries caused by gliders (Petauridae) is eaten.

Unusual foods include crustaceans (Mangrove Honeyeater) and lizards (Wattled Honeyeater *Foulehaio carunculata*). A few honeyeaters also depredate birds' eggs and, occasionally, nestlings (e.g. Noisy Friarbird *Philemon corniculatus*, Red Wattlebird *Anthochaera carunculata*).

Honeyeaters are active and agile while foraging, often stretching or hanging upside-down to reach flowers or insects. They have strong legs and sharp claws. The smaller honeyeaters (*Acanthorhynchus*, *Myzomela*) occasionally hover at flowers, though this is energetically more demanding than perching and probably only used where flowers are inaccessible from a perch. There is a tendency for bills to be longer and more decurved in the more nectarivorous genera, though correspondence of shape of bills and flowers is loose and generalized. The brush-tongue is the most obvious adaptation for nectar feeding, though honeyeaters have rather simple digestive systems compared with more strictly insectivorous passerines. Honeyeaters sometimes defend foraging and breeding territories from conspecifics and other honeyeaters. Such territories may consist of a few flowering trees or shrubs or even part of a flowering tree. Intruders may be driven considerable distances from the territory.

Honeyeaters are very important pollinators of native plants in Aust. and NZ, and probably elsewhere (Armstrong 1979; Godley 1979; Ford & Paton 1986). Many species of the plant families Myrtaceae, Proteaceae and Epacridaceae are pollinated by birds. Bird flowers are usually red, yellow or white, though some are cryptically coloured. They are open and cup-shaped, tubular or gullet-shaped, with inflorescences often being presented as a large brush; for details of shapes of flowers used by different species of honeyeater in Wet–Dry Tropics of NT, see Franklin & Noske (In press). Honeyeaters too may be seed dispersers, and are both pollinators and seed dispersers of some of the mistletoes (Loranthaceae).

Honeyeaters may be solitary, especially when holding feeding territories. Mostly they breed as pairs, though these may be loosely associated in dispersed colonies. Several species are facultatively co-operative in the breeding season (e.g. *Melithreptus*, some *Lichenostomus*), whereas a few are obligate co-operative breeders. The miners *Manorina* live in large, dense colonies, from which other honeyeaters and other insectivorous birds are aggressively excluded; females defend the nesting sites, whereas males roam more widely and contribute to feeding young at many different nests. There have, however, been few studies of territoriality in the Meliphagidae; see Pyke *et al.* (1996) for review of territoriality in honeyeaters.

It is likely that most species are socially monogamous, though Noisy Miners appears to be promiscuous (McFarland & Ford 1991). Females of Crescent Honeyeaters may wander into neighbouring territories, and males make only a modest contribution to parental behaviour, suggesting that some extra-pair copulations may occur (Clarke & Clarke 1999). The few species whose breeding system has been examined genetically (including Noisy Miner) are monogamous. The Stitchbird of NZ may be polygynous, polyandrous or polygynandrous (Castro *et al.* 1996); males have exceptionally large testes and cloacal protuberances, and the species indulges in face-to-face copulation (the latter probably forced extra-pair copulation).

Outside the breeding season, many honeyeaters are social, joining loose, wandering flocks. The migratory species, e.g. Yellow-faced Honeyeater, may gather into large flocks. Whereas large numbers of honeyeaters may gather at rich nectar sources, these tend to be loose congregations rather than structured groups. Sometimes occur in mixed-species feeding flocks (e.g. Sage 1994). Allopreening observed in a few species, notably *Melithreptus* (Noske 1983) *contra* claim of Immelmann (1961) that mutual preening does not occur. Little is known about roosting, but Regent Honeyeaters and *Melithreptus* sometimes roost communally (*contra* Immelmann's [1961] general claim that honeyeaters do not tolerate physical contact after fledging).

Almost all observers of honeyeaters have commented on their aggressive and pugnacious nature. Two types of aggression commonly noted: CHASES, in which attacking bird pursues fleeing bird beyond the latter's point of takeoff; and DISPLACEMENTS, in which attacking bird lands on or near the perch vacated by the attacked bird (e.g. McFarland 1986). Flocks at feeding sites are often noisy, with frequent displacements and chases. Occasionally these result in fights where two or more birds fall to the ground with claws locked together. Pursued birds may be pecked, leading to feathers flying and, exceptionally, may be killed (Dow 1978). Conversely, honeyeaters that have been studied closely have been found to be quiet, even shy, especially during the breeding season.

One of the most complex behaviours, shown best in the miners *Manorina* but also in some *Lichenostomus* and *Phylidonyris*, is the CORROBOREE (Dow 1975; see species accounts). A dozen or more birds gather into a tight group with much calling and wing-fluttering. Sometimes one bird, or even a predator, appears to be the focus of the display. Possible functions include defence against predators and conspecific intruders, or even a show of togetherness by members of a group. With a few exceptions (Noisy Miner, New Holland Honeyeater), the displays of honeyeaters have not been methodically studied and described. The frequency of white or coloured feather-tufts and colourful bare skin suggests that honeyeaters use a wide variety of displays for intraspecific communication.

Most honeyeaters have strong and clear calls, and several species have attractive songs (Pizzey 1980). The simplest songs consist of a few whistles (New Holland Honeyeater), whereas more complex twittering phrases are quite common (some *Lichenostomus*). Black-chinned Honeyeater *Melithreptus gularis*, Singing Honeyeater and Spiny-cheeked Honeyeater have rich and varied songs (Immelmann 1961). However, the NZ honeyeaters, Tui *Prosthemadera novaeseelandiae* and Bellbird *Anthornis melanura*, are classed among the world's best songsters (Hartshorne 1973), on the basis of their pureness of tone and complexity. In contrast, some honeyeaters have harsh (wattlebirds *Anthochaera*) or even rather comical (friarbirds *Philemon*) calls. Song-flights are quite common (some *Lichenostomus*, Tawny-crowned Honeyeater). Mimicry has been recorded in the songs of a few honeyeaters (e.g. Regent Honeyeater, Stitchbird), though its function is not clear.

Many species have characteristic flight calls, especially those that migrate (e.g. White-naped Honeyeater). Probably all give alarm calls, with at least New Holland Honeyeater apparently having separate alarm calls for aerial and terrestrial predators. Such alarm calls often draw other honeyeaters towards the caller, which may lead to mobbing of the predator or corroborees or both. Whereas nestlings and juveniles tend to give distress calls when handled, adult honeyeaters are usually silent when captured. Nestlings and recently fledged juveniles also beg, typically using a simple whistling or piping call.

Most Aust. honeyeaters have long breeding seasons, with different species having peaks of breeding activity in late winter, spring or early summer. The NZ honeyeaters, and a few Aust. species (e.g. Noisy Friarbird) are more seasonal. In most cases honeyeaters make many attempts at breeding in a season, even after successfully raising young. Nests are cup-shaped, occasionally oval with a side entrance, and placed in a fork of branches or suspended from foliage or twigs. *Notiomystis* and at least one species of *Moho* are exceptional among honeyeaters in nesting in tree-cavities. Blue-faced Honeyeaters usually choose nests of other species, especially Grey-crowned Babblers *Pomatostomus temporalis*. Nests are made of twigs, grass, creepers, bark, fern, vines, often bound with spider web, and lined with plant down and animal hair, including wool. Hair is sometimes plucked from live animals, including Koalas *Phascolarctos cinereus* and people.

Honeyeater eggs range from white, through cream, buff, salmon to pink, and may be finely spotted to heavily blotched with light to dark lilac, red, purple, chestnut or black, typically more heavily at the blunt end. The most frequent clutch-size is two eggs in most species, though clutches of three or four are common in *Philemon* and *Manorina*. Two females are suspected of laying in the larger clutches of Blue-faced Honeyeater. Laying intervals are 24 h in a few well-studied species. Incubation periods range from 12 to 17 days, and fledging period from 11 to 20 days, occasionally longer (Ford & Trémont 2000). In most species, nest-building, incubation and brooding of nestlings is carried out primarily or exclusively by the female, though occasionally the male and even auxiliaries may participate. Both parents, and in a number of species, helpers, feed the young and guard the young from predators. Evidence from a few species indicate that young birds become independent from 26 to 42 days after fledging. However, this is a progressive process, with young starting to feed themselves in about half of this time. Breeding success, in well-studied species in Aust., ranges from 5.6% to 69.6% of nests. The highest value is for Rufous-banded Honeyeater *Conopophila albogularis* in a tropical urban environment, the lowest value is for Noisy Miner. Nest predators include Cats, snakes, currawongs *Strepera*, butcherbirds *Cracticus* and other birds. Nestlings may be attacked by green tree-ants *Oecophylla*, and by larval bot-flies *Passeromyia*. Honeyeater nests may be parasitized by a range of cuckoos (see species accounts, and *HANZAB* 4). Infanticide and egg-destruction of other species has been occasionally recorded (Dow 1975).

Some honeyeaters have coped well with the impact of European settlement in Aust. Several species (White-plumed, Rufous-banded, and Brown *Lichmera indistincta* Honeyeaters) are among the commonest native suburban birds. Noisy Miners have become common in fragmented and degraded woodlands in agricultural regions in se. Aust. Perhaps most species in Aust., though, have declined in abundance as their forest, woodland or heathland habitat has been cleared. There have been local extinctions or substantial declines of remnant populations (e.g. Yellow-plumed Honeyeater *Lichenostomus ornatus* in the WA Wheatbelt, Black-chinned Honeyeater in the Mt Lofty Ras of SA). A major effort has been made to save the last population of the distinctive subspecies *cassidix* of Yellow-tufted Honeyeater *Lichenostomus melanops* in Vic., which declined as most of its habitat was lost; it also suffers from competition with Bell Miner *Manorina melanophrys*. In mallee of se. Aust. the Black-eared Miner *Manorina melanotis* has almost disappeared as a species through hybridization with Yellow-throated Miner M. *flavigularis*, which has been favoured by clearing, fragmentation and opening up of the mallee. One of the most difficult species to conserve is the Regent Honeyeater, which is now classed as endangered. It is highly mobile, visiting a wide range of nectar and other food sources over a large area. The details of its movements, and the habitats it may depend on, are poorly known. Several other wide-ranging species of arid and semi-arid regions are considered rare or even threatened, though this may be partly a result of our lack of knowledge.

Island species of honeyeaters are often restricted to small ranges and are uncommon. In NZ, the Stitchbird was reduced to a single population on Little Barrier I., as a result of nest-predation by introduced mammals. It has since been translocated to several other islands (Castro *et al.* 1994), although its long-term future there may depend on ongoing management, such as provision of nest-boxes and feeders. Many of the honeyeaters in Wallacea are endemic to only one island (e.g. on Buru, Seram, Wetar). Their status is poorly known, despite a number of recent expeditions, and they are vulnerable to the clearing of forest, which is happening throughout Indonesia (Collar *et al.* 1994). The large forest-dwelling *Gymnomyza* honeyeaters appear to be declining in New Caledonia and Samoa, if not on Fiji (Collar *et al.* 1994). The most disastrous situation, however, exists on the Hawaiian Is. Three species (*Chaetoptila*, two species of *Moho*) are extinct, the survival of Kauai Oo M. *braccatus* on Kauai seems doubtful, and the exact status of Bishop's Oo M. *bishopi* on Maui is not known, though it apparently still exists. They probably declined from forest clearance, introduced mammalian predators and, finally, avian malaria, which has decimated the honeycreepers of Hawaii (van Riper *et al.* 1986).

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Anthornis melanura **Bellbird**
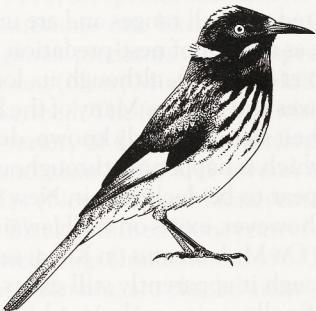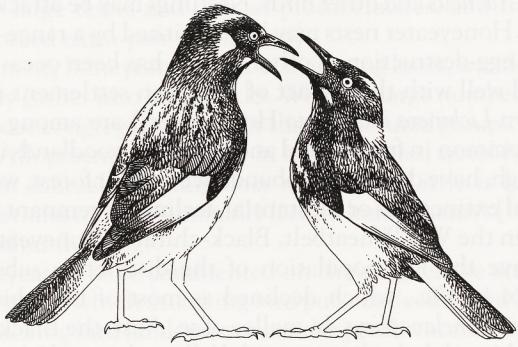
Certhia melanura Sparrman, 1786, *Mus. Carlsonianum* 1: n. 5 — Promontoriun Bonae Spei = Queen Charlotte Sound, New Zealand.

This replacement generic epithet combines the preoccupied genus name *Anthomiza* (Greek ἄνθος, a flower, and μυζάω, to suck) and Greek ὄρνις, a bird, and refers to the nectar diet of this bird. Because of its curved bill, the Bellbird, named for its liquid bell-like song, was originally described in the genus *Certhia*, and distinguished from other 'treecreepers' by its black tail (Greek μελανουρος, black-tailed).

OTHER ENGLISH NAMES Chatham Island or Three Kings Bellbird; Mocker, Mockie or Mockiemock.

POLYTYPIC Nominate *melanura*, NI, SI and Stewart I., NZ, and many offshore islands, including Auckland Grp; *melanocephala*, G.R. Gray, 1843, Chatham Is, NZ (extinct); *obscura*, Falla, 1948, Three Kings Is, NZ; *oneho*, Bartle & Sagar, 1987, Poor Knights Is, NZ.

FIELD IDENTIFICATION Length 17–20 cm; wingspan *c.* 22 cm; weight: male 32.5 g, female 25 g. Medium-sized NZ honeyeater with short slightly decurved bill; low sloping forehead; and strong legs and feet. Shape of rather long tail distinctive, especially in adult male: rather narrow at base, and flared and deeply notched at tip. Much smaller than Tui *Prosthemadera novaeseelandiae*; slightly smaller, slimmer but longer tailed than Stitchbird *Notiomystis cincta*. Sexes differ in

plumage at all ages. No seasonal variation. Adult male largely dark olive-green, with iridescent purple sheen to head, contrasting bluish black wings and tail, prominent pale yellow tuft of feathers on fore-flanks, and pale vent and undertail-coverts. Adult female duller than male: plain olive-brown with little contrast between head, wings, tail and body (with only weak bluish sheen on head), and with short white moustachial stripe. Both sexes of adult have red iris. Juveniles separable: both sexes duller than adult female, with no iridescence on head, and with pale-yellowish moustachial stripe, and brown iris; juvenile male has blacker wings and tail than juvenile female. Slight geographical variation, mainly in colour of iridescence of head, and size. **Adult male** Head and neck, dark olive-green with iridescent purple to violet-blue sheen, strongest on forehead and ear-coverts. Upperbody, olive-green, slightly brighter on rump. Uppertail, black-brown with narrow iridescent blue-black edge to outer webs of all but outer feathers. Upperwing: coverts largely dark olive-green, with blackish inner webs to greater coverts; and remiges, blackish with varying iridescent blue sheen; folded wing appears concolorous with mantle and scapulars, with strongly contrasting blackish remiges with iridescent bluish sheen in fresh plumage. Underbody, dark olive-green grading to paler olive on lower belly and rear flanks and with prominent patch of pale-yellow feathers on fore-flanks, often covering angle of folded wing; vent and undertail-coverts, pale yellow to off-white; and thighs, grey. Undertail mostly black-brown. Underwing mainly grey, with dark-olive leading edge to primary coverts, pale-yellow wash to secondary coverts, and brown tinge to remiges. Bill, black. Iris, red. Legs and feet, blue-grey. **Adult female** Rather plain, and much browner than adult male. Head and neck, olive-grey to olive-brown with weak blue iridescence, strongest on forehead and crown (but rarely visible in field); and with thin white moustachial stripe. Upperparts, dark olive-brown. Uppertail, dark brown, edged olive on outer webs of all but outer feathers, and with no iridescence. Upperwing: coverts largely dark olive-brown, with dark brown inner webs to greater coverts; and remiges, dark brown with olive outer edges (and no iridescence); folded wing appears concolorous with mantle and scapulars, with contrasting brown remiges. Underparts mostly olive-brown, with patch of very pale yellow feathers on fore-flanks, often covering angle of folded wing, but less prominent than in adult male; and with pale olive to off-white vent and undertail-coverts. Undertail, brownish grey. Underwing much as adult male. Bare parts as adult male. **Juvenile male** Duller and greyer than adult male or female and with little or no iridescence. Head and neck, olive-grey, paler on chin and throat, and with short pale-yellow moustachial stripe. Upperparts, dark grey with olive suffusion. Uppertail, black-brown, like adult male, but with no iridescent bluish edges to feathers. Upperwing similar to that of adult male but most coverts greyer, with less olive, and with little iridescent sheen to remiges. Underbody grades from brownish olive on breast and anterior flanks to greyish olive on belly and lower flanks, with off-white vent and mottled grey-brown and white undertail-coverts; do not have pale-yellowish patch on fore-flanks. Undertail, dark brown. Underwing much as adult male but with cream leading edge and no yellow wash to secondary coverts. Bill, black. Gape, fleshy and yellow for at least 14 days after fledging. Iris, brown. **Juvenile female** Similar to juvenile male but slightly paler and greyer. Differences from juvenile male: head and neck mainly dark olive-brown, greyer olive on ear-coverts; lores duller than in juvenile, brown; upperparts, brown; uppertail and upperwing much as adult female and show little contrast with upperbody; breast, belly and flanks, light grey-brown, and undertail-coverts, buff; undertail and underwing as adult female except for cream leading edge to underwing (as in juvenile male).

Similar species None, and adults should not be confused with other species. Adult females and juveniles sometimes confused with female and juvenile **Stitchbird** but occur together only on a few small islands and Bellbird readily distinguished by: slimmer appearance; longer and distinctively shaped tail that is rarely, if ever, held cocked; rather plain olive-brown upperwings (all plumages of Stitchbird show conspicuous white panel in wing, though it is smaller in juvenile Stitchbird); and short pale moustachial stripe (none in Stitchbird); further, warning *titch* call of Stitchbird is distinctive, uttered often and unlike any Bellbird call. Should not be confused with Silvereye *Zosterops lateralis* which, while sharing predominantly olive-green plumage, is much smaller, with very different shape and habits.

Usually seen singly, or in pairs and family groups during breeding season. Larger numbers occur together at concentrated feeding sources e.g. flowering kowhai *Sophora* in spring and fruiting podocarps in autumn, where they may associate with Tui, Silvereyes and New Zealand Pigeons *Hemiphaga novaeseelandiae*. Active and agile when foraging in trees and bushes; rarely forage on ground or in open. Occasionally catch insects in flight. Flight slightly undulating and sometimes erratic, appearing hesitant over longer distances. Long, flared and notched tail, rather deep belly and small head distinctive features in flight. Whirring noise of wings characteristic, especially in territorial disputes. Generally tame and easily seen, but best way to locate birds in thicker vegetation is by voice, which is similar to, and can be confused with, that of Tui (for further details, see Voice).

HABITAT Occur from coast to high altitudes, up to >1220 m asl; in dense forest, including forest regrowth; also occur in subalpine scrub above tree-line. Common in urban areas, usually near forest remnants.

Mainly occur in mixed podocarp-hardwood forests of lowlands, especially areas with very dense and diverse vegetation (Blackburn 1968; Gravatt 1971; Gill 1983; O'Donnell & Dilks 1994), such as forests of Northern Rata *Metrosideros robusta* with a dense subcanopy and shrub layer of young canopy trees and shrubs, including *Coprosma*, Kawakawa *Macropiper excelsum*, Mapou *Myrsine australis* and *Olearia* (Reed 1976; Norton 1980; Wilson *et al.* 1988; Fitzgerald *et al.* 1989); or forests dominated by Quintinia *Quintinia acutifolia* and Kamahi *Weinmannia racemosa*, with emergent Rimu *Dacrydium cupressinum*, and Kiekie *Freycinetia banksii* in shrub layer (Dawson 1964). Occur in coastal broadleaf forests, such as Pohutukawa *Metrosideros excelsa* forest (Edwards 1955; Kikkawa 1964; CSN 38); and inhabit dense stands of understorey vegetation in broadleaf forests, such as Mountain Ribbonwood *Hoheria glabrata* (Lambert 1970). Also occur in mixed beech forests, such as low forests of Bog Pine *Halocarpus bidwillii*, Yellow-silver Pine *Lepidothamnus intermedius* and Mountain Beech *Nothofagus solandri*; and in open beech forest at high altitudes, usually with diverse and complex understorey (Stead 1932; Dawson & Bull 1975; Guest 1975; Wilkinson & Guest 1977; Dawson *et al.* 1978; Clout & Gaze 1984; Gaze 1984; Wilson *et al.* 1988). Present in small remnants of native forest (Bartle & Sagar 1987). Also found in tea-tree or Leatherwood *Olearia colensoi* scrub; and flax *Phormium* and tall grass such as *Festuca arundinacea* near swamps (Challies 1962, 1966; Lovegrove 1975; Pierce 1980; Oliver; CSN 22, 42). Regularly in urban parks and

gardens, and on golf courses, especially if remnant native bush nearby; occasional records in farmland, including orchards (Stead 1932; Gibson 1961; Baker 1986; Guest & Guest 1987; Oliver; CSN). Sometimes inhabit plantations of eucalypts and acacias; and occasionally in forests of pines *Pinus* or willows *Salix* (Clout & Gaze 1984; Oliver; CSN).

In detailed study, during spring, in lowland forests of w. Paparoa Ra., SI, found mainly in coastal forest dominated by Rimu, Northern Rata, Hinau and Kamahi, with closed canopy, abundant epiphytes and dense shrublayer; also occurred in forest dominated by Red Beech *Nothofagus fusca* and Silver Beech *N. menziesii*; mixed Rimu–Kahikatea *Dacrycarpus dacrydioides*–Red Beech *N. fusca*–Silver Beech forest; mixed open Rimu–Kahikatea–Hard Beech *N. truncata*–Silver Beech forest with sparse canopy; and least often in areas of regenerating forest (Onley 1980).

DISTRIBUTION AND POPULATION Endemic to NZ.

NI FAR NORTH: Resident on Three Kings Is (Turbott & Buddle 1948; Ramsay & Watt 1971; Bartle & Sagar 1987; NZCL). Generally absent on mainland; rare reports on w. coast, e.g. round Hokianga Harbour (e.g. NZ Atlas; CSN 19 [Suppl.] 39), may have been misidentified Tuis (Craig & Douglas 1984b). NORTHLAND: Recorded at a few scattered sites centred on Whangarei, mostly between Helena Bay and Bream Head, but sometimes farther S to Bream Tail and Mangawhai; these are probably birds straying from resident populations on nearby offshore islands of Poor Knights and Hen and Chickens Grps (Sibson 1953; Kinsky & Sibson 1959; Merton & Atkinson 1968; Craig & Douglas 1984b; Bartle & Sagar 1987; Kendrick 1994; NZ Atlas; CSN). AUCKLAND and SOUTH AUCKLAND: Few records on mainland, mostly adjacent to Little Barrier and Tiritiri Matangi Is, from whence birds may stray (Turbott 1953; Craig & Douglas 1984b). Said not to have been recorded on Great Barrier I. since 1964 (Bell 1976), though several NZ Atlas records in w. and s. parts of the island date from 1969 at the earliest. Very occasionally recorded W to near se. Kaipara Harbour. Introduced to Whangaparaoa Pen. and Waiheke I. (see below). Rare reports from within City of Auckland may have been misidentified Tuis (Craig & Douglas 1984b). Sometimes recorded W of Firth of Thames, in area bounded by line joining Maraeti, Clevedon, Hunua and Kaiaua, including Hunua Ras. Widespread on Coromandel Pen., as well as Cuvier and Mercury Is (Hicks *et al.* 1975; Lovegrove 1975; NZ Atlas; CSN). WAIKATO: Absent in N, but widespread S of line joining Raglan, Waingaro, Hakarimata Ra. and Hamilton; though generally sparsely scattered in NE, from Hamilton and Matamata S to L. Arapuni and Tokoroa (NZ Atlas; CSN). BAY OF PLENTY, VOLCANIC PLATEAU and GISBORNE–WAIROA: Widespread but scattered (NZ Atlas; CSN), including offshore islands such as Cuvier I. and Mercury Grp (Edgar 1962; Skegg 1962; Blackburn 1967, 1970; Reed 1976; Craig & Douglas 1984b). HAWKES BAY: Widespread S to Havelock North, and along e. slopes of Ruahine Ra., but few records elsewhere, e.g. Makaretu, Kopua (NZ Atlas; CSN). WAIRARAPA: Mostly between e. Tararua Ra. and Ruamahanga R., though occasionally recorded elsewhere, including round Patiahua in N, Aorangi Mts in S, and at a few isolated sites elsewhere (NZ Atlas; CSN). WELLINGTON: Generally widespread, though rarely occur in SW (NZ Atlas). Also on Kapiti I. (Wilkinson & Wilkinson 1952; NZ Atlas; CSN 32). MANAWATU: Scattered records in S, E and N, from areas S of Levin, NE along w. slopes of Tararua and Ruahine Ras, to near Taihape; generally absent elsewhere (NZ Atlas; CSN). WANGANUI: Widespread, but scattered in some areas (NZ Atlas;

CSN). TARANAKI: Widespread W to line joining Patia and Uruti; farther W, mostly confined to Egmont NP (NZ Atlas; CSN). **SI** NELSON and MARLBOROUGH: Widespread, though scattered in Richmond Ra., and, farther S, apparently absent from area W of Inland Kaikoura Ra. (NZ Atlas; CSN). CANTERBURY: In N, widespread in coastal and subcoastal areas from s. Seaward Kaikoura Ra. S to n. Pegasus Bay; very occasionally round Rangiora; and widespread on Banks Pen. Generally absent from lowlands between Amberley and Timarau, but widespread farther W in uplands from near Hanmer Springs SW to round Stavely. Also occur from middle reaches of Rangitata R. S to Waimate, but, in S, not W of Hunter Hills. Occasionally recorded along middle reaches of Waitaki R. (NZ Atlas; CSN). OTAGO: Scattered records from middle reaches of Waitaki R., S through Kakanui Mts to coast near Palmerston. Widespread in S, including Otago Pen. Scattered in SW, round L. Wakatipu, and widespread in NW, in areas W of Pisa Ra., including Ls Wanaka and Hawea. However, mostly absent from central Otago (Child 1975; NZ Atlas; CSN). SOUTHLAND: Widespread, including on Stewart I. and associated islands, such as Ruapuke, Muttonbird and Codfish Is (Blackburn 1965, 1968; NZ Atlas; CSN); also on Solander and Little Solander Is (Wilson 1973; Cooper & Morrison 1984; Cooper *et al.* 1986; McLean & Russ 1994). WEST COAST: Widespread (NZ Atlas; CSN).

Chatham Is Extinct; formerly throughout (NZCL). Last recorded in 1906, on Little Mangere I. (Fleming 1939). Doubtful reports from Pitt I. in *c.* 1952 (Lindsay *et al.* 1959). Extinction possibly result of degradation of forest (Tennyson & Millener 1994; *contra* Fleming 1939).

Snares I. Reported in 1888, but not since (Warham 1967; Oliver).

Auckland Is Occur throughout (Bartle & Paulin 1986; NZCL).

Breeding Probably breed throughout range.

Introductions Several releases to areas where formerly occurred in an attempt to re-establish the species. **1932**
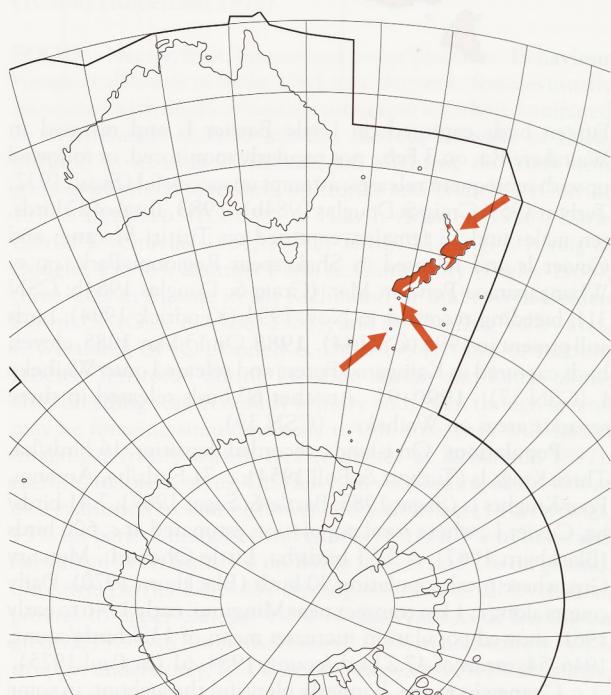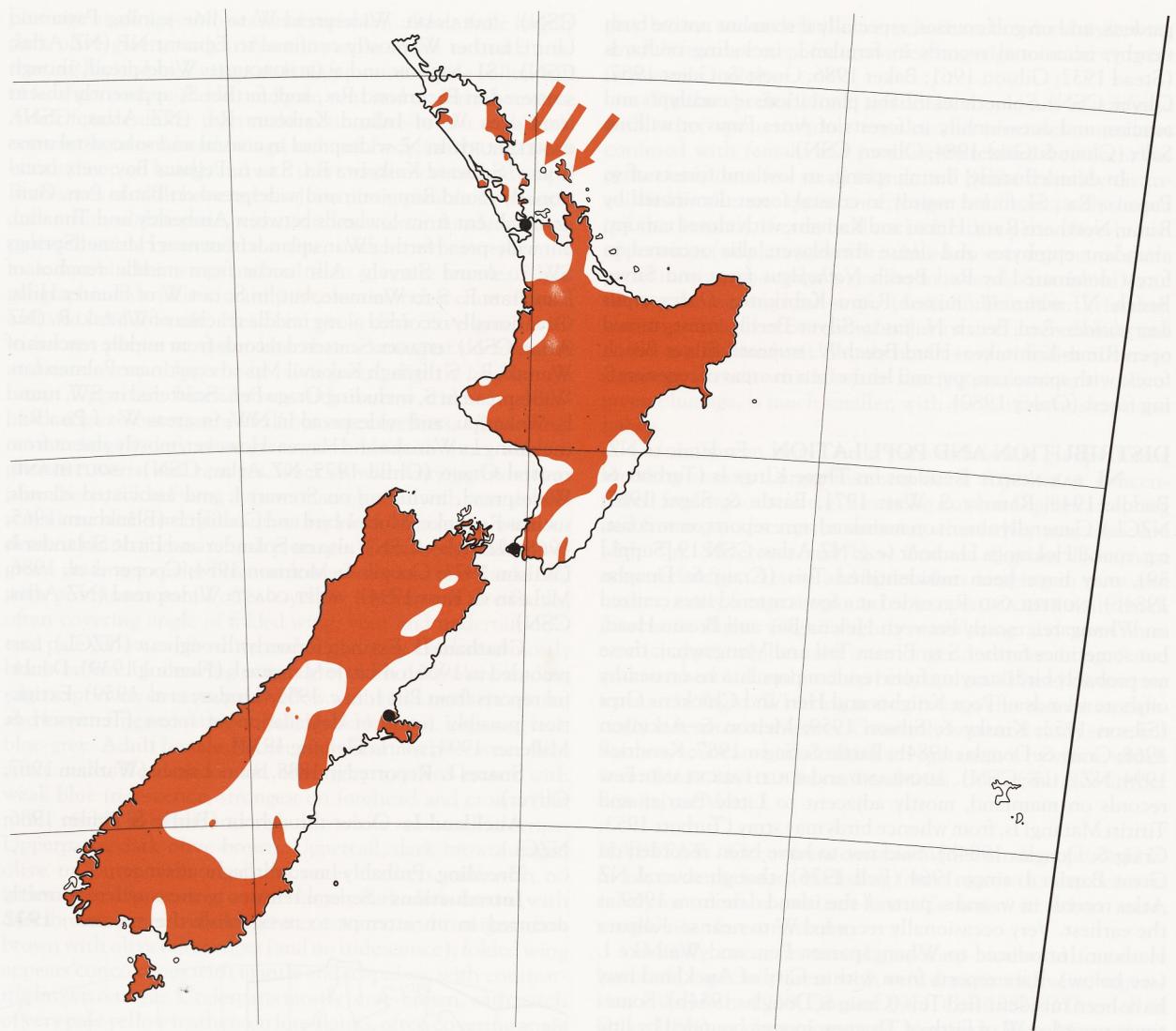
Fifteen birds captured on Little Barrier I. and released in Waitakere Ra. on 3 Feb.; not regularly monitored, or followed up with subsequent releases; attempt unsuccessful (Stead 1932; Turbott 1953; Craig & Douglas 1984b). **1983** Total of 22 birds, ten males and 12 females, captured on Tiritiri Matangi and Cuvier Is and released in Shakespear Regional Park, on e. Whangaparaoa Pen., in Mar. (Craig & Douglas 1984b; CSN 31); breeding recorded in Nov. 1993 (Kendrick 1994); birds still present in 1995 (CSN 44). **1988** On 13 May 1988, eleven birds captured in Kaingaroa Forest and released onto Waiheke I. (CSN 37). **1990–91** Another 60 birds released in three separate areas on Waiheke I. (CSN 39).

Populations On islands, recorded densities: 16 birds/ha, Three Kings Is (Turbott & Bull 1954); c. 71 birds/ha, Aorangi, Poor Knights Is (Sagar 1985; Bartle & Sagar 1987); 7.41 birds/ha, Cuvier I., where total population estimated at c. 600 birds (Blackburn 1967), c. 3.53 birds/ha, Little Ohena I., Mercury Grp, where total population 20 birds (Blackburn 1970). Daily counts along c. 1 km transect near Minginui, early 1946 to early 1961, showed population increase: mean of 13.3 birds/count, 1946–54; mean of 47.2 birds/count, 1954–61 (St Paul 1975).

Change in range Formerly plentiful throughout, in some

places the most abundant bird species (Turbott 1953, 1967). On **NI**, populations N of Waikato R. declined rapidly after c. 1860 and were probably locally extinct by 1866; populations in Gisborne–Wairoa, where 'the bush fairly swarmed with them', also declined at about the same time (Turbott 1967). However, populations apparently increased in several areas on NI during 1940s. Round Clevedon, records in early 1940s were the first since 1880 (CSN 1). Round Moumoukai, S of Clevedon, Bellbirds first recorded in 1942; populations soon increased and range expanded; local population had peaked by 1954, but then declined; few records by late 1950s, with only remnant populations surviving by early 1960s; single birds very occasionally seen now (McKenzie 1979; Craig & Douglas 1984b; CSN 1–9). On nearby Coromandel Pen., populations said to have increased in mid- to late 1950s (CSN 8). Populations at Rotorua said to have increased rapidly from mid-1940s till at least late 1950s (Phillipps & Lindsay 1948; CSN 1, 7, 8). At Wellington, more numerous in 1945–46 than during previous 21 years (CSN 2). Survived on Cavalli and Motuihe Is till 1950s (Sibson 1953; Turbott 1953; Craig & Douglas 1984b). In mid-1950s, said to have increased round New Plymouth (CSN 7). Rarely seen round Gisborne, but many birds recorded during

spring 1973 (CSN 20), and population increased till at least 1975 (CSN 22). More recently, increased numbers in Blowhard Bush, result of control of predators (CSN 43). On **SI**, populations in Canterbury declined in late 19th century: a few still present in Christchurch in late 1890s, but virtually extinct by 1900; numbers declined throughout Canterbury till 1910 (Stead 1932; *contra* Hutton & Drummond 1904), after which they increased considerably, and were again plentiful in some areas by early 1930s (Stead 1932). This increase said to have continued into 1940s (Graham 1948). Populations round Avon R., Christchurch, increased in 1978–79 (CSN 26).

THREATS AND HUMAN INTERACTIONS Formerly hunted by Maori with a spear called a *here*, up to 12 m long and tipped with a serrated barb made from bone, which held the bird when struck; other 'contrivances' sometimes also used (Hutton & Drummond 1904). Early decline in populations attributed by early authors to effects of bushfires, predation (by feral Cats and rats) and introduced honeybees (Reischek 1887; Hutton & Drummond 1904; Turbott 1953, 1967), though the honeybee theory recognized as 'an utter fallacy' (Hutton & Drummond 1904). Decline on NI certainly coincided with spread of rats (Atkinson 1973), which thought to destroy eggs and nestlings (CSN 3, 32). A temporary decline of numbers on Red Mercury I. coincided with air-drop of rat poison, but was probably caused by seasonal movement; no adverse effects were recorded (Robertson *et al.* 1993). The major threat today is continued logging of native forest and clearance of scrub or forest remnants on farms (D.J. Onley). Near Karamea, in native forest predominantly of Rimu *Dacrydium cupressinum* and Hard Beech *Nothofagus truncata*, 5-min counts over 3 days in winter found numbers were significantly lower in logged than in unlogged forests (Onley 1983). Common Brushtail Possum *Trichosurus vulpecula* now recognized as a major threat to health of forests, being particularly destructive to rata *Metrosideros* emergents and therefore affecting supplies of nectar for Bellbirds (D.J. Onley).

MOVEMENTS Described as resident (Moncrieff 1929; Turbott 1953; Kikkawa 1960, 1966; Thoresen 1967; CSN 22) with local movements (Sagar 1985), migratory (Moncrieff 1929; Wilson *et al.* 1988) or with seasonal patterns of occurrence (Moncrieff 1929; St Paul 1975; Guest & Guest 1987). Occasionally visit islands (Emmens 1954; Wodzicki 1978), and therefore can cross water. Movements suggested to be related to availability of food (McLean 1912; Moncrieff 1929; Bull 1959; Gravatt 1970; St Paul 1975), appearance coinciding with flowering or fruiting of food trees, and departure when food supply decreases. Said to become more generally dispersed during spring, when seeking flowering trees (McLean 1912). On Tiritiri Matangi I., males move more often than females, especially to food sources, and move farther (Craig *et al.* 1981b; Craig & Douglas 1984b). However, on Poor Knights Is females and juveniles generally move around more, with males defending territories throughout year (Sagar 1985; see below). Described as resident on Green I., Mercury Is, NI (Thoresen 1967); Canterbury region (Turbott 1953; CSN 22); and Dunedin, SI (Kikkawa 1960, 1966; Baker 1986). Present throughout year on Little Barrier I. (Gravatt 1970), at Kawerau (CSN 39), Minginui (CSN 6), Orongorongo Valley, Wellington (Gibb 1996), Aramoho (CSN 41), Taumuranui (Moncrieff 1929), Ohikanui Valley (in low numbers; Wilson *et al.* 1988), Kowhai Bush (Dean 1990), Pembroke (Moncrieff 1929) and Macandrew Bay, Otago Pen. (CSN 45). Present throughout

year on Poor Knights Is, where males defend territories all year but females become non-territorial after breeding season, though local movements by either sex may occur during year to exploit localized sources of food or water (Sagar 1985).

Movements and appearance on both NI and SI appear to be seasonal, with birds spending summer in 'bush' (probably inland or high altitudes) and moving to coast, lower altitudes, plantations or urban areas over winter (Oliver; CSN 19 Suppl.), possibly augmenting local populations (Wilson *et al.* 1988; CSN 22). During winter, regular migration recorded from 'bush' to coasts, plantations on plains, river beds or urban areas: New Plymouth, NI; Canterbury, including Otaio R. area; Palmerston North and Macandrew Bay, in Otago, and Southland (Moncrieff 1929; CSN 6, Suppl. 19), SI. Winter visitor to Christchurch (CSN 36, 42) and Heathcote–Avon Estuary, SI (CSN 26), and more commonly seen during winter in South Auckland, Te Puke (CSN 41), Rotorua (CSN 6) and Te Kuiti (Guest & Guest 1987). During winter, numbers increase at Tihoi and decrease at Minginui; possibly result of some of Minginui population moving to Tihoi area over winter, when food resources decrease in Minginui (St Paul 1975). Described as spring visitor to Nelson, and a regular autumn visitor to Dunedin (Moncrieff 1929). Increase in numbers in Dunedin may be due to breeding, with apparent population decline before winter due to juvenile dispersal (Kikkawa 1966).

Bird counts in Ohikanui Valley and nearby areas, SI, 1975–77, found highest numbers in Buller R. Valley, outside Ohikanui Valley, in June, and lowest in Dec.; opposite to count results from central Ohikanui Valley, suggesting that Buller, at lower altitude, may be a wintering site for birds from higher altitudes in Ohikanui Valley. Numbers increase between June and Sept. in lower Ohikanui Valley, followed by decline in Dec., suggesting that birds return through this area to spend summer at higher altitudes in Valley. Found throughout year in Inangahua Valley, with no seasonal fluctuation (Wilson *et al.* 1988).

Banding Of 1014 banded up to 1974, 110 recoveries (10.8%) (Robertson 1975).

FOOD Nectar, fruit, insects and insect products. **Behaviour** Forage at all levels in forest. On Little Barrier I., females usually associated with flocks of insectivorous species, often dominated by Whiteheads *Mohoua albicilla*; moving in wake of flock, foraging in manner of treecreeper, alighting on trunk near ground-level and spiralling up trunks and branches (Gravatt 1971). DETAILED STUDIES: On Hen I. (Merton 1966); Little Barrier I. (Gravatt 1969, 1971); Tiritiri Matangi I. (Craig & Douglas 1984b); Hanmer Park, n. Canterbury (Fegley 1988); three sites in SI, one in Mt Richmond SF and two in Golden Downs SF (Gaze & Clout 1983); and in Windbag Valley area, s. Westland, SI (O'Donnell & Dilks 1994). SIZE OF FEEDING FLOCKS: Territorial during breeding season and forage alone; after breeding season usually solitary and, even though several may be foraging simultaneously in one tree, they will defend foraging territory within tree (Heather & Robertson 1997). FEEDING HEIGHTS, SITES: On Hen I. (n=96 feeding obs.): 46% of observations were among flowers, 16% in foliage, 14% on twigs, 15% on bark of branches and trunks of trees, 3% in holes and fisssures, 1% on fruit, 3% on flying insects and 2% on ground. On Little Barrier I. (n=337 feeding obs.), fed at all levels from ground to upper canopy: 1.8% of observations of feeding on ground, 19.9% in lower understorey, 9.5% in mid-storey, 34.7% in upper understorey, 18.7% in subcanopy, and 15.4% in canopy; heights of these observations: 6.5% on ground, 12.0% at 0.1–

1.5 m above ground, 14.2% at 1.6–3.0 m, 14.2 at 3.1–4.5 m, 15.3% at 4.6–6.0 m, 15.3% at 6.1–7.5 m, 12.5 at 7.6–9.0 m, 5.9% at 9.1–10.5 m, 2.0% at 10.6–12.0 m, and 2.0% above 12 m. When feeding on insects on Little Barrier I. (n=183 feeding obs.): 50.8% collected from trunks, 38.8% from branches, 3.8% from twigs, 1.6% from leaves, 0.5% from terminal shoots, 3.3% from litter on ground, and 1.1% aerially. In Windbag Valley area (n=4270 feeding obs.), fed at all levels of forest: 24% in upper understorey, 28% in shaded canopy, 22% in unshaded canopy, 20% among emergent leaves, and 6% from air. At Hanmer Park, birds foraging in pine *Pinus* forest (n=44 feeding obs.) mostly fed on ground and in lower 60% of forest; when foraging in native beech *Nothofagus* forest with mixed understorey of manuka *Leptospermum* and kanuka *Kunzea* (n=53 feeding obs.), 37% of feeding was in subcanopy (Fegley 1988). Fed on ground twice as often in pine forest (18% of obs.) as in native forest (9%); in pine forest, 11% of birds fed on insects and honeydew from underside of branches and foliage, whereas in native forest, 26% fed at such sites. Birds feeding on upper surface of foliage and branches accounted for 50% in pine forest and 19% of observations in native forest. Birds feed from tree trunks 45% of observations in native forest compared with only 23% in pine plantation (Fegley 1988). In n. SI, fewer birds fed in conifer plantations than in adjacent native forests, and birds most abundant in areas where honeydew most plentiful; birds used plantation forests more during summer than winter months, when they were seen feeding in or next to native forests (Clout & Gaze 1984). FOOD SOURCES: Feed on nectar, fruit, insects and their products (Turbott 1967; Gravatt 1969, 1971; Falla *et al.* 1978; Moon & Lockley 1982; Gaze & Clout 1983; O'Donnell & Dilks 1994). During spring and summer, take nectar and fruit, though, in Jan., take many insects (mostly cicadas). During autumn and winter, take mainly fruit, usually whole, though some fruits squashed to extract juice (St Paul 1975). Overall, probably take more insects than nectar or fruit; spend much time in all seasons searching for insects in crevices in bark, on twigs and branches, and sometimes on ground (Falla *et al.* 1978). Considered more insectivorous than Tuis and Stitchbirds (Gravatt 1971; O'Donnell & Dilks 1994). During winter, females forage for insects more than males do (Gravatt 1971). On Little Barrier I. (n=284 feeding obs.: 57 in spring; 76 in summer; 68 in autumn; and 83 in winter), fed on nectar in 80.7% of observations in spring, 65.8% in summer, 27.9% in autumn and 34.9% in winter; on insects 19.3%, 32.9%, 61.8%, 57.8%; and fruit –%, 13.3%, 10.3%, 7.2%. In Windbag Valley area, obtain food from many species of plants (summarized in Table 1). Use of different sources of food, with exception of honeydew, varies seasonally. Feed on nectar throughout year, but proportion varied from c. 5% of observations during June–July to 41% in Oct. Honeydew taken in most months, mainly from Kamahi *Weinmannia racemosa*, with rest from Southern Rata *Metrosideros umbellata*, and represented 2–5% of total feeding observations. Amount of fruit in diet also varied seasonally, being greatest during June (16% of obs.); fruit of Rimu *Dacrydium cupressinum* was most important, comprising 31% of fruit eaten. Insects taken from 28 species of plants, mostly from canopy, understorey and epiphytes; most important in Aug., when comprised c. 90% of feeding observations. At three sites in SI (n=6237 5-s obs. throughout year), 50% of observations were of foraging (monthly range 36%–70%) with remaining time spent preening, singing and loafing; when foraging, 21% of observations were of feeding on honeydew secreted by scale insects *Ultracoelostoma assimile* (Coccidae), 17% on insects, 0.3% on fruit, and 12% on other food types including nectar.

Table 1. Plant species used for feeding by Bellbird in Windbag Valley area, s. Westland (% of total feeding obs.) (O'Donnell & Dilks 1994).

PLANT SPECIES	FOOD ITEMS			
	General (4270 obs.)	Nectar (605 obs.)	Fruit (278 obs.)	Invertebrates (436 obs.)
CANOPY SPECIES				
Dacrydium cupressinum	10.4	–	30.9	7.6
Dacrycarpus dacrydioides	1.9	–	3.6	3.7
Elaeocarpus hookerianus	0.3	–	2.2	–
Lagarostrobos colensoi	0.2	–	–	1.4
Libocedrus bidwillii	0.1	–	–	–
Metrosideros umbellata	10.9	25.1	–	7.6
Nothofagus menziesii	10.0	–	–	13.3
Podocarpus hallii	0.2	–	0.7	3.0
P. totara	0.1	–	–	–
Prumnopitys ferruginea	2.2	–	1.1	1.4
P. taxifolia	0.1	–	–	–
Weinmannia racemosa	33.2	1.3	–	37.4
Dead trees (various)	0.6	–	–	0.7
SHRUB HARDWOODS				
Aristotelia serrata	0.4	–	1.4	–
Ascarina lucida	0.2	–	6.8	0.5
Carpodetus serratus	0.3	–	0.3	–
Coprosma	1.0	–	9.4	1.2
C. foetidissima	0.9	–	7.9	–
C. lucida	0.1	–	4.0	–
C. rotundifolia	0.4	–	4.0	–
Coriaria arborea	0.1	–	0.7	0.5
Fuchsia excorticata	9.7	54.7	1.4	2.5
Griselinia littoralis	0.8	–	0.7	1.6
Hedycarya arborea	0.3	–	0.4	–
Mylicytus ramiflorus	0.2	–	–	0.2
Myrsine australis	0.5	–	3.2	–
M. divaricata	0.4	–	2.9	0.2
Neomyrtus penunculata	0.8	–	6.1	–
Pinnantia corymbosa	0.1	–	–	–
Phyllocladus aspleniifolius	0.8	–	–	0.7
Pseudopanax colensoi	0.1	–	–	10.1
P. crassifolius	1.5	2.0	7.9	1.6
P. edgerleyi	0.2	–	1.1	–
P. simplex	0.3	0.2	0.4	–
Pseudowintera colorata	0.7	0.2	2.5	0.7
Schefflera digitata	0.3	0.7	–	0.7
OTHERS				
Astelia fragrans	<0.1	–	–	0.2
Earina autumnalis	–	0.5	–	–
Ferns	0.1	–	–	–
Freycinetia baueriana	0.3	0.7	–	–
Metrosideros	10.9	11.9	–	1.4
Mosses	0.4	–	–	0.9
Muehlenbeckia australis	<0.1	–	–	–
Orchids	0.1	–	–	–
Paraxilla	0.6	3.3	0.4	–
Ripogonum scandes	0.7	–	2.9	0.5
Rubus	0.1	–	–	0.2
Tree-ferns	–	–	–	0.3
NOT IN PLANTS				
Ground or aerial feeding	1.7			

Honeydew is a major food item in most SI forest habitats, except in Windbag Valley area, because these are dominated by beech trees *Nothofagus* that are commonly infested with scale insects (P.D. Gaze). At Nelson Lakes NP, SI, the poisoning of introduced vespulid wasps has resulted in significant increase in abundance of honeydew and an apparent increase in density of Bellbirds, suggesting that these wasps were competing with

Bellbirds for this resource (D.J. Butler; P.D. Gaze). FEEDING METHODS: Probe flowers for nectar; insects usually gleaned from leaves or bark of branches and trunks of trees, or caught aerially by sallying (Stenhouse 1957; St Paul 1975; Oliver); collect honeydew by hopping up trunk of trees, taking each droplet with brush-like tongue (Gaze & Clout 1983). When feeding on nectar, usually grasp flower-bearing stems with feet, and hang in all positions to probe flowers (Turbott 1967). On Hen I., feed on nectar by probing flowers; and on insects mainly by sallying, including sally-strikes at flying insects and sally-hovering to pick insects from flowers; also by gleaning, especially when on ground. In Windbag Valley area, most invertebrates collected by gleaning (c. 80% of 436 feeding obs.); remaining insects caught by sallying, mostly aerially, to catch flying insects. On Tiritiri Matangi I., access to food source determined by social hierarchy; males dominate females and often exclude them from a site. ADAPTATIONS: Slightly downcurved bill and long bifurcated, brush-like tongue suitable for collecting nectar (Soper 1965). Tongue like that of Tui, canaliculated along its length, but to a lesser degree; its tip is comparatively more deeply cleft into four segments, each with fine hair-like processes to form a brush (McCann 1964).

Detailed studies On HEN I. (57 feeding obs.; Merton 1966): **Plants** DICOTYLEDONS: Araliaceae: *Pseudopanax lessonnii* fru. 1.8%; Corynocarpaceae: *Corynocarpus laevigata* nectar 1.8, sap 1.8; Gesneriaceae: *Rhabdothamnus solandri* nectar 1.8; Meliaceae: *Dysoxylum spactabile* nectar 39.5; Verbenaceae: *Vitex lucens* nectar 35.8; Tiliaceae: *Entelea arborescens* sap 1.8. **Animals** INSECTS: Unident. 5.2; Diptera 1.8; Hemiptera 8.7.

On LITTLE BARRIER I. (145 birds observed feeding on nectar over 12 months; Gravatt 1969, 1970): **Plants** DICOTYLEDONS: Araliaceae: *Neopanax arboreum* 1 bird observed feeding on this species (Sept.); *Schefflera digitata* 1 (Feb.); Caprifoliaceae: *Alseuosmia macrophylla* 2 (Sept.–Oct.); Corynocarpaceae: *Corynocarpus laevigata* 2 (Aug.); Epacridaceae: *Cyathodes fasciculata* 1 (Oct.); *C. juniperina* 1 (Aug.); Meliaceae: *Dysoxylum spactabile* 4 (June, Aug.); Myrtaceae: *Meterosideros excelsa* 29 (Nov.–Jan.); *M. fulgens* 2 (June–July); *M. perforata* 1 (Jan.); *M. robusta* 12 (Dec.–Jan.); Oleaceae: *Nestegis* 2 (July–Aug.); Phytolaccaceae: *Phytolacca octandra* 1 (Apr.); Pittosporaceae: *Pittosporum tenuifolium* 2 (Oct.); *P. umbellatum* 22 (Aug.–Sept.); Proteaceae: *Knightia excelsa* 4 (Sept., Nov.); Scrophulariaceae: *Hebe* 1 (Sept.); Verbenaceae: *Vitex lucens* 56 (all year); Violaceae: *Melicytus ramiflorus* 1 (May).

At DUNEDIN BOTANIC GARDENS (direct obs. of nectar feeding, July 1983–July 1985; number of days, and months, on which feeding recorded; Baker 1986): **Native plants** MONOCOTYLEDONS: Agavaceae: *Phormium* 9 days (Nov.–Jan.). DICOTYLEDONS: Araliaceae: *Pseudopanax* 20 (June–Sept.); Fabaceae: *Sophora* 28 (May–Oct.); Myrtaceae: *Meterosideros* 13 (Nov.–Feb.); Onagraceae: *Fuchsia excorticata* 37 (May–Dec.); Pittosporaceae: *Pittosporum umbellatum* 4 (July–Aug.); Verbenaceae: *Vitex lucens* 10 (Apr.–Aug.). **Introduced plants** MONOCOTYLEDONS: Liliaceae: *Kniphofia* 8 (Jan.–Feb.); *Lapageria rosea* 3 (Apr.–May). DICOTYLEDONS: Amaryllidaceae: *Bomarea caldasii* 4 (Apr.–June); Berberidaceae: *Mahonia* 7 (Apr.–June); Elaeocarpaceae: *Crinodendron hookeranum* 4 (Dec.–Jan.); Ericaceae: *Arbutus unedo* 18 (Mar.–Aug.); *Arctostaphylos manzanita* 3 (July–Aug.); *Erica* 3 (June–July); *Rhododendron* 10 (June–Aug.); Fabaceae: *Cytisus proliferuus* 1 (June); Lamiaceae: *Colquhounia coccinea* 2 (Mar.); Mimosaceae: *Albizia lophantha* 14 (Apr.–Aug.); Myrtaceae: *Callistemon* 10 (Dec.–Feb.); *Eucalyptus* 41 (Apr.–Feb.); *Melaleuca* 17 (Jan.–June); *Syzygium paniculatum* 1 (Apr.); Pittosporaceae: *Hymenosporum flavum* 1 (May); Proteaceae: *Banksia* 48 (Feb.–Oct.); *Grevillea* 21 (Dec.–Oct.); *Protea* 13 (Jan.–June); Rosaceae: *Prunus subhirtella* 5 (June–July); Rutaceae: *Correa* 5 (June–Sept.); Saxifragaceae: *Ribes sanguineum* 5 (Aug.–Sept.); Styracaceae: *Styrax japonica* 1 (Mar.).

At DUNEDIN, OTAGO (obs. of feeding on native plants, July 1990–June 1992; Baker 1992): **Plants** GYMNOSPERMS: Podocarpaceae: *Podocarpus* fru. (Apr.–May). MONOCOTYLEDONS: Agavaceae: *Cordyline australis* fru. (May); *Phormium* nectar (Nov.–Feb.). DICOTYLEDONS: *Pseudopanax* nectar (June–Sept.); Cornaceae: *Korokia* fru. (June–Aug.); Elaeocarpaceae: *Aristotelia serrata* fru. (Jan.–Feb.); Fabaceae: *Clianthus puniceus* nectar (Apr.–Sept.); *Sophora* nectar (Apr.–Dec.); Loranthaceae: *Tupeia antarctica* fru. (May–June); Malvaceae: *Hoheria* nectar (Feb.); Moraceae: *Streblus heterophyllus* fru. (May); Myoporaceae: *Myoporum laetum* fru. (July); Myrtaceae: *Lophomyrtus bullata* fru. (July); *Meterosideros* nectar (Nov.–Jan.); Myrsinaceae: *Myrsine* fru. (Apr.); Onagraceae: *Fuchsia excorticata* nectar (all year); Pittosporaceae: *Pittosporum* nectar (July–Sept.); Polygonaceae: *Muehlenbeckia australis* fru. (Feb.–Mar., July); Rubiaceae: *Coprosma* fru. (Feb.–Sept.); Scrophulariaceae: *Hebe* nectar (June, Aug.); Solanaceae: *Solanum laciniatum* fru. (Apr.–July); Verbenaceae: *Vitex lucens* nectar (Apr.–Sept.); Violaceae: *Melicytus ramiflorus* fru. (Mar.–July).

At DUNEDIN (direct obs. of feeding on fruit and nectar from native plants, July 1992–Dec. 1997; number of days when feeding recorded; Baker 1999): **Plants** GYMNOSPERMS: Podocarpaceae: *Dacrycarpus dacrydiodes* fru., 3; *Podocarpus totara* fru., 18. MONOCOTYLEDONS: Agavaceae: *Cordyline australis* fru., 1; *Phormium* nectar, 30. DICOTYLEDONS: Araliaceae: *Pseudopanax* fru., 3, nectar, 48; Coriariaceae: *Coriaria arborea* fru., 1; Cornaceae: *Corokia* fru., 1; *Griselinia littoralis* fru., 3; Elaeocarpaceae: *Aristotelia serrata* fru., 7; Escalloniaceae: *Carpodetus serratus* fru., 3; Fabaceae: *Clianthus puniceus* nectar, 4; *Sophora* nectar, 86; Icacinaceae: *Pennantia corymbosa* fru., 1; Loranthaceae: *Ileostylus micranthus* fru., 4; *Tupeia antarctica* fru., 7; Malvaceae: *Hoheria* nectar, 4; Moraceae: *Streblus heterophyllus* fru., 2; Myoporaceae: *Myoporum laetum* fru., 1; Myrsinaceae: *Myrsine australis* fru., 26; Myrtaceae: *Lophomyrtus bullata* fru., 5; *L. obcordata* fru., 3; *Metrosideros excelsa* nectar, 6; *M. robusta* nectar, 1; *M. umbellata* nectar, 9; Onagraceae: *Fuchsia excorticata* nectar, 123; Pittosporaceae: *Pittosporum crassifolium* nectar, 2; *P. eugenioides* nectar, 1; *P. umbellatum* nectar, 8; Polygonaceae: *Muehlenbeckia australis* fru., 13; Proteaceae: *Knightia excelsa* nectar, 1; Rubiaceae: *Coprosma areolata* fru., 9; *C. crassifolia* fru., 1; *C. grandifolia* fru., 2; *C. linariifolia* fru., 4; *C. lucida* fru., 9; *C. parviflora* fru., 1; *C. propinqua* fru., 11; *C. repens* fru., 1; *C. rhamnoides* fru., 1; *C. robusta* fru., 54; *C. rotundifolia* fru., 7; *C. tenuifolia* fru., 2; Scrophulariaceae: *Hebe* nectar, 4; Solanaceae: *Solanum laciniatum* fru., 3; Verbenaceae: *Vitex lucens* nectar, 16; Violaceae: *Melicytus alpinus* fru., 5; *M. obovatus* fru., 2; *M. ramiflorus* fru., 10.

On KAPITI I. (obs. of plants visited for nectar; Aug. 1991–Aug. 1994; [1] = frequent visits, whenever flowers available; [2] = occasional visits; Castro & Robertson 1997): **Plants** MONOCOTYLEDONS: Agavaceae: *Phormium tenax*[1]. DICOTYLEDONS: Araliaceae: *Pseudopanax arboreous*[1]; Cornaceae: *Griselinea littoralis*[2]; Corynocarpaceae: *Corynocarpus laevigatus*[2]; Cunoniaceae: *Weinmannia racemosa*[1]; Elaeocarpaceae: *Elaeocarpus dentatus*[1]; Fabaceae: *Sophora*[1]; Loganaceae: *Geniostoma rupestre*[1]; Meliaceae: *Dysoxylum spectabile*[1]; Monimiaceae: *Laurelia novaezelandiae*[1]; Myoporaceae: *Myoporum*

laetum[1]; Myrtaceae: *Kunzea ericoides*[1]; *Metrosideros excelsa*[1]; M. *fulgens*[1]; M. *robusta*[1]; Onagraceae: *Fuchsia excorticata*[1]; Pittosporaceae: *Pittosporum cornifolium*[1]; *P. crassifolium*[1]; *P. eugenioides*[1]; *P. tenuifolium*[1]; *P. umbellatum*[2]; Proteaceae: *Knightia excelsa*[1]; Verbenaceae: *Vitex lucens*[1].

Other records Plants (Nectar unless stated.) Fruit[1,11,18,21]. LICHEN[1]. GYMNOSPERMS: Podocarpaceae: *Dacrycarpus dacrydioides*[25,28], fru.[14,27,35]; *Dacrydium cupressinum* fru.[14]; *Podocarpus totara* fru.[30,35]; *Prumnopitys taxifolia* fru.[14,27,28]. MONOCOTYLEDONS: Agavaceae: *Cordyline* fru.[21]; C. *australis*[19]; C. *robusta*[25]; *Phormium colensoi*[2,12]; *P. tenax*[1,5,8,9,11,15,19,21]; Iridaceae: *Watsonia*[22]; Liliaceae: *Aloe*[44]. DICOTYLEDONS: Apocynaceae: *Parsonsia heterophylla*[19]; Araliaceae: *Neopanax arboreum*[28]; *Pseudopanax*[19,41]; Elaeocarpaceae: *Aristotelia serrata*[23], fru.[12]; *Elaeocarpus dentatus*[19]; Epacridaceae: *Dacrophyllum*[21]; Ericaceae: *Arbutus unedo* fru.[3]; Escalloniaceae: *Carpodetus serratus*[25,26], fru.[14,19,26,27]; *Ixerba brexioides*[12]; Fabaceae: *Chamaecytisus prolifer*[23,24]; *Sophora microphulla*[10,15,21,26,28,36], fru.[21]; Fagaceae: *Nothofagus solandri* sap[20]; Gesneriaceae: *Rhabdothamnus solandri*[43]; Icacinaceae: *Pennantia corymbosa* fru.[27,28]; Lauraceae: *Beilschmiedia taraire*[19]; Malvaceae: *Hoheria populnea*[21]; Meliaceae: *Dysoxylum spactabile*[8,15,19,38]; Mimosaceae: *Acacia*[21,33], pollen[29]; Moraceae: *Ficus* fru.[6,13,21]; Myoporaceae: *Myoporum*[19]; Myrsinaceae: *Myrsine australis* fru.[34,40]; Myrtaceae: *Callistemon citrinus*[41]; *Eucalyptus*[19,21,31]; E. *leucoxylon*[41]; *Leptospermum*[19]; *Metrosideros excelsa*[15,19,21,22]; M. *fulgens*[17]; M. *robusta*[1,5,8,15,21,39,41]; M. *umbellata*[12]; Oleaceae: *Ligustrum vulgare* fru.[35]; *Olea*[28]; Onagraceae: *Fuchsia*[14,15,21,25,26,27,28,40,41], buds[27], fru.[8,14,26,27,28]; F. *exorticata*[7,11], fru.[12]; Pittosporaceae: *Pittosporum crassifolium*[10,12,19]; *P. eugeniodes*[19]; *P. tennifolium*[19]; Proteaceae: *Banksia*[37,41]; *Grevillea*[40]; *Knightia excelsa*[15,19,21]; Rosaceae: *Crataegus* fru.[25,26]; *Malus sylvestris* nectar, fru.[21]; *Prunus*[41]; *P. persica*[31], fru.[21]; Rubiaceae: *Coprosma* fru.[14,21,26,31,33]; C. *lucida* fru.[11,28]; C. *robusta* fru.[41,42,45]; *Nertera depressa* fru.[21]; Rutaceae: *Citrus*[13,22]; Salicaceae: *Salix nigra*[30]; Saxifragaceae: *Ribes* fru.[25,26,27,28]; Theaceae: *Camellia japonica*[43]; Tiliaceae: *Entelea arborescens*[27], fru.[26]; Verbenaceae: *Vitex lucens*[15,17,19,44]; Vitaceae: *Vitis vinifera* fru.[13]; Winteraceae: *Pseudowintera axillaris* fru.[16]. **Animals** INSECTS[1,4,11,17,18,21,28]: eggs[32]; Hemiptera: honeydew[35]; Cicadidae[14,27,28]; Pseudococcidae: honeydew[15]. **Other matter** Sugar water[8]; burnt bones[46]; agricultural lime[46].

REFERENCES: [1] Stead 1932; Sibson [2] 1947, [3] 1993; [4] Dawson & Cresswell 1949; [5] Dunckley 1949; [6] Potter 1949; [7] McCann 1952; [8] Wilkinson & Wilkinson 1952; [9] Black 1956; [10] Edgar 1962; [11] Turbott 1967; Gravatt [12] 1969, [13] 1970; [14] St Paul 1975; [15] Falla *et al.* 1978; [16] Norton 1980; [17] Gaze & Fitzgerald 1982; [18] Moon & Lockley 1982; [19] Craig & Douglas 1984b; [20] Hailman & Hailman 1991; [21] Oliver; CSN [22] 2, [23] 3, [24] 4, [25] 6, [26] 7, [27] 8, [28] 9, [29] 21, [30] 22, [31] 23, [32] 24, [33] 25, [34] 28, [35] 29, [36] 34, [37] 35, [38] 37, [39] 38, [40] 39, [41] 41, [42] 42, [43] 43, [44] 44, [45] 45; [46] D.J. Onley.

Young Fed entirely on insects (Stead 1932); in another study, fed on insects, including caterpillars and other larvae, and spiders; feeding process extremely rapid, and parents arrive, feed chicks and leave in a few seconds (Soper 1965). On Kapiti I., one brood fed almost exclusively on artificial sugar water (Wilkinson & Wilkinson 1952). On Aorangi I., Poor Knights Is, both parents fed nestlings roughly equally till 12 days old; subsequently, overall feeding rate remained similar (1 visit/3–4 min), but female made 2–3 times more visits than male; parents continued feeding young for at least 7 days after leaving nest. Of 50 recognizable items: 46 were adult insects (including moths), ten were insect larvae, and two were nectar (Sagar 1985).

Intake On Kapiti I., energy intake for birds feeding on nectar from five species of plants estimated at c. 0.2–1.3 kJ/min, which mostly satisfies estimated energetic requirements (0.25 kJ/min). Average number of flowers visited by individuals while foraging for 1 min at various plant species were: *Geniostoma rupestre* 47.4 fl./min (6.29; 10.2 min); *Dysoxylum spectabile* (early flowering) 37.2 (5.35; 6.0), late flowering 42.0 (5.85; 8.6); *Pseudopanax arboreus* (male fl.) 85.6 (3.27; 3.1); *Pittosporum crassifolium* 28.5 (3.35; 17.5) (Castro & Robertson 1997).

SOCIAL ORGANIZATION Based on contribution by E. Marks. Most information from long-term studies on social organization on Tiritiri Matangi I. (Craig & Douglas 1984a, 1986; Craig 1985); study of breeding on Poor Knights Is (Sagar 1985); and studies of interspecific hierarchies (Craig et al. 1981b; Craig 1984). Outside breeding season, on Tiritiri Matangi, social organization is related to individuals competing for access to limited sources of nectar (Craig & Douglas 1986); birds will use a range of strategies, from gathering at nectar sources and forming dominance hierarchies, to holding individual feeding territories with resident males each defending food at site near its breeding territory (see Territories, below); males do not give preferential treatment to mates (Craig & Douglas 1984a). On Poor Knights Is, at end of breeding season, immatures sometimes join winter feeding flock; during non-breeding season, adult males continue to maintain territories held in breeding season; females become non-territorial and, especially during autumn, sometimes join feeding flocks of juveniles and immatures (Sagar 1985). Before start of breeding season, said that pairs re-form (NZRD); and pairs hold territories in breeding season (see below). Often associate with other species of honeyeaters when foraging. Also associate with other passerines such as Grey Warbler *Gerygone igata* and New Zealand Tomtit *Petroica macrocephala* (Oliver). On Little Barrier I., in July, just as likely as not to be found in a mixed-species flock (McLean *et al.* 1987).

Bonds Monogamous. Retain mate year after year (Craig & Douglas 1984a; Craig 1985). Courtship begins in winter, before breeding season starts; after mating, pairs stay together (NZRD); courtship displays noted late Aug. (Sagar 1985). Males occasionally visit nests of neighbouring pairs (NZRD). Once, when female was chased by a male, her nearby mate chased intruding male, leaving female to feed undisturbed for a while; though suspected male probably chased intruder because he had invaded area rather than to help mate (Craig 1985). On Poor Knights Is, pair-bond ends at end of breeding season (late Dec.); and in NI, pair-bonds mostly break down during non-breeding season (Craig & Douglas 1984a). Sexually mature at 1 year (NZRD). **Parental care** Only female builds nest, incubates, and broods nestlings, but both parents feed nestlings (Stead 1932; Sagar 1985); both defend territory, though male possibly takes greater role, whereas female more prominent in defence of nest. Once fledged, young stay near nest and fed by both parents for at least 7 days (Stead 1932; Sagar 1985), but fledgelings can depend on parents for up to several weeks; on Poor Knights Is, juveniles first seen alone c. 6 weeks after first fledgelings known to have flown (Sagar 1985); after fledging, young stay together for 10–14 days while they learn to forage for themselves (NZRD).

Breeding dispersion Nesting solitary. On Poor Knights Is, 10–11 nesting pairs in 0.45 ha, with minimum distance between nests 12 m (Sagar 1985). **Territories** On Poor Knights Is, adult males defended territories all year, and all of 20 banded males occupied same territories for up to 5 years, with only slight adjustments to some boundaries. At any time of year, birds of either sex left territory for brief periods to use localized

sources of food, to drink or to bathe (Sagar 1985). BREEDING SEASON: On Poor Knights Is, during breeding season, female shares territory with male and both chase other Bellbirds from area (Sagar 1985). Male largely responsible for defence of breeding area (Craig 1984), though female prominent in defence of nest (see Social Behaviour: Parental anti-predator strategies). Resident female may dominate non-resident males at food sources near her breeding territory (NZRD). NON-BREEDING SEASON: On Poor Knights Is, at end of breeding season, females become non-territorial; males continue to hold territories, but territorial boundaries less defined during winter (Sagar 1985). On Tiritiri Matangi I., resident males defended and resident females ranged over areas similar to those occupied when breeding; social organization in foraging areas during winter was complex, shifting with changes in distribution of resources from exclusively held territories to access based on dominance hierarchies, e.g. at one concentrated resource, a flowering *Vitex* tree, a linear hierarchy was formed among 35 banded males and 14 banded females that visited; at a dispersed resource, flowering *Dysoxylum* trees, both males and females held feeding territories (Craig 1985; Craig & Douglas 1986); see below. HIERARCHIES: Males dominate females at all sources of nectar, and during non-breeding season will often displace mate (Craig 1985; Craig & Douglas 1986); but females said to dominate males at nest (Craig 1985). Dominance allows access to good feeding areas; dominance by males at food sites leads to sexes having different diets and feeding in different areas (Craig & Douglas 1984a; Craig 1985). In hierarchy at flowering *Vitex* tree in winter: males dominated females, though high-ranking females displaced non-resident and younger males; older birds more dominant than younger birds; residents more dominant than non-residents; highest-ranking male and female had nested closest to tree during breeding season; adult resident males were most dominant. Dominant birds spent longer in tree each day than subordinate birds, spent more time foraging in morning when nectar levels highest, and repelled other birds trying to feed. Area of tree used by most dominant males was similar to that used by intermediate males in hierarchy, but dominant males each spent most time in a core-range of the tree (their preferred part of the tree) that was twice as large as core-ranges of intermediate males; when dominant males left trees, intermediates became dominant and significantly increased size of their core-ranges (Craig & Douglas 1986). FEEDING TERRITORIES: On Tiritiri Matangi I., as *Dysoxylum* trees in area began to flower, birds moved from *Vitex* tree to establish feeding territories in *Dysoxylum*. Initially only males held territories, excluding all other conspecifics, and females forced to feed elsewhere. As flowering increased, females established their own feeding areas, excluding other females but not nearby resident males. Resident males returned to, and defended, similar sites to those held while breeding, regardless of density of flowers. Usually male territories did not overlap with those of other males, though sometimes overlapped with territory of mate. Territories of females overlapped mostly with other females' territories. Females defended ranges that were smaller (793 m² [296; 19]) than those of males (1973 m² [751; 9]); range of female territory size varied much, largest being more than ten times larger than smallest. Resident males that bred in area defended larger territories (2405 m² [958; 6]) than males new to area (1108 m² [164; 3]); similiarly, resident females defended larger territories (1230 m² [576; 8]) than other females (474 m² [104; 11]) (Craig 1985; Craig & Douglas 1986). INTERSPECIFIC HIERARCHIES: Interspecific aggression and hierarchies occur among honeyeaters at food resources: Bellbird subordinate to the larger Tui, but dominant over Stitchbird; both Tui and Bellbird have wing-slots that make wing-noises associated with aggression and courtship; not known whether female Bellbirds dominate male Stitchbirds (Craig et al. 1981b; Craig 1984, 1985). Tui feeds on flowers with highest levels of nectar; Bellbird feeds mainly on those with intermediate levels. Only individuals of the most dominant species were able to maintain exclusive access to resource, and this only happened in trees with low numbers of flowers. In trees with many flowers, defence was uneconomic, and access to flowers by the three species was in direct relationship to status and likely returns (Rasch & Craig 1988). Also reported attacking other species, e.g. once observed attacking House Sparrows *Passer domesticus* at feeding table (Gibson 1961).

Roosting Nocturnal, but roosting behaviour unknown. Start singing before sunrise (Stead 1932). Said that Alarm Call often heard at dusk, possibly to bring pairs together for roosting (NZRD).

SOCIAL BEHAVIOUR

Based on account prepared by E. Marks. Studies as for Social Organization; also notes in Stead (1932). Females less conspicuous in some seasons (Craig & Douglas 1984b).

Agonistic behaviour Pugnacious (Stead 1932), though level of aggression displayed varies with individuals and concentration of resources (Craig & Douglas 1986). Adult males and females have wing-slots that produce noise in aggressive encounters, but in juveniles, which are subordinate to all adults, these are absent or very small (Craig 1984, 1985). Dominance of male is partly result of larger size of both body and wing-slots compared with females and juveniles (Craig & Douglas 1986). Terrritories and hierarchies established by chasing and Song (Craig & Douglas 1986); territorial disputes normally resolved by aggressive displays, vocal threats and aerial chases (Wilson & Wilson 1999). SINGING: Both sexes sing (Stead 1932) and there is much variation in Song (see Voice). On Tiritiri Matangi I., Songs used by all residents to advertise their presence in feeding territories (Craig & Douglas 1986). Birds sing and counter-sing, which identifies locations of neighbouring birds and possibly allows birds to space themselves in relation to one another (NZRD). Once, after chase, group of five males gathered, sitting c. 1 m apart with tails slightly spread, feathers of breasts and backs raised, heads forward and bills pointed downward; moved their bodies from side to side and sang; lasted c. 5 min (Stead 1932). Rarely, males gather in groups of up to 15 birds within c. 10 m radius and exchange Song (J.L. Craig); seen especially in breeding season, late in day, and often near good sources of food (Stead 1932); both Oliver and Marples (1944) also noted groups. Sing throughout year, though to different degrees over year (see Voice). Males and females attracted to playback of calls (Craig & Douglas 1984b). **Threats** Aggressive postures include raising wings slightly and vibrating them rapidly. Fluffing of body feathers is also common (J.L. Craig). When chasing in flight, make whirring noises with wings (Stead 1932; Craig 1984). **Fighting** Once, in Dec., two males seen fighting in stream; one pushed other under water by placing its foot on it, while flapping to hold position, till other bird drowned; afterwards, victor preened and rested (Wilson & Wilson 1999). In another conflict between two males, birds dug claws into head and body of opponent and remained locked together on ground, breast to breast, for some time; after fight, one flew short distance and rested (Taylor 1969). **Alarm** Give Alarm Calls when predators nearby. Seen mobbing a Southern Boobook *Ninox*

novaeseelandiae with other species of passerines (Wilkinson 1927). Alarm Call apparently serves to attract other birds (NZRD).

Sexual behaviour Courting in winter involves male giving Quiet Song (see Voice) while conducting VERTICAL HOVERING DISPLAY in front of female; during this display, male holds body almost vertically and hovers or flies slowly upward, making loud whirring noise with wings (NZRD). This is similar to display noted by Stead (1932), though he gives no context: male sometimes flew from tree, and with body held almost upright, flew up and down 2–3 times in *c*. 1 m waves, calling and whirring wings; then flew away calling, with same noisy flight (Stead 1932). During spring and when mating, pairs fly swiftly together, one above the other, a few centimetres apart, in fast synchronized flight through vegetation. Once, in Nov., pair flew low, then dropped to ground and thrust bills at each other; then flight resumed, male rising first, before female picked up a twig, flew to a tree, deposited it and then flew after male; no calls given (Guthrie-Smith 1914). After mating, pairs stay together constantly and often duet (NZRD). **Courtship feeding** Before female starts to incubate, male sometimes feeds her; female receives food with bill open and wings quivering; also fed on nest when incubating (Stead 1932). **Copulation** Once, male sat on branch near female, fluffed his feathers and sang for *c*. 3 min before attempting copulation, but female flew away (Sagar 1985). Two out-of-season copulations seen, after which females were allowed to forage in males' areas (Craig 1985).

Relations within family groups When male approaches nest to feed nestlings, female leaves nest and forages nearby, returning only after male leaves (Sagar 1985). Young often leave nest before able to fly, and perch nearby (Stead 1932); for several days after leaving nest, give loud begging calls almost continuously (Stead 1932; Sagar 1985). **Parental anti-predator strategies** Female sits tightly (Guthrie-Smith 1914; Stead 1932). Female attacks any intruder near eggs or young when necessary (NZRD). To distract a predator, female may: stay a few centimetres away, crouch low and give plaintive call; hop agitatedly nearby and give Alarm Call (Stead 1932); or fall to ground and flap through undergrowth (NZRD). Male appears in response to female's Alarm Calls and sings near nest (NZRD).

VOICE Quite well known. Study by Marples (1944), at Dunedin, SI, on number of Song-types and of seasonality of Song. Study by Craig (1984) on wing-noise, includes sonagram. Andersen (1909, 1911, 1913, 1915, 1918, 1926) at different times and locations recorded >40 calls in musical notation. McLean (1912) also provides calls in musical notation. Has been classed as one of the best 22 songsters of the world (Hartshorne 1973). Notes are simple but varied, the resemblance of one note to the tolling of a distant bell being responsible for the vernacular name (Buller 1888). The usual notes are clear whistles, such as can be produced on a piccolo, although the instrument is more shrill and cannot sound *pianissimo*; other notes are flute-like or bell-like, and extremely mellifluous, particularly when sung slowly (Andersen 1926). Sing all year, though less in winter (Stead 1932; St Paul 1975) with Song at its best during spring (McLean 1912). Sing at dawn for *c*. 20 min, starting before sunrise, though Dawn Song said not to be given in some areas where the species appears to be numerous; also sing at dusk (Potts 1882; Stead 1932; St Paul 1975). Song in morning and evening comprised three distinct sounds resembling the chiming of bells; Song during the day more a warbling sound (Reischek 1887; St Paul 1975). Usually silent when foraging, except at concentrated nectar sources

(NZRD); on Three Kings Is a 'mellifluous chorus' was noted from at least a dozen birds at a flowering food source (Turbott & Buddle 1948). Such choruses of many birds may occur at any time of day (St Paul 1975). Birds can sing in perfect unison, giving illusion that one bird is singing ventriloquially (St Paul 1975). Sing in flight (St Paul 1975). Both sexes sing (Buller 1888; McLean 1912; Andersen 1923). Male has Dawn Song, Full Song and Quiet Song, and there is Female Song (NZRD). Song of male fuller and louder, allowing the sexes to be distinguished (Potts 1882; Andersen 1926; Stead 1932; Craig & Douglas 1984b). Male is said to sing more than the female (Stead 1932), but also said to be silent for part of year (Andersen 1926). After mating, pairs stay together constantly and often duet (NZRD). On Three Kings Is, both male and female have same harsh call-note, pitched a little higher in female (Turbott & Buddle 1948). Song varies with locality, although basic pattern similar (Stead 1932; NZRD). Birds in one location answer each other with same notes, and different calls will be heard in other locations, while, on return to first location (after an unspecified time), call will be found to have changed (Oliver 1922). Song of subspecies *obscura* on Three Kings Is said to differ from that on mainland (Falla 1948); that of extinct subspecies *melanocephala* on Chatham Is said to have been richer and fuller than that of mainland (Travers 1873). Some notes indistinguishable from those of Tui, with which often confused, but Bellbird usually delivers its notes at some pace; notes of Tui are said to be richer, more rollicking, more fluid, more resonant and more varied than those of Bellbird; and Tui is more likely than Bellbird to intersperse harsher sounds among its notes (McLean 1912; Oliver 1922; Andersen 1923, 1926; Stead 1932; Falla *et al.* 1979; Craig & Douglas 1984b; NZRD). A duet between Tui and Bellbird has been reported, both birds being in view in same tree (Andersen 1911, 1915, 1926). Playback of Song within a forest patch will attract both males and females (Craig & Douglas 1984b). MIMICRY: Andersen (1926) thought Bellbird not a mimic, but conceded that many would disagree. Oliver (1922) thought mimicry of Tui by Bellbird was likely. McLean (1912) reported a female giving a soft rendering of sucking, guttural notes of a Tui. NON-VOCAL SOUNDS: Loud wing-noises, which include a wide range of frequencies, with major components in the lower frequencies, particularly <1 kHz, are heard in flight during chases and displays, most conspicuously during aggressive interactions but also during courtship displays (Craig 1984). Wing-noise also audible when birds fly from branch to branch and when they pursue insects (Potts 1882; McLean 1912). Sonagrams show that there are breaks in the wing-noise and that it ends abruptly, suggesting that birds control its production (Craig 1984), a conclusion that had been drawn by an earlier observer (Stead 1932). The noises appear to be produced by slots in wing from emargination of ninth primary. Such wing-slots are larger in males than females, and absent or extremely small in young birds (Craig 1984, 1985). Snapping of bill may accompany Song (Reischek 1887).

Adult SONG: Most Song varies greatly in form and length (J.L. Craig). This section discusses general aspects of Song, while separate sections below cover the categories of Song distinguished by NZRD, namely Dawn Song, Full Song and Quiet Song of male, and Female Song. A variety of Songs are given but they are easily distinguished, being chiefly broken peals of 5–8 notes (McLean 1912; Marples 1944). See sonagram **A**. At one site in Dunedin, four Songs were given during 5-year study. In addition there were four other Songs made for 1–5 days, probably from birds passing through. The first Song, of
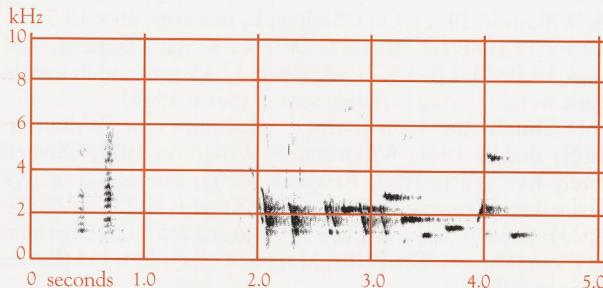
A L.B. McPherson; Abel Tasman NP, SI, Oct. 1984; P107

seven notes, was given all year, but with a peak of occurrence in May (but sometimes as late as Aug.) and a minimum in Oct. The second Song, of two notes, a *zizz*, a further two notes, followed by a phrase of six notes, the third of these being high-pitched and heavily accented; and the third Song, a series of descending notes, usually four, but sometimes three or five; both had peaks of occurrence in June or July, but did not occur for 4–5 months during spring and summer. The fourth Song, not described, had a similar occurrence to second and third but with peak somewhat earlier in year. In areas 2–3 km away, there were unfamiliar songs or variants of familiar ones. Second Song was sometimes given by groups of males perched within a metre or two of each other, and all singing with great energy (Marples 1944). Another observer commented that singing in chorus appeared to be only by males, and was often performed near a food source, particularly during the breeding season (Stead 1932). Rarely, males gather in groups of up to 15 birds within a *c*. 10 m radius, and exchange Song (J.L. Craig). During court-ship, male sings in front of female (NZRD), and at Poor Knights Is, NI, one male sang for 3 min before attempting copulation (Sagar 1985). Members of a pair sing and counter-sing with neighbouring birds to ascertain relative position of neighbours (NZRD). Song also used to advertise presence in feeding territories (Craig & Douglas 1986). If predator near nest, male responds to Alarm Calls of female by singing near nest (NZRD). DAWN SONG: Simple song of 2–6 pure bell-like notes, occasion-ally interspersed with quieter notes, monotonously repeated for 10–40 min, at any time of day, but particularly at dawn, less often at dusk, and more often in breeding season (Stead 1932; NZRD; J.L. Craig). May be sung by neighbouring males in unison (NZRD). FULL SONG: Varies; includes bell-like notes as well as *chonks*, *clonks*, harsh *jarrs*, and quiet notes. Males give long choruses where ranges overlap, particularly at rich food sources. Part or all of Full Song is given at any time of day and it is often used in counter-singing between neighbours (NZRD). QUIET SONG: Quiet Song is audible only to 10 m, and is used during Vertical Hovering Display (see Social Behaviour) (NZRD). Whisper-song of Andersen (1918, 1926) probably corresponds to Quiet Song: it was sung very softly, with 'curious interjections' separating the phrases. Often the *tlank* or other interjection was heard, and snatches of Whisper-song could be heard on closer approach; for another, sung at dusk for 2–3 min, nothing but the interjection *kwak*, at regular intervals of *c*. 2 s, could be heard at 6 m, and at 3 m the Whisper-song, of mellow though highly pitched notes, occasionally broadening to a bell sound, was barely audible, although there was a perceptible rise and fall in intensity (Andersen 1918, 1926). Another observer reported sucking, sobbing, wheezing and coughing notes, like those of Tui, but given very softly (McLean 1912). FEMALE SONG: Consists of 7–15 relatively pure notes, preceded by several titters (NZRD). It differs from male Songs and often

consists of same stereotyped pattern (J.L. Craig). Females use it to counter-sing against each other and to duet with their mates. They may sing on nest (NZRD). ALARM CALL: Staccato call (NZRD). See sonagram **B**. Given when alarmed and when mobbing predators; it attracts conspecifics (NZRD). Occasion-ally given while foraging, particularly during heavy rain, and often at dusk, perhaps to bring pairs together for roosting (NZRD). Given when Cat or owl present (Wilkinson 1927). Repeated scolding *tink-tink-tink* (McLean 1912), chattering cry of warning, attracting conspecifics (Potts 1882), succession of notes 'like a policeman's rattle', attracting conspecifics (Buller 1888), and sharp, shrill note, quickly repeated, given by female when flushed from nest (Stead 1932), all probably same call. **Other calls** Continuous whistling when feeding (Oliver 1922). Squeaks given by fighting birds (McLean 1912). Plaintive cry given by female, while crouching, after being flushed from nest (Stead 1932).
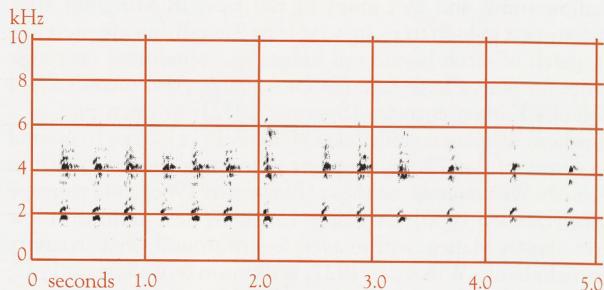
B L.B. McPherson; Abel Tasman NP, SI, Oct. 1984; P107

Young Nestlings and fledgelings utter high-pitched beg-ging calls, particularly when parents nearby (NZRD). A high-pitched, single sharp note was repeated by a young bird, its gape still white at the base; 3 weeks later the note was F instead of A, and was repeated incessantly twice per second for minutes at a time, stopping only for a couple of seconds when food was given (Andersen 1918). Incessant squeaky begging calls given almost continuously for at least 1 week after young leave nest, becom-ing much less frequent once young begin to forage for them-selves (Stead 1932; Sparrow 1982; Sagar 1985). Low twittering from flying young, still being fed by parents (Moncrieff 1928). While still in juvenile plumage, young males learn Song from nearby adult birds, their first attempts being low yet harsh squeaks 'lacking in tone' (Potts 1882; Stead 1932; NZRD).

BREEDING Detailed study over three seasons on Poor Knights Is (Sagar 1985); and notes from Stewart I. (Guthrie-Smith 1914) and Kapiti I. (Wilkinson 1927; Wilkinson & Wilkinson 1952). Some information from Chatham I. (Oliver). Said to be host of Long-tailed Cuckoo *Eudynamys taitensis* (Cunningham 1966).

Season Breed Sept.–Jan., rarely to Mar.; sometimes raise two broods in season (Turbott 1967; Moon 1992; Heather & Robertson 1997; Oliver). NOMINATE MELANURA: Eggs, Nov.–Jan. (NMNZ; NZ NRS); one brood of fledgelings, late Oct. (Turbott 1967). NI: Young, late Dec. and early May (Potts 1884; CSN 32); fledgelings, late Dec., early Jan. and early Apr. (Sagar 1985; CSN 32, 41, 44). SI: Nest, Oct. (CSN 24); fledgelings, early Jan. (Sparrow 1982). SUBSPECIES ONEHO: On Poor Knights Is, breed late Sept. to late Dec.; probably single-brooded, but sometimes lay replacement clutch after failure; laying, late Sept. to late Nov., with peak mid-Oct. to mid-Nov.; eggs at least

late Oct. to early Dec.; young, late Oct. to early Nov. and late Nov. to early Dec.; fledgelings, late Oct. to late Dec. (Sagar 1985). SUBSPECIES MELANOCEPHALA: On Chatham I., bred Aug.–Oct. (Potts 1884).

Site Well concealed and sheltered from elements, among foliage of tree or shrub, occasionally in crevice in rock face or in hole in tree-trunk (Sagar 1985; Oliver). Favourite nesting trees are rata *Metrosideros* and Manuka *Leptospermum scoparium*; also recorded in dense clumps of creeper, particularly *Rubus*, and in thick grass on a steep bank (Potts 1884; Stead 1932; Falla *et al*. 1975). On Poor Knights Is, two distinct types of site preferred: (1) in dense canopy layer of shrubs, mainly Mahoe *Melicytus ramiflorus*, *Coprosma macrocarpa* and *Myrsine divaricata*; (2) in rock faces, usually concealed behind dense vegetation such as *Muehlenbeckia*, though sometimes in bare crevice. Of 70 nests, 36 (51.4%) in canopy, 15 (21.4%) in rock crevice, and rest on branches overgrown with dense *Parsonsia*, against trunk or on low branch surrounded by dense foliage, in hollow trunk and in canopy of tall tree. In Minginui area, mostly nest in high trees, up to at least 9 m tall, but also nest low in patch of scrub beside tall forest, and sometimes on rough ledge on side of large tree (St Paul 1975). Also recorded in a Kanuka *Kunzea ericoides* (Sparrow 1982); in open part of a Tawhero *Weinmannia silvicola* (McLean 1912); close to ground in centre of flax *Phormium* plant (Kinsky & Sibson 1959); in Kamahi *Weinmannia racemosa* (Blackburn 1968); and in grape vine (Dawson 1950). On Kapiti I., usually nest in shrub or low tree, mostly Mahoe, within a few feet of ground; once in cavity in rocky bank (Wilkinson 1927; Wilkinson & Wilkinson 1952; CSN 32). On SI, one nest in rata (CSN 24). On Stewart I., one nest in garden hedge between two buildings; another in a deserted building, which birds entered through broken door, with nest beneath sagging roof of Totara *Podocarpus totara* bark (Guthrie-Smith 1914). On Chatham I., nested in Karaka *Corynocarpus laevigatus*, where Supplejack *Rhipogonum scandens* vines provided shelter; also in Karamu *Coprosma robusta* and under crown of tree-fern (Oliver). MEASUREMENTS (m): Height of five nests, including two approximations, 5.1 (6.18; 0.9–16) (McLean 1912; Buddle 1941; Sparrow 1982; CSN 24; Oliver). On Poor Knights Is, 21.4% of nests built on ground.

Nest, Materials Untidy cup-shaped nest; outer cup of twigs, leaves, rootlets, grass and moss; inner cup of fine grass, moss and sometimes scales of Mamaku (Black Tree-fern) *Cyathea medullaris*, lined with feathers, sometimes moss (Guthrie-Smith 1914; Wilkinson 1927; Wilkinson & Wilkinson 1952; Sagar 1985; Oliver). Potts (1884) said that feathers usually all same colour, from same type of bird; from petrels, New Zealand Pigeon *Hemiphaga novaeseelandiae*, Kaka *Nestor meridionalis*, or parakeet *Cyanoramphus* (Guthrie-Smith 1914; Wilkinson 1927; Sagar 1985). Female collects material and builds nest (Wilkinson & Wilkinson 1952). One female collected dry grass from beside path (Sparrow 1982). One nest completed in *c*. 3 days (Sparrow 1982). One female began building second nest 6–7 days after first brood fledged; once, second nest *c*. 40 m from first (Sparrow 1982). MEASUREMENTS: Diameter of nest, *c*. 15 cm (Wilkinson & Wilkinson 1952).

Eggs Pink or pinkish white, with spots and blotches of brown to reddish brown, mainly at larger end (Guthrie-Smith 1914; Wilkinson & Wilkinson 1952; Sagar 1985; Oliver). On Chatham I., pink, with large reddish-brown blotches at larger end, smaller blotches elsewhere (Oliver). MEASUREMENTS: 22.4 (0.98; 21.0–24.1; 15) × 16.5 (0.49; 15.1–17.0) (NMNZ; Oliver); Poor Knights Is: 22.7 (0.76; 21.1–23.8; 21) × 16.1 (0.49; 15.1–17.0) (Sagar 1985); vary from 22.5 × 16 to 25 × 17 (Wilkinson

& Wilkinson 1952). On Chatham I., two eggs, 26 × 18.5 and 25.5 × 19 (Oliver). WEIGHT: On Poor Knights Is, newly laid eggs, 3.1 (0.23; 2.8–3.5; 7); equal to *c*. 12.4% mean adult female body weight during breeding season (Sagar 1985).

Clutch-size Usually three, sometimes four (Wilkinson 1927; Buddle 1941; Wilkinson & Wilkinson 1952; Oliver); rarely five (Potts 1884; Reischek 1887); one brood of five fledgelings (Sparrow 1982). On Poor Knights Is, 2.87 (0.63; 2–4; 23): C/2 × 6, C/3 × 14, C/4 × 3 (Sagar 1985). On Chatham I., three (Oliver). On Tiritiri Matangi I., 3.6 (3–4; 11) (Bartle & Sagar 1987).

Laying Eggs laid at 1-day intervals (Sagar 1985). Lay replacement clutch after loss of eggs; one pair incubating replacement clutch 15 days after loss of first eggs (Sagar 1985).

Incubation By female only (Wilkinson & Wilkinson 1952; Sagar 1985). Begins attentively with completion of clutch; before completion, eggs may be left for several hours (Sagar 1985). Leave nest for short periods during early stages of incubation; near hatching, sit very closely (Wilkinson & Wilkinson 1952). One female spent 3–5 min foraging away from nest for every 12–20 min spent incubating (Sagar 1985). Male feeds female on nest (Stead 1932; Wilkinson & Wilkinson 1952; Sparrow 1982). A clutch of three fresh eggs that was swapped for three well-incubated eggs was not rejected by adults (Buddle 1941). INCUBATION PERIOD: *c*. 13 days (Wilkinson & Wilkinson 1952), or *c*. 14 days (Heather & Robertson 1997); interval between laying and hatching of last egg (n=2), 14.5 and 15.5 days (Sagar 1985). Eggs in two-egg clutches hatched within 24 h of each other, eggs in three-egg and four-egg clutches hatched over 2 days (Sagar 1985). A clutch of three eggs hatched within 24 h (Buddle 1941).

Young Altricial, nidicolous. At hatching, eyes closed, with down only on crown and along back. Develop a covering of down within a few days; at 7 days, eyes opening; at 10 days, remiges have emerged from pins; at 15 days, young active and perch on rim of nest (Sagar 1985). Only female broods (Buddle 1941; Sagar 1985); during first 5–6 days, young brooded for *c*. 42% of daylight hours; thereafter, brooded only at night (Sagar 1985). Both sexes feed young (Buddle 1941; Wilkinson & Wilkinson 1952; Sagar 1985); up to 12 days old, nestlings fed equally by both sexes, with one feeding visit made every 3–4 min; after 12 days female made 2–3 times more feeding visits than male (Sagar 1985). At one nest, when male approached nest to feed young, female left nest and foraged in nearby vegetation, returning only after male departed (Sagar 1985). At another nest, female left when male approached; male fed young, removed faecal sac, swallowed it and then flew away; 5 min later, female returned, fed young, removed faecal sac, then brooded young till male returned; male usually absent for 8–10 min (Buddle 1941). Both sexes carry faecal sacs away or eat them (Buddle 1941; Sagar 1985).

Plate 43   (P. Slater)

Yellow Chat *Epthianura crocea* (page 1229)
NOMINATE CROCEA: **1** Adult male breeding; **2** Adult male non-breeding; **3** Adult female breeding; **4** Juvenile; **5** Immature male non-breeding; **6** Immature female non-breeding; **7** Adult female breeding
SUBSPECIES TUNNEYI: **8, 9** Adult male breeding

Orange Chat *Epthianura aurifrons* (page 1220)
10 Adult female

Fledging to independence FLEDGING PERIOD: c. 14 days (Wilkinson & Wilkinson 1952); 19 days (n=1); several young still in nest at 16 days (Sagar 1985). After fledging, young remain near nest, usually in dense vegetation, and are fed by both sexes (Sparrow 1982; Sagar 1985); fed for at least 7 days, and may be dependent on parents for several weeks (Sagar 1985). Female continues to feed young for first day or two after fledging; young begin to forage for themselves after 3 days; continue to be fed occasionally for c. 10 days (Wilkinson & Wilkinson 1952). One brood, 5–6 days after fledging, fed only by male; at 10–11 days, brood had moved c. 50 m from nest area, still fed by male but also foraged for themselves; at 16–17 days, still fed occasionally by male (Sparrow 1982).

Success On Poor Knights Is, of 116 eggs in 42 nests, 101 (87.0%) hatched; four nests (9.5%) failed to hatch any eggs, of which three were deserted and one was destroyed, probably by petrel crashing into it at night; of 21 young in eight nests, 20 (95.2%) fledged; overall, 82.8% eggs produced fledgelings. One clutch taken by rats (Guthrie-Smith 1914). Three partly eaten corpses of fledgelings found (CSN 44).

PLUMAGES Prepared by A.M. Dunn. Fledge in juvenile plumage. Partial post-juvenile (first pre-basic) moult to immature plumage starts within a few months of fledging. Immature plumage resembles adult plumage in nominate, but differs slightly from adult in subspecies *oneho* from Poor Knights Is. Attain adult plumage with complete first immature post-breeding (second pre-basic) moult when 12–14 months old. Thereafter, complete post-breeding (pre-basic) moults each cycle produces successive adult plumages without change in appearance. Sexes differ in plumage. Four subspecies; nominate *melanura* and subspecies *oneho* described below; see Geographical Variation for descriptions of the other two subspecies. Description of nominate *melanura* based on examination of skins of 29 adult males, 20 adult females, two juvenile males, three juvenile females, 12 immature males and 12 immature females. Description of *oneho* based on examination of skins of six adult males, two adult females, one juvenile male, one juvenile female and one immature male.

Adult male (Definitive basic). NOMINATE MELANURA: HEAD AND NECK: Forehead, crown, nape, hindneck, sides of neck and ear-coverts, dark olive (46–49) with iridescent purple (127A–172B) sheen and concealed dark-grey (83) bases to feathers; iridescent sheen strongest on forehead and ear-coverts, and covers most of each feather; sheen becomes weaker on crown and nape, where confined to tips of feathers, and usually absent on hindneck and sides of neck; sheen not visible from some angles. Lores and eye-ring, black (89). Chin, olive-black (ne) with strong iridescent purple (172A–172B) sheen. Throat, dark greyish olive (c49) with weak iridescent purple (172A–172B) sheen on throat. UPPERPARTS: Mantle, back, scapulars and uppertail-coverts, dark olive to olive (46–50). Rump, olive

(c50), marginally brighter than rest of upperparts. UNDERPARTS: Breast, belly and most of flanks, grade from dark greyish olive (c49) on upper breast to olive (c50) on lower belly and rear-flanks. Patch of feathers on anterior flanks (rarely concealed by folded wing), pale yellow (c157). Vent, pale yellow (c157) to yellowish white (ne). Undertail-coverts, grey-olive (c42) with pale-yellow (c157) to off-white (ne) shaft-streaks of varying width; outer undertail-coverts almost completely off-white (ne). Thighs, olive-grey (c42). UPPERTAIL: T1–t5, black-brown (119) with narrow (1–2 mm wide) iridescent blue-black (173) edge to outer webs that extend from base to c. 1 cm from tip, and with narrow indistinct grey-olive (c43) fringe to tips. T6 similar to other rectrices, but lacks iridescent blue-black outer edge. UNDERTAIL: Dark brown (c121) with black (c89) edge to outer webs of t1–t5. UPPERWING: Marginal and median coverts, dark olive (c46) with concealed grey (84) bases. Greater secondary coverts and smaller feathers of alula, grey-black (82) with broad dark-olive (c46) fringe to outer webs and tips. Largest feathers of alula, grey-black (82) with weak blue-black (c90) iridescence to outer web. Greater primary coverts and tertials, grey-black (82) with narrow dark-olive (c46) fringe to outer webs. Secondaries and inner primaries (p1–p3), black-brown (119) with very narrow (<1 mm) olive (50) edge that extends for c. 2 cm along distal half of outer web, and with narrow, weak, iridescent blue-black (c90) edge to basal half of outer web. Outer primaries (p4–p10), black-brown (119) with weak blue-black (c90) iridescence to basal half of outer web; p9 has strongly emarginated tip (see Structure and Ageing). Iridescence to remiges and alula disappears with wear. UNDERWING: Secondary coverts, grey (84) with pale-yellow (c157) wash. Marginal and median primary coverts, dark olive (46) with grey (84) bases. Greater primary coverts, grey (84). Remiges, dark brownish grey (ne). SUBSPECIES ONEHO: Mostly as adult male nominate, but iridescent sheen to head and neck slightly bluer; feathers of forehead, crown, nape, ear-coverts, chin and throat have violet (c72) sheen (cf. purple [172A–172B] of nominate).

Adult female (Definitive basic). NOMINATE MELANURA: Females much browner than males. HEAD AND NECK: Forehead, crown, nape, hindneck and sides of neck, grey-olive (43) to dark grey-olive (ne) with iridescent dark-blue (c170) sheen and concealed grey (84) bases to feathers; iridescent sheen much weaker than in male, strongest on forehead and crown, very weak on nape, and absent from hindneck and sides of neck. Ear-coverts, olive-brown (c29) with very weak iridescent dark-blue (c170) sheen. Lores and eye-ring, grey-black (c82). Short white moustachial stripe extends for c. 1 cm from gape. Malar area, olive-brown (c29) with light-brown (c223D) tips to feathers. Chin and throat grade from light brown-grey (44) or light brown (c223D) to slightly richer light brown (c26). UPPERPARTS: Dark olive (c48). UNDERPARTS: Breast, belly and most of flanks, buffy olive (ne). Patch of feathers on anterior flanks (rarely concealed by folded wing), yellow-white (ne). Vent, cream (c54) to off-white (ne). Thighs, light brown (c223D). Undertail-coverts, buffy olive (ne) with pale-yellow (c157) to off-white (ne) shaft-streaks of varying width; outer undertail-coverts almost completely off-white (ne). UPPERTAIL: T1–t5, dark brown (121) with narrow (1–2 mm wide) olive (50) edge to outer webs that extends from base to c. 1 cm from tip. T6, dark brown (121). UNDERTAIL: Brownish grey (c79). UPPERWING: Marginal and median coverts, dark olive (c48) with concealed brownish-grey (79) bases. Greater secondary coverts and smaller feathers of alula, dark brown (121) with broad dark-olive (c48) fringe to outer webs and tips. Largest feathers of alula, dark brown (121). Greater primary coverts

and tertials, dark brown (121) with narrow dark-olive (c48) fringe to outer web. Secondaries and inner primaries (p1–p7), dark brown (121) with very narrow (<1 mm) olive (50) edge to outer webs; on p4–p7, olive edge confined to basal half of feather. Outer primaries (p8–p10), dark brown (121); p9 has strongly emarginated tip (see Structure and Ageing). UNDERWING: Secondary coverts, grey (84) with pale-yellow (c157) wash. Marginal and median primary coverts, light brown (c223D) with grey (84) bases. Greater primary coverts, grey (84). Remiges, dark brownish grey (ne). SUBSPECIES ONEHO: Mostly as adult female nominate, but iridescent sheen to feathers on head and neck slightly greener; feathers of forehead, crown, nape, and ear-coverts have green-blue (c64) sheen (cf. blue [c170] of adult female nominate).

Nestling Mostly naked at hatching, with some down on crown and along back; attain covering of grey down within a few days (Sagar 1985).

Juvenile male NOMINATE MELANURA: Much duller and greyer than either adult male or female, with no iridescence on head. HEAD AND NECK: Forehead, crown, nape, hindneck and sides of neck, dark grey (83) with dark-olive (c49) suffusion. Ear-coverts, grey-olive (c43). Lores and eye-ring, black (89). Short yellowish-white (ne) moustachial stripe extends for c. 1 cm from gape. Malar area, dark grey (c83). Chin and throat, light grey (85) with dark-olive (c46) suffusion; feathers also have softer or looser texture than adults. UPPERPARTS: Dark grey (83) with dark-olive (c46) suffusion; strength of dark-olive suffusion varies between individuals. UNDERPARTS: Breast, belly and flanks, grade from grey (84) on upper breast to brownish grey (80) on lower belly, all with slight grey-olive (c43) suffusion. No yellow feathers on flanks (cf. adults). Vent, off-white (ne). Undertail-coverts, light grey-brown (c45) with off-white (ne) bases. Thighs, brownish grey (c79). UPPERTAIL: Similar to adult male, but with little or no iridescence to edges. T1–t5, black-brown (119) with narrow black (89) edge to basal half of outer web and narrow indistinct olive-grey (c42) fringe to distal half of rectrices. T6, black-brown (119). UNDERTAIL: Dark brown (c121). UPPERWING: Similar to adult male, but small coverts much greyer with less olive coloration, and dark-olive fringes and edges to larger coverts and remiges slightly browner. Marginal and median coverts, dark grey (83) with dark-olive (c46) suffusion to tips. Rest of primary and secondary coverts, alula and tertials, as adult male, but with slightly browner shade of olive on fringes and edges of feathers; fringes and edges dark olive (c48) (cf. dark olive [46] in adult male). Primaries and rest of secondaries, as adult male, but with weaker iridescence to basal half of outer webs and slightly browner shade of olive on edges of feathers; fringes and edges dark olive (c48) (cf. olive [50] in adult male). P9 not strongly emarginated at tip (cf. adult male). UNDERWING: Marginal coverts, cream (c92). Rest of coverts, grey (84). Remiges, dark brownish grey (ne). SUBSPECIES ONEHO: As juvenile male nominate.

Juvenile female NOMINATE MELANURA: Similar to adult female, but slightly browner in upperparts and slightly greyer in underparts, and with no iridescence on head. Browner than juvenile male. HEAD AND NECK: Forehead, crown, nape, hindneck and sides of neck, dark olive-brown (c129). Ear-coverts, grey-olive (c43). Lores and eye-ring, dark brown (c121). Short yellowish-white (ne) moustachial stripe extends for c. 1 cm from gape. Malar area, brown (c28). Chin and throat, brownish grey (80) with light-brown (c223D) suffusion to tips of feathers. UPPERPARTS: Brown (c28). UNDERPARTS: Breast, belly and flanks, light grey-brown (c45) with light-brown (c223D) suffusion to tips of feathers. Vent, cream (c92). Thighs, brown (28).

Undertail-coverts, buff (c124). TAIL: As adult female. UPPERWING: As adult female, but p9 not strongly emarginated at tip. UNDERWING: Marginal coverts, cream (c92). Rest as adult female. SUBSPECIES ONEHO: As juvenile female nominate.

First immature male (First basic). NOMINATE MELANURA: As adult male, but retain juvenile remiges and rectrices. P9 not strongly emarginated at tip (cf. adult male). SUBSPECIES ONEHO: Similar to adult male, but with less iridescence on head and neck, and retained juvenile remiges and rectrices duller than in adult. P9 not strongly emarginated at tip (cf. adult male).

First immature female (First basic). NOMINATE MELANURA: As adult female, but retain juvenile remiges and rectrices. P9 not strongly emarginated at tip (cf. adult female). SUBSPECIES ONEHO: No specimens available; probably as adult female, but with retained juvenile remiges and rectrices.

Aberrant plumage Several have been recorded; all involve abnormal amounts of yellow or white in plumage (Gaze 1984; Oliver). One yellow individual described in detail had uniform pale-yellow body with white tail, undertail-coverts, primaries and secondaries; head and throat were paler than rest of the body; eye was dark brown, legs were pale pink and bill lacked normal intensity of colour (Gaze 1984).

BARE PARTS Based on photos (Williams 1963; Brathwaite 1974; Moon 1979, 1992; Moon & Lockley 1982; Barnett 1985; NZRD) and published descriptions as cited. Sexes similar. **Adult** Bill, black (89) or dark grey (83). Inside mouth, pink (c7). Iris, crimson (108) or dark red-brown (c221A) or red (14). Orbital ring, grey-black (82). Legs and feet, dark blue-grey (78) or dark grey (c83). Claws, black-brown (119). **Nestling** Based on photo (Moon 1992): edge of bill and gape, pale yellow (157); inside mouth, orange (17); skin on side of head and ventrally, dull pink (c5); dorsal skin, dark grey (c83). **Juvenile** Bill, black (Bartle & Sagar 1987). Gape, yellow, fleshy (Bartle & Sagar 1987); obvious at least 14 days after fledging (D.J. Onley). Iris, brown. Legs and feet, glaucous (Bartle & Sagar 1987).

MOULTS Based on examination of skins of 58 adults and 29 juveniles and first immatures (CM, NMNZ) and published information. **Adult post-breeding** (Pre-basic). Complete, primaries outward. Few data available from skins; only four had active moult of primaries. One from SI was just starting moult of primaries in Feb. with PMS of 3; another from Chatham Is was starting in Dec. with PMS of 9. Two from SI were finishing moult of primaries in Apr., with PMS of 38 and 44. Active moult of body recorded in Dec., Feb., Mar. and Apr. Active moult of tail recorded in Mar. and Apr. On Poor Knights Is, moult occurs late Nov. to late Jan.; moult of body starts with feathers of head; moult of body under way by early Dec.; most adults have active moult of primaries by early Jan. (Bartle & Sagar 1987). On Tiritiri Matangi I., moult of primaries active Feb.–Apr. (Bartle & Sagar 1987). On NI, moult of primaries active in Mar. and finished by Apr. (Bartle & Sagar 1987). At Punakaiki, SI, moult of primaries and tail active late Feb. to Mar., and some moult of body continues into Apr. (Bartle & Sagar 1987). At Geraldine, SI, have light moult of head during late Jan., active moult of primaries Feb.–Apr., and moult of body can continue into May (Bartle & Sagar 1987). On Auckland Is, two had active moult of wing, tail and body in Feb. (Bartle & Sagar 1987). On Three Kings Is, adults collected during Feb. appeared freshly moulted (Bartle & Sagar 1987), and adults were recorded moulting late Dec. to early Jan. (Turbott & Bull 1954). **Post-juvenile** (First pre-basic). Partial; involves plumage of body and wing-coverts. Eight were

recorded with active moult of body: one from Chatham Is in Dec., four from SI in Feb., one from Poor Knights Is in Feb., one from Three Kings Is in Mar., and another from SI in Apr. On Poor Knights Is, undergo moult of body Feb.–Mar. (Bartle & Sagar 1987). At Punakaiki, occurs before Apr. (Bartle & Sagar 1987). **First immature post-breeding** (Second pre-basic). Complete; primaries outward. No data from skins. On Poor Knights Is (Bartle & Sagar 1987): occurs Nov.–Jan.; moult of body begins in Oct., and particularly active on head, chin and throat; moult of wing-coverts starts in late Nov.; moult of primaries starts in early Dec.; indistinguishable from adults by early Jan.

MEASUREMENTS NOMINATE *MELANURA*: (1–2) NI, SI, Stewart I. and Auckland I., skins; Spur = length of spur on p9 formed by emargination at the tip of the feather (CM, NMNZ): (1) Adults; (2) Juveniles and immatures. (3–9) Adults, skins (Bartle & Sagar 1987): (3) Northland; (4) Islands in Hauraki Gulf; (5) NI (except Northland and islands in Hauraki Gulf); (6) W. SI; (7) E. SI; (8) Stewart I.; (9) Auckland I. (10) NI, SI and Stewart I., juveniles and immatures, skins (Bartle & Sagar 1987). (11–12) Tiritiri Matangi I., live (Bartle & Sagar 1987): (11) Adults; (12) Juveniles and immatures. (13) Punakaiki–Charleston area, adults, live (Bartle & Sagar 1987). (14–15) Geraldine, live (Bartle & Sagar 1987): (14) Adults; (15) Juveniles and immatures. (16) Orongorongo Valley, adults, live (Robertson *et al.* 1983). (17) Tiritiri Matangi I. and Whangaparaoa Pen., adults (and probably first immatures), live (Craig *et al.* 1981a,b). (18) Little Barrier I., adults and immatures, live; Wing U = chord of unstraightened wing; Bill N = length of bill from tip to anterior edge of nostril (Gill & Veitch 1990). (19) Live birds from Tiritiri Matangi I. and skins from unspecified locations (Craig 1984). (20) Kowhai Bush (near Kaikoura, SI), adults, live; Claw M = length of claw on middle toe; Claw H = length of claw on hindtoe (Gill 1980).

		MALES	FEMALES	
WING	(1)	90.5 (2.71; 86–96; 29)	81.4 (3.18; 73–86; 18)	**
	(2)	87.4 (2.56; 81–91; 14)	78.9 (2.56; 75–83; 14)	**
	(3)	83, 85, 88	80 (4.69; 75–85; 5)	
	(4)	87.8 (2.56; 83–92; 14)	77.5 (1.19; 75.8–79.3; 8)	**
	(5)	87.3 (2.05; 83–90; 8)	75, 76, 79	
	(6)	92.1 (2.25; 88–97; 19)	80.6 (2.84; 75.0–84.5; 11)	**
	(7)	91.0 (2.45; 86–96; 12)	82.0 (2.0; 80–85; 5)	**
	(8)	94.4 (1.59; 92–97; 9)	79.5, 85.0, 86.0	
	(9)	94.0 (2.28; 89–97; 17)	84.2 (1.33; 82–86; 6)	**
	(10)	86.6 (3.81; 77–92; 10)	78, 81	
	(11)	84.1 (2.1; 79.5–87.9; 40)	75.1 (1.52; 71.1–77.9; 23)	**
	(12)	81.7 (1.79; 77.8–84.7; 21)	73.5 (1.53; 69.6–76.2; 25)	**
	(13)	91.0 (1.92; 88–95; 14)	80.4 (1.71; 77–83; 13)	**
	(14)	89.0 (2.35; 86–92; 33)	79.5 (2.29; 75–85; 28)	**
	(15)	87.7 (1.49; 86–90; 7)	79.2 (2.23; 77–83; 6)	**
	(16)	86.1 (2.43; 80–92; 200)	76.4 (2.33; 66–81; 94)	**
	(17)	83.5 (2.54; 22)	75.2 (1.65; 17)	**
	(20)	87.9 (2.67; 85–92; 14)	77.3 (1.67; 75–79; 8)	**
WING U	(18)	84.6 (2.52; 80–88; 19)	74.6 (2.20; 71–78; 11)	**
SPUR	(1)	5.2 (0.68; 4.0–7.0; 29)	5.2 (0.63; 4.3–6.7; 19)	ns
	(19)	3.9 (1.51; 57)	3.3 (1.88; 22)	ns
TAIL	(1)	86.2 (3.82; 77–93; 29)	71.4 (4.67; 62–78; 18)	**
	(2)	82.3 (4.21; 73–89; 13)	70.8 (3.21; 65–76; 12)	**
	(3)	76, 78, 79	68.8 (4.49; 64–75; 5)	
	(4)	81.7 (3.77; 74–85; 14)	69.3 (1.96; 65.6–71.8; 8)	**
	(5)	84.1 (3.56; 77–87; 8)	67, 69, 74	
	(6)	87.7 (3.47; 83–96; 19)	69.7 (3.07; 63–74; 11)	**
	(7)	85.3 (4.32; 78–92; 12)	70.6 (2.3; 67–73; 5)	**
	(8)	88.6 (1.74; 85–91; 9)	69.8, 72.9, 79.0	

		MALES	FEMALES	
	(9)	88.2 (3.95; 83–94; 15)	74.4 (2.41; 71–77; 5)	**
	(10)	78.5 (8.23; 62–90; 10)	70, 70	
	(11)	81.5 (2.97; 76.7–87.6; 38)	68.4 (1.94; 65.1–71.7; 23)	**
	(12)	78.2 (2.22; 73.1–83.7; 21)	66.3 (2.04; 62–70; 25)	**
	(13)	89.5, 89.9, 96.0	73.9 (4.42; 66.4–80.0; 8)	
	(14)	88.0 (3.08; 83–94; 8)	73.5 (1.98; 71–76; 6)	**
	(16)	84.5 (4.23; 74–92; 144)	70.6 (3.15; 65–79; 59)	**
	(17)	80.4 (2.90; 22)	68.5 (2.01; 17)	**
	(18)	82.5 (2.90; 77–86; 14)	65.3 (5.54; 59–71; 6)	**
	(20)	86.4 (2.90; 81–93; 14)	71.8 (2.82; 68–77; 8)	**
BILL S	(1)	20.8 (0.99; 18.7–22.8; 29)	19.2 (1.22; 16.4–21.2; 19)	**
	(2)	20.4 (1.05; 18.2–21.8; 13)	18.7 (1.06; 16.1–20.6; 14)	**
	(20)	22.0 (0.86; 20.3–23.4; 14)	20.2 (0.73; 18.5–20.9; 8)	**
BILL F	(3)	14.2, 14.2, 14.5	13.3 (0.84; 11.8–13.8; 5)	
	(4)	14.2 (0.62; 13.4–15.4; 13)	–	
	(5)	13.6 (0.65; 12.9–14.6; 7)	11.6, 12.1, 12.3	
	(6)	13.7 (0.67; 12.3–14.6; 19)	12.5 (0.60; 11.3–13.5; 11)	**
	(7)	13.6 (0.69; 12.3–14.4; 10)	13.1 (0.79; 12.0–13.9; 4)	ns
	(8)	13.4 (0.77; 12.4–14.7; 9)	13.1, 13.2, 13.9	
	(9)	13.2 (0.38; 12.6–14.0; 15)	12.1 (0.76; 11.6–13.2; 4)	**
	(10)	13.2 (0.65; 12.1–14.0; 10)	11.4, 12.7, 13.4	
	(11)	14.5 (0.50; 13.3–15.5; 17)	13.9 (0.39; 13.1–14.4; 19)	**
	(12)	14.0 (0.51; 13.2–14.8; 11)	13.5 (0.28; 13.1–13.9; 15)	**
	(14)	14.6 (0.98; 13.4–17.1; 26)	14.1 (0.54; 13.2–15.2; 19)	*
	(15)	14.8 (0.72; 14.1–15.8; 4)	12.2, 13.7, 14.0	
	(16)	14.2 (0.79; 13–17; 148)	13.3 (0.83; 12–16; 61)	**
BILL N	(18)	9.9 (0.37; 9.6–10.4; 6)	–	
BILL W	(20)	5.2 (0.18; 5.0–5.6; 14)	5.2 (0.23; 4.9–5.5; 8)	ns
BILL D	(20)	4.4 (0.26; 4.0–5.1; 14)	4.1 (0.11; 3.8–4.2; 8)	**
THL	(4)	40.5 (0.94; 39.2–41.2; 4)	38.0 (0.77; 37.0–39.3; 9)	**
	(5)	39.3, 39.9, 40.8	36.3	
	(6)	41.2 (0.88; 40–42; 7)	37.0 (1.11; 35.3–38.7; 7)	**
	(7)	40.7 (0.66; 40.2–41.6; 4)	38.3	
	(8)	41.1 (0.70; 40.2–42.3; 9)	38.2, 38.9, 39.0	
	(9)	40.6 (0.34; 40.2–41.3; 8)	37.1 (0.70; 36–38; 5)	**
	(10)	39.4, 40.0, 41.2	36.7, 37.9, 39.1	
	(11)	41.1 (0.63; 40.1–42.2; 40)	38.3 (0.52; 37.3–39.5; 23)	**
	(12)	40.9 (0.65; 39.8–42.3; 18)	38.2 (0.48; 37.1–39.0; 21)	**
	(13)	41.6 (0.71; 40.5–42.7; 13)	38.5 (0.64; 37.2–39.3; 7)	**
	(14)	41.0 (0.58; 39.6–42.2; 27)	38.3 (0.56; 37.3–39.5; 21)	**
	(15)	40.3 (0.54; 39.8–41.2; 5)	36.4, 37.5, 38.3	
	(17)	41.1 (0.74; 22)	38.4 (0.50; 17)	**
TARSUS	(1)	26.4 (0.84; 24.5–28.1; 29)	25.0 (1.40; 22.6–27.6; 17)	**
	(2)	26.7 (0.87; 24.8–28.4; 14)	24.7 (1.17; 22.4–26.4; 15)	**
	(3)	26, 26, 29	22.9, 28.0	
	(4)	25.7 (1.07; 23.0–27.1; 14)	24.2 (0.74; 23.2–24.9; 8)	**
	(5)	26.0 (1.19; 23.6–27.5; 8)	21.7, 22.9, 23.2	
	(6)	27.2 (1.28; 25.0–29.1; 19)	24.8 (1.2; 23.1–27.0; 11)	**
	(7)	26.5 (1.53; 24.2–28.8; 12)	24.8 (0.82; 24.0–25.8; 4)	*
	(8)	27.0 (1.03; 25.2–28.2; 9)	25.0, 25.3, 25.6	
	(9)	26.9 (1.37; 24–29; 16)	25.9 (1.2; 25.0–27.7; 6)	ns
	(10)	25.9 (1.33; 22.6–27.3; 9)	24.2, 25.3, 25.8	
	(11)	26.1 (0.53; 25.1–27.2; 40)	24.3 (0.43; 23.6–25.2; 23)	**
	(12)	25.9 (0.55; 24.8–27.2; 21)	24.1 (0.48; 23–25; 25)	**
	(13)	26.8 (0.84; 25.8–28.0; 14)	25.7 (0.87; 24.5–27.5; 13)	**
	(14)	26.4 (1.05; 23.3–28.5; 31)	24.8 (1.34; 19.7–27.3; 23)	**
	(15)	26.9 (1.08; 25.6–28.1; 7)	24.5 (0.46; 24.0–25.3; 6)	**
	(16)	26.1 (0.86; 24–28; 127)	24.4 (0.98; 20–26; 49)	**
	(18)	26.3 (0.66; 25.4–27.5; 15)	25.0 (1.02; 24.0–26.8; 7)	**
	(20)	28.3 (0.71; 27.3–29.2; 11)	26.7 (1.39; 24.1–28.4; 8)	**
TOE C	(4)	20.5 (1.28; 18.1–22.0; 9)	–	
	(5)	19.6 (0.85; 18.4–21.0; 8)	16.5, 17.2, 19.1	
	(6)	20.9 (1.31; 18.6–23.2; 17)	19.5 (0.69; 18.2–20.7; 10)	**
	(7)	21.3 (0.63; 19.9–22.0; 8)	18.4, 20.0, 20.0	
	(8)	21.4 (0.53; 20.3–22.0; 8)	18.5, 20.1, 20.2	
	(9)	23.3 (1.25; 21.1–25.0; 14)	21.2 (1.34; 19.8–22.7; 4)	**
	(16)	20.8 (1.19; 17–24; 147)	19.9 (1.18; 17–23; 61)	**
	(18)	17.9 (1.22; 16.0–19.6; 11)	16.0 (0.96; 14.7–17.6; 8)	**
CLAW M	(20)	6.8 (0.39; 6.3–7.7; 13)	6.2 (0.14; 6.0–6.4; 8)	**
CLAW H	(20)	9.7 (0.28; 9.3–10.2; 9)	8.6 (0.20; 8.4–9.0; 6)	**

Adult females have significantly longer Wing (P<0.05) than juvenile and immature females. Adult males have significantly longer Wing (P<0.01) and Tail (P<0.01) than juvenile and immature males. The length of spur on p9 in unsexed juveniles, 0.3 mm (0.80; 16), is significantly smaller than that of both adult males and adult females (P<0.01) (Craig 1984).

SUBSPECIES MELANOCEPHALA, Chatham Is: (21–22) Skins (NMNZ, CM): (21) Adults; (22) Juveniles and first immatures. (23–24) Skins (Bartle & Sagar 1987): (23) Adults; (24) Juveniles and immatures.

		MALES	FEMALES	
WING	(21)	108.5 (1.73; 107–111; 4)	93, 94	
	(22)	105.0 (2.24; 102–108; 5)	91, 92	
	(23)	106.4 (3.7; 102–112; 7)	92.8 (1.79; 92–96; 5)	**
	(24)	102, 105, 108	–	
SPUR	(21)	5.3 (0.46; 4.8–5.9; 4)	3.9, 4.3	
TAIL	(21)	105.2 (2.50; 102–108; 4)	85, 87	
	(22)	97.5 (4.12; 92–102; 4)	78, 79	
	(23)	100.1 (5.6; 93–108; 7)	82.8 (2.41; 81–87; 5)	**
	(24)	87, 94, 95	–	
BILL S	(21)	22.9 (0.64; 22.3–23.8; 4)	20.4, 21.3	
	(22)	22.6 (0.82; 21.5–23.7; 5)	20.3, 20.3	
BILL F	(23)	15.2 (1.28; 13.3–16.8; 7)	13.3 (0.51; 12.7–13.8; 5)	**
	(24)	13.1, 14.1, 15.4	–	
THL	(23)	45.9 (1.14; 44.7–47.5; 5)	41.4 (1.02; 39.9–42.7; 5)	**
	(24)	44.9, 45.2, 45.5	–	
TARSUS	(21)	34.1, 35.6, 35.8	30.7, 31.5	
	(22)	34.3, 34.5, 34.8	31.3	
	(23)	37.3 (3.57; 34–44; 7)	31.2 (2.14; 29–35; 5)	**
	(24)	34.6, 34.7, 34.8	–	
TOE C	(23)	25.4 (0.93; 24.3–26.2; 4)	21.6 (2.05; 18–23; 5)	**

Adults males have significantly longer Wing and Tail than juvenile and immature males (P<0.05); other measurements not significantly different.

SUBSPECIES OBSCURA, Three Kings Is: (25–26) Skins (NMNZ): (25) Adults; (26) Juveniles and immatures. (27) Adults, skins (Bartle & Sagar 1987).

		MALES	FEMALES
WING	(25)	93, 95, 97	82
	(26)	89, 91	80, 81
	(27)	93.1 (3.80; 88.7–98.0; 4)	82
SPUR	(25)	6.1, 6.5, 6.7	5.4
TAIL	(25)	87, 90, 92	70
	(26)	80, 80	70, 71
	(27)	84.0 (2.58; 81–87; 4)	71, 72
BILL S	(25)	24.9, 24.9	21.4
	(26)	23.3, 24.4	20.5, 22.2
BILL F	(27)	17.1 (1.05; 15.9–18.3; 4)	14.3, 15.0
THL	(27)	44.9	40.0
TARSUS	(25)	28.3, 30.3	26.3
	(26)	28.3, 28.9	25.4, 25.7
	(27)	27.9 (26.8–29.2; 4)	25.0, 26.7
TOE C	(27)	21.8 (1.61; 19.6–23.5; 4)	19.0, 23.0

SUBSPECIES ONEHO, Poor Knights Is: (28–29) Skins (NMNZ): (28) Adults; (29) Juveniles and immatures. (30–31) Live (Bartle & Sagar 1987): (30) Adults; (31) Juveniles and immatures.

		MALES	FEMALES	
WING	(28)	88.8 (2.99; 85–91; 6)	78, 80	
	(29)	85, 85	77	
	(30)	87.7 (2.40; 81–94; 251)	77.0 (2.10; 72–83; 142)	**
	(31)	84.0 (2.28; 78–90; 167)	74.3 (2.03; 70–78; 67)	**
SPUR	(28)	4.7 (0.47; 4.4–5.5; 6)	5.0, 5.2	
TAIL	(28)	86.3 (3.56; 81–90; 6)	68, 73	
	(29)	81, 84	71	
	(30)	88.1 (2.56; 79–94; 48)	71.4 (3.01; 66–75; 16)	**
	(31)	83.1 (2.06; 79–87; 41)	71.9 (3.98; 67–78; 9)	**
BILL S	(28)	21.9 (0.79; 21.2–23.3; 6)	21.0	
	(29)	21.9, 22.7	20.0	
BILL F	(30)	15.4 (0.60; 14.0–17.4; 48)	14.8 (0.76; 13.4–16.8; 33)	**
	(31)	14.2, 15.7	13.8	
THL	(30)	42.0 (0.76; 40.2–43.5; 144)	38.9 (0.63; 37.5–40.5; 64)	**
	(31)	41.5 (0.83; 39.4–43.1; 67)	38.9 (0.67; 37.5–40.0; 28)	**
TARSUS	(28)	27.3 (0.76; 26.2–28.5; 6)	25.1, 25.6	
	(29)	26.5, 26.9	24.7	
	(30)	27.4 (1.05; 23.2–30.0; 115)	25.6 (1.13; 22.3–27.2; 73)	**
	(31)	27.5 (0.86; 25.0–29.3; 34)	25.7 (0.77; 24.7–27.5; 16)	**
TOE C	(30)	21.7 (1.24; 19.8–23.2; 8)	20.5, 20.6	

WEIGHTS NOMINATE MELANURA: (1–2) NI and SI, from museum labels (NMNZ): (1) Adults; (2) Juveniles and first immatures. (3–6) Adults, skins (Bartle & Sagar 1987): (3) NI (except Northland and islands in Hauraki Gulf); (4) W. SI; (5) E. SI; (6) Auckland I. (7–9) Adults, live (Bartle & Sagar 1987): (7) Tiritiri Matangi I.; (8) Punakaiki–Charleston area; (9) Geraldine. (10) Orongorongo Valley, adults, live (Robertson et al. 1983). (11) Tiritiri Matangi I. and Whangaparaoa Pen., adults (and probably first immatures), live (Craig et al. 1981a,b). (12) Little Barrier I., adults and immatures, live (Gill & Veitch 1990).

	MALES	FEMALES	
(1)	31.3 (5.17; 21.8–39.5; 10)	–	
(2)	32.8 (3.79; 27.0–36.5; 6)	17.7, 23.0, 28.0	
(3)	27.3, 28.3	–	
(4)	33.8 (2.35; 30–37; 9)	23, 28	
(5)	30.5, 36.5, 39.5	–	
(6)	35.5, 35.5, 35.5	29, 32	
(7)	31.7 (2.83; 24.0–37.5; 31)	25.4 (3.21; 20.5–32.0; 20)	**
(8)	32.9 (3.58; 29.0–42.1; 13)	26.1 (1.06; 24.3–27.6; 7)	**
(9)	34.8 (2.05; 31–40; 32)	26.1 (1.68; 23–31; 27)	**
(10)	30.7 (2.42; 21–38; 202)	23.6 (2.16; 20–32; 94)	**
(11)	30.7 (2.15; 14)	25.0 (3.36; 25)	**
(12)	29.7 (2.49; 25–34; 14)	21.6 (0.58; 21–22; 6)	**

SUBSPECIES ONEHO, Poor Knights Is: (13–14) From museum labels (NMNZ): (13) Adults; (14) Juveniles and first immatures. (15–16) Live (Bartle & Sagar 1987): (15) Adults; (16) Juveniles and immatures.

	MALES	FEMALES	
(13)	37.3 (7.17; 32–47; 5)	26, 30	
(14)	22, 28	20.5	
(15)	36.2 (3.37; 25–47; 86)	26.8 (2.52; 22–35; 46)	**
(16)	33.9 (2.15; 30–38; 44)	25.0 (2.11; 18–28; 45)	**

No weights available for subspecies melanocephala or obscura.

STRUCTURE Wing moderately long, broad and wedge-shaped. Ten primaries: p6 longest; p10 38–43 mm shorter, p9 12–15, p8 3–5, p7 0–1, p5 0–1, p4 2–3, p3 10–12, p2 14–17, p1 16–18. P4–p8 emarginated on outer web; p4–p10 on inner web. In adults, emargination of p9 very pronounced (See Ageing). Nine secondaries, including three tertials; tips of longest tertials

fall between p2 and p3 on folded wing. Tail long and slightly forked; 12 rectrices; t6 longest, t1 9–12 mm shorter. Bill moderately long and narrow with a slight downward curve to pointed tip; about half length of head. Tarsus moderately long and slender; scaling: fused scutes in front and holothecal to rear. Tibia fully feathered. Middle toe with claw, 21.1 (1.26; 19.5–22.9; 6). Outer toe 74–84% of middle, inner toe 69–81%, hindtoe 83–96%.

AGEING Five features readily distinguish younger birds from adults: fleshy yellow gape; yellow moustachial stripe; lack of iridescence on head; brown irides; and lack of emarginate ninth primary (Bartle & Sagar 1987). The fleshy yellow gape of juveniles usually disappears before post-juvenile moult, but occasionally persists longer in females (Bartle & Sagar 1987). Yellow moustachial stripe and lack of iridescence on head are plumage characters replaced in post-juvenile moult (Bartle & Sagar 1987; this study). Irides change from brown to red Apr.–June of first winter (Bartle & Sagar 1987). Shape of tips of outer primaries differs between adults and juveniles, particularly on p9. In juveniles, p9 broader and with more rounded tip, with little if any emargination; in adults, p9 strongly emarginate.

SEXING In adults, sexes readily distinguished by plumage, but also differ slightly in shape of emarginated p9. Emargination at tip of p9 tends to be more pronounced in adult males (Bartle & Sagar 1987; this study), but there is some overlap between sexes (see Spur in Measurements). Juveniles readily sexed on colour of tail: black in males and brown in females.

GEOGRAPHICAL VARIATION Four subspecies currently recognized (NZCL). Within mainland populations of nominate *melanura*, trend towards lighter birds in N and darker birds in S. This trend caused by variation in amount of melanin in plumage and suggested that amount of melanin influenced by humidity at time of moulting, with birds from wetter areas having darker plumage than those from drier areas. Nominate *melanura* and subspecies *oneho* described above; other subspecies described below.

SUBSPECIES MELANOCEPHALA from Chatham Is extinct since c. 1906 (NZCL). Differed from all other subspecies in having yellow eyes (cf. red in adults of other subspecies) (Bartle & Sagar 1987; Oliver; NMNZ). Adult males much larger than other subspecies in all measurements (Bartle & Sagar 1987; Oliver; see Measurements). Descriptions of subspecies *melanocephala* based on examination of skins of four adult males, two adult females and two juvenile males. **Adult male** Mainly differed from nominate in having much darker head and neck. HEAD AND NECK: Forehead, crown, nape, hindneck, sides of neck and ear-coverts, dark olive (c49) with strong irridescent dark-blue (74) to blue-black (173) sheen to feathers; iridescence much stronger than in nominate. Lores and eye-ring, black (89). Chin and throat slightly darker than in nominate male: dark greyish olive (ne) with weak iridescent blue-black (c173) sheen. UPPERPARTS: As nominate male. UNDERPARTS: Similar to nominate, but slightly darker on upper breast and slightly yellower on lower belly and rear-flanks. Breast, belly and most of flanks grade from dark greyish-olive (ne) on upper breast to yellow-olive (c52) on lower belly and rear-flanks. Patch of feathers on anterior flanks much darker than in nominate male, yellowish grey (ne). Vent, straw-yellow (c57). Undertail-coverts, grey-olive (c43) with off-white (ne) to straw-yellow (c57) edge to outer web. TAIL, WING: As nominate male. **Adult female** Differed only slightly from nominate female in plumage. HEAD AND NECK: Iridescent sheen to feathers of forehead, crown and nape, slightly different shade of blue from that of nominate female, blue (c69). Chin and throat slightly paler than nominate female: grade from cream (54) on chin to buff (c124) on throat. Rest as nominate female. UPPERPARTS: Slightly lighter than nominate female; dark olive (c46). UNDERPARTS: As nominate female or slightly greyer. TAIL, WING: As nominate female. **Juvenile male** Very similar to adult female *melanocephala* and more olive than nominate juvenile male. HEAD AND NECK: Forehead, crown, nape, hindneck, sides of neck and ear-coverts, grey-olive (c43); similar to adult female *melanocephala*, but with little or no iridescence to feathers. Lores, eye-ring, moustachial stripe and malar area, as nominate juvenile. Chin and throat slightly darker than juvenile male nominate, olive-grey (42–43); feathers also have softer or looser texture than in adults. UPPERPARTS: Much browner than either adult female *melanocephala* or juvenile male nominate; brown (c28). UNDERPARTS: Breast, belly and flanks grade from grey-brown (c91) on upper breast to light grey-brown (c119C) on lower belly. Vent, greyish cream (ne). Undertail-coverts, light grey-brown (c45). Thighs, olive-brown (c29). TAIL: Much browner than either adult male *melanocephala* or juvenile male nominate, but slightly darker than adult female *melanocephala*. Rectrices, dark brown (c219) with olive (c50) edge to outer webs, and very weak iridescent dark-blue (c74) sheen to rest of outer webs of t1–t5. UPPERWING: As juvenile male nominate, or slightly browner. UNDERWING: As juvenile male nominate. **Juvenile female** No specimens available. **First immature male and female** (First basic). No specimens in complete immature plumage available, but plumage of individuals in post-juvenile moult indicate that probably appear as adults but with retained juvenile remiges and rectrices.

SUBSPECIES OBSCURA occurs on Three Kings Is. Larger than nominate (Bartle & Sagar 1987; see Measurements), but not as large as *melanocephala*. Description of *obscura* based on examination of three adult male skins, one adult female skin and one juvenile male skin. **Adult male** Similar to nominate with marginally darker plumage and slightly different iridescent sheen to head and neck. HEAD AND NECK: Dark olive of forehead, crown, nape, hindneck and sides of neck and ear-coverts, on average slightly darker than that of nominate; dark olive (c49). Iridescent sheen to feathers of forehead, crown, nape, ear-coverts, chin and throat, violet (c71). UPPERPARTS: On average slightly darker than adult male nominate. Mantle, back, scapulars and uppertail-coverts, dark olive (49). Rump, olive (c51). UNDERPARTS: On average slightly duller than nominate. Breast, belly and flanks, dark grey-olive (ne). A few feathers on upper flanks, yellowish white (ne); fewer than in nominate, and probably mostly concealed by folded wing. Vent and undertail-coverts, yellowish white (ne). TAIL: As nominate male. UPPERWING: Very similar to nominate male, but dark-olive (c49) fringes and edges to coverts and tertials marginally darker than nominate male; and secondaries and inner primaries lack dark-olive edge to outer web. Rest as nominate male. UNDERWING: As nominate male, but marginal coverts slightly darker olive (49). **Adult female** Very similar to female nominate, but on average slightly paler on underparts. HEAD AND NECK: Mostly as adult female nominate, but chin and throat slightly paler, light grey-brown (c45). UPPERPARTS: As nominate female or marginally browner. UNDERPARTS: Breast, belly and flanks, light grey-brown (c45). A few feathers on upper flanks, yellowish white (ne); fewer than in nominate, and probably mostly concealed by folded wing. Vent and undertail-coverts, off-white (ne). Thighs, light grey-brown

(119C). TAIL, WING: As nominate female. **Juvenile male** As juvenile male nominate. **Juvenile female** No specimens available, but probably as juvenile female nominate.

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Tui *Prosthemadera novaeseelandiae* (page 1191)
NOMINATE *NOVAESEELANDIAE:* **1** Adult; **2** Juvenile; **3** Adult

Bellbird *Anthornis melanura* (page 1173)
NOMINATE *MELANURA:* **4** Adult male; **5** Adult female; **6** Juvenile male; **7** Juvenile female; **8** Adult male

Stitchbird *Notiomystis cincta* (page 954)
9 Adult male; **10** Adult female; **11** Juvenile; **12** Adult male