

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

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

The Passeriformes divide into two main groups:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Family 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 *Melipotés*, 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 *Prothemadera*.

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*, *Melipotés*, *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 strong with scutellate, bilaminipantar 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), *Melipotés* (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. *Melipotés*).

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'sian region. Several species are characteristic of mangroves (e.g. Mangrove *Lichenostomus fasciocularis* 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.

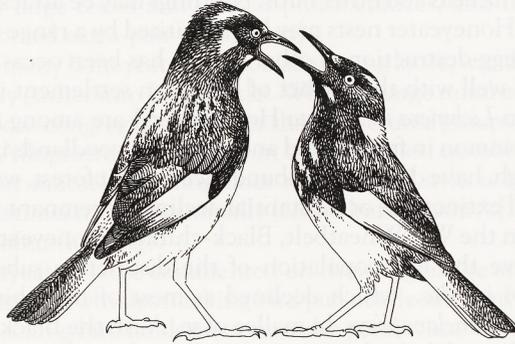
Island species of honeyeaters are often restricted to small ranges and are uncommon. In NZ, the Stitchbird was reduced to a single population on Little Barrier I., as a result of nest-predation by introduced mammals. It has since been translocated to several other islands (Castro *et al.* 1994), although 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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Merops novaeseelandiae Gmelin, 1788, *Syst. Nat.* 1(1): 464 — Nova Seelandia = Queen Charlotte Sound, New Zealand.

The generic epithet refers to the curled feathers and filamentous plumes on the neck of the Tui (Greek *πρόσθεμα*, an appendage, and *δηρή*, the neck). New Zealand received its name from the Dutch explorer Abel Tasman, who explored the west coast in 1642, naming it Nova Zeelandia, after his home (Latin *novus*, new, and Modern Latin *Zeelandia*, Zealand).

OTHER ENGLISH NAMES Chatham Island Tui, Parson Bird, Poey Bird.

POLYTYPIC Nominate *novaeseelandiae*, NI, SI and Stewart I., NZ, and many offshore island groups, including Auckland and Kermadec Is; *chathamensis*, Hartert, 1928, Chatham Is, NZ.

FIELD IDENTIFICATION Length 27–32 cm; wingspan c. 40 cm; weight: nominate *novaeseelandiae*: male 120 g, female 85 g; subspecies *chathamensis*: male 155 g, female 110 g. Largest NZ honeyeater. Large honeyeater with a sturdy gently decurved bill, low sloping forehead, broad rounded wings and tail, and strong legs and feet. Much larger than Bellbird *Anthornis melanura* and Stitchbird *Notiomystis cincta*. Sexes alike in plumage but males larger than females. No seasonal variation. First impressions of adult in field are of glossy black bird with white patches on upperwing: adult mainly black, browner on back and flanks, with strong blue, green and purple iridescence to much of plumage (colour varying with angle of light), and with white tuft of feathers on throat, white patch on upperwing, and lacy white hindneck-collar. Juvenile separable: head and body dull greyish or brownish black, glossy only on wings and tail, and white confined to patch on upperwing. **Adult** Most plumage strongly iridescent, appearing shiny dark blue, green-violet or even golden, depending on light. Head and neck, black with strong dark-green to dark bluish-olive iridescence, except for modified feathers forming white ball-like tufts on sides of throat (which usually appear as single tuft in field), and small, pointed, slightly curled feathers with distinct white shaft-streaks that form pale lacy hindneck-collar extending onto sides of neck and upper mantle. Rest of mantle, back, scapulars and rump, black-brown, with mainly golden straw-yellow iridescence, though can appear slightly iridescent blue to green in some lights. Uppertail-coverts, black with strong blue to blue-green or dark-violet iridescence. Uppertail, black, with dark-green iridescence, strongest on outer webs of feathers; sometimes has straw-yellow sheen. Upperwing, black or black-brown with strong dark-green to dark-blue iridescence except for conspicuous white patch on leading innerwing formed by largely white marginal and median secondary coverts. Folded wing appears entirely iridescent with white patch

on shoulder. Breast and upper belly, black with dark green to dark bluish-olive iridescence, and sometimes with golden sheen; rest of belly and vent, black-brown, with no iridescence but often with yellowish-brown tips to feathers; flanks, dark grey, and thighs, black-brown, and both often fluffed up and covering edge of closed wing; undertail-coverts, black with dark-green to dark-blue iridescence. Undertail, black, without iridescence. Underwing, blackish with slight dark-green to dark-blue iridescence to marginal coverts. Bill, black or black-brown. Iris, black-brown. Legs and feet, black to grey-black. **Juvenile** Duller than adult with iridescence only on uppertail and upperwing and none or very little on body. Head, neck, upperbody and underbody, mostly black-brown to grey-black, usually with very fine pale streaks to head, neck, upperbody and breast (but streaks absent on some birds); chin and throat contrastingly greyer than rest of head and neck, and there is often a pale patch across lower throat in area where white throat-tufts present in adult; scapulars and uppertail-coverts often have very weak dark-green to dark-blue iridescence. Wing and tail much as adult except iridescence reduced or absent, especially on marginal coverts. Bare parts as adult except gape yellowish and swollen up to c. 5 weeks of age.

Similar species Adults unmistakable. Combination of black glossy plumage, white tufts on throat, pale lacy collar and white patch on upperwing, diagnostic. Juveniles, and even adults seen fleetingly, could be confused with similar-sized and dark **Common Starling** *Sturnus vulgaris* and **Common Blackbird** *Turdus merula*, but white patch on upperwing diagnostic in all plumages of Tui; Starlings also short-tailed with pointed triangular wings and should rarely present identification problems; Blackbirds are similar in size and shape to Tui with rather broad rounded wings and tail, and identification may depend on better views.

Occur singly, in pairs or family groups on breeding territo-

ries, but regularly in larger numbers at good sources of nectar or fruit, where sometimes associate with Silvereyes *Zosterops lateralis*, Bellbirds and New Zealand Pigeons *Hemiphaga novaeseelandiae*. Sometimes inconspicuous on breeding territory, especially in tall forests, but obvious, noisy, active and aggressive when feeding in groups on flowering or fruiting plants. Often vigorously chase conspecifics and other species from food. Regularly commute to rich sources of food, flying high, often in small, loose flocks. In flight, have broad rounded wings with fingered tips and rather long rounded tail. Long-distance flight undulating, with shallow, fluttering and erratic wing-beats. Appear to have difficulty in maintaining height, slipping sideways and correcting with a quick flurry of wing-beats. Over short distances and through trees, flight strong, swift and agile, often with noisy whirring wing-beats. Make steep display dives, plummeting on closed wings into canopy with a noisy whoosh of wings and wild raucous calls.

HABITAT Mainly mixed, often dense, podocarp–broadleaf forest, both in continuous tracts of forest, and small remnants and regrowth. Also occur in suburbs, especially in n. NI, and widespread in non-native forests, including parks. Occur in temperate zone and subantarctic region. Mostly inhabit lower altitudes, including coasts, though sometimes recorded up to nearly 1500 m asl (Challies 1966; McKenzie 1979; Wilson *et al.* 1988; Fitzgerald *et al.* 1989; Freeman 1994; O'Donnell & Dilks 1994; CSN; D.J. Onley).

Inhabit mixed, often dense podocarp–broadleaf, podocarp–broadleaf–beech or podocarp–beech forest, usually with dense, sometimes diverse, canopy of Hinau *Elaeocarpus dentatus*, Pukatea *Laurelia novaeseelandiae*, Mahoe *Meliclytus ramiflorus*, Porokaiwhiri *Hedycarya arborea*, Rewarewa *Knightia excelsa*, Kamahi *Weinmannia racemosa*, Pate *Schefflera digitata*, Horopito *Pseudowintera axillaris* or beech *Nothofagus*, often with tall emergents, such as Northern Rata *Metrosideros robusta*, Rimu *Dacrydium cupressinum*, Miro *Podocarpus ferrugineus* and Matai *P. taxifolia*, and sometimes dense understorey of *Coprosma* and Kawakawa *Macropiper excelsum* (Kikkawa 1960; Challies 1966; Guest 1975; Dawson *et al.* 1978; Norton 1980, 1982; Onley 1983; Clout & Gaze 1984; Wilson *et al.* 1988; Fitzgerald *et al.* 1989; O'Donnell & Dilks 1994; CSN). Also occur in beech forest with mixed canopy of Red *Nothofagus fusca*, Silver *N. menziesii* or Mountain *N. solandri* Beech, though only occasionally recorded in forest dominated by single species of beech, especially high-altitude Mountain Beech forest (Guest 1975; St Paul 1975; Dawson *et al.* 1978; Wilson *et al.* 1988; CSN). Sometimes recorded in rainforest dominated by *Quintinia acutifolia* and Kamahi (Dawson 1964). Occasionally occur in regrowth (St Paul 1975). Also recorded in tall Kanuka *Kunzea ericoides* forest with dense secondary cover (Kikkawa 1964) and in coastal shrubland and Manuka *Leptospermum scoparium* scrub (Dawson 1951; Blackburn 1968; Daniel 1982; CSN 28); and occasionally occur in thickets of flowering Kowhai *Sophora tetraptera*, *Olearia* or Houpara *Pseudopanax lessonii* (Dawson 1951; McKenzie 1979; CSN). Once recorded among mangroves (CSN 31). Also occur in remnant native vegetation, sometimes near urban areas (Stewart 1980; CSN 4, 22) and in settled areas planted with exotic species, such as privet *Ligustrum*, oaks *Quercus*, willows *Salix* and eucalypts, sometimes with dense understorey of native shrubs and small trees (Turbott 1967; Owen & Sell 1985; Gill 1989; CSN); often occur in urban parks and gardens (Prickett 1959; Guest & Guest 1987, 1993; CSN); sometimes also recorded in orchards (CSN 39, 41). In detailed study in w. Paparoa Ra., found in

variety of lowland forest types: mainly in mixed forest with canopy dominated by Red Beech and Silver Beech, with emergent Rimu and Kahikatea *Dacrycarpus dacrydioides*; also recorded in mixed closed Red Beech–Silver Beech forest with tall emergent Rimu; low sparse mixed Rimu–Hard Beech *Nothofagus truncata*–Silver Beech forest with some areas of Mountain Beech and Yellow–Silver Pine *Lepidothamnus intermedius*; low coastal forest with closed canopy, mainly of Kamahi, and large emergent Rimu and Northern Rata; and least often recorded in remnant patches of Rimu and beech forest (Onley 1980).

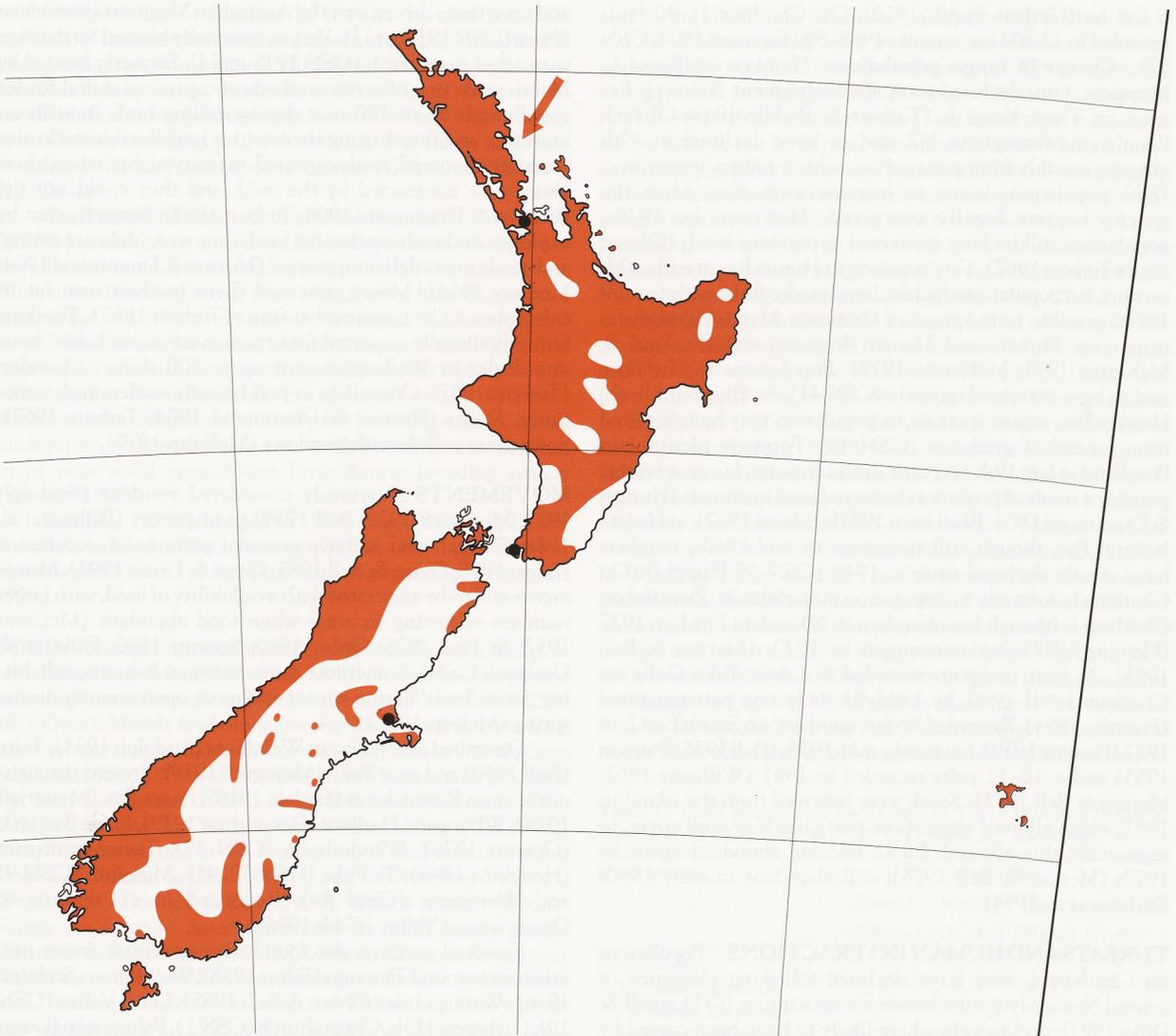
On Kermadec Is, mainly inhabit mixed coastal Pohutukawa *Metrosideros excelsa*–Nikau *Rhopalostylis sapida*–Mapou *Myrsine australis* forest or mixed Pohutukawa–Ngaio *Myoporum laetum* forest, as well as forest edges; occur less often in rainforest dominated by Pohutukawa, Nikau and Hutu *Ascarina* (Edgar *et al.* 1965; Merton & Veitch 1986).

On Pitt and South East Is, Chatham Is, occur in all habitat types except paddocks on Pitt I. (D.J. Onley); and including mixed broadleaf forest of Ngaio with Kawakawa and Lowland Ribbonwood *Plagianthus betulinus*, where inhabit both canopy and understorey; also recorded in areas with dense flowering flax *Phormium* (O'Donnell & Dilks 1993; CSN 37).

DISTRIBUTION AND POPULATION Endemic to NZ. Account summarized from NZ Atlas, CSN and published information as cited.

NI Generally widespread. **FAR NORTH, NORTHLAND:** Recorded at a few scattered sites from Spirits Bay and Tom Bowling Bay, S to Kowhai Beach (Edgar 1971; Pierce *et al.* 1993); widespread S of Kaitaia, including on offshore islands, such as Hen & Chickens Grp (Merton & Atkinson 1968), but absent from Poor Knights Is (Bartle & Sagar 1987). Formerly recorded on Three Kings Is, but not since 1887 (Turbott & Buddle 1948; Oliver). **AUCKLAND, s. AUCKLAND, WAIKATO:** Widespread, including on islands such as Mokohinau Grp, Great Barrier, Little Barrier, Noises and Tiritiri Matanga (Reed 1972; Bell 1976; Cunningham & Moors 1985; Gill & Veitch 1990). **BAY OF PLENTY:** Generally widespread, though not often in coastal areas (Edgar 1978). Rarely recorded on Cuvier I. (Blackburn 1967a; CSN 26); also occur on Mercury and Alderman Grps and Mayor I. (Hicks *et al.* 1975). **VOLCANIC PLATEAU, GISBORNE–WAIROA:** Widespread but scattered. **HAWKES BAY:** Widespread, but scattered in S. **WAIRARAPA:** Scattered records in E, but widespread elsewhere. **WELLINGTON:** Widespread, including on Kapiti I. (Wilkinson & Wilkinson 1952). **MANAWATU:** A few records at scattered sites in s. and central areas, e.g.





Palmerston N (Guest & Guest 1993), but quite widespread in N. **WANGANUI:** Widespread, though scattered in extreme NE. **TARANAKI:** Generally widespread, but absent from areas S and W of Egmont NP. **SI** Most records in W; scattered elsewhere. **NELSON:** Widespread. **MARLBOROUGH:** Widespread in N, including Marlborough Sounds, in area bounded by Wairau R., St Arnaud Ra. and Spenser Mts. A few scattered records farther E, from Blenheim S to near Clarence. **CANTERBURY:** Widespread in NW, S to L. Sumner (Wilkinson & Guest 1977). Rarely recorded elsewhere: mostly on Banks Pen., with a few other records at sparsely scattered sites on Canterbury Plains, mainly along Waimakariri, Rakaia and Waitaki Rs. **OTAGO:** A few scattered records from near Dunedin S to Chaslands Mistake. Also a few records along Clutha R. and round Ls Wakatipu, Wanaka and Hawea, and their catchment streams; otherwise, mostly absent. **SOUTHLAND:** Mostly recorded in S, from Catlins SF Park, W to near Invercargill, and N to Hokonui Hills and near Dipton. Farther W, rarely in s. Longwood Ra., and widespread in area from Te Waewae Bay, N to Kaherekoau Mts and W to Cameron Mts and L. Hakapoua–Big R. (Muller 1969). Widespread on Stewart I. and other associated islets, including Ruapuke I. and Muttonbird Grp (Blackburn 1968; Muller

1969); also on Centre I. in Foveaux Str. (Cooper 1991). Absent from much of Fiordland, but a few records centred on Preservation and Chalky Inlets; a few scattered records in E, between L. Monowai and Te Anau; odd records elsewhere; more widespread N of line joining Caswell Sound and N. Mavora L. (Sibson 1967; Lambert 1970). **WEST COAST:** Widespread, though mainly W of main divide (O'Donnell & Dilks 1986).

Kermadec Is Confined to Raoul I., where abundant (Merton 1970; Merton & Veitch 1986; Robertson 1996).

Chatham Is Recorded on Pitt, South East and Mangere Is (Freeman 1994; Nilsson *et al.* 1994; Tennyson & Millener 1994; CSN), and, till the mid-1990s, on Chatham I. (Dilks *et al.* Undated).

Snares Is Single immature seen during 1961 (Warham 1967).

Auckland Is Little information. Recorded on 1972–73 expedition (Bell 1975); not recorded on main island in Dec. 1976 (Bartle & Paulin 1986).

Breeding Probably breed throughout much of range. A pair bred on Pitt I., Chatham Is, in 1990, for the first time in 20th century (Butler & Merton 1992).

Populations At Tutira, Hawkes Bay, four nests recorded in

c. 0.8 ha (Guthrie-Smith 1910). On Chatham I., 30 birds recorded in 12,500 ha, summer 1988–89 (Freeman 1994; CSN 37). **Change in range, populations** Numbers on Raoul I., Kermadec Grp, declined soon after settlement (Oliver). Extinct on Three Kings Is (Turbott & Buddle 1948; Oliver). Populations throughout NZ said to have declined in 19th century, possibly from persecution, with numbers lowest in c. 1880; populations began to increase soon after, when the species became legally protected. However, by 1920s, populations still had not recovered to previous levels (Oliver; *contra* Turbott 1967). Very common in Hunua Ras in early 20th century, but populations had declined markedly by early to mid-1970s, possibly from spread of Common Mynas *Acridotheres tristis* (see Threats and Human Interactions) (St Paul & McKenzie 1974; McKenzie 1979). Populations in Gisborne said to have increased recently (CSN 41). At Blowhard Bush, Hawkes Bay, recent increase in population may have resulted from control of predators (CSN 43). Formerly plentiful in Fiordland in late 19th and early 20th centuries, but now scarce, possibly a result of predation by introduced mammals (Hutton & Drummond 1904; Blackburn 1967b; Sibson 1967); at Haast–Jackson Bay, though still numerous in mid-1960s, numbers have greatly declined since c. 1940 (CSN 19 [Suppl.]). On Chatham Is, formerly widespread on major islands. Plentiful on Chatham I. (though less abundant in N) and on Pitt I. in 1937 (Fleming 1939), but uncommon by 1970s (Merton & Bell 1975). At least five pairs recorded in Lower Tuku Gully on Chatham I. till 1990; by 1992–93, only one pair remained (Freeman 1994). Recorded ‘in fair numbers’ on South East I. in 1937 (Fleming 1939), but rare by mid-1950s (Bell 1955; Dawson 1955) and c. 10–12 pairs recorded in 1961 (Williams 1962; Merton & Bell 1975). Stock were removed from the island in 1961, which allowed vegetation, particularly ground cover, to regenerate; this allowed Tui to become abundant again by 1970s (Merton & Bell 1975); still abundant in early 1990s (Nilsson *et al.* 1994).

THREATS AND HUMAN INTERACTIONS Populations on Chatham I. may have declined following clearance of coastal Ngaio *Myoporum laetum* for agriculture (O’Donnell & Dilks 1993); declines elsewhere likely to have been caused by clearance of lowland forest (Wilson *et al.* 1988). 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). Declines due to habitat clearance may have been offset by adaption to foraging in exotic nectar-bearing plants such as eucalypts and acacias (Oliver). Nestlings often killed by Stoats *Mustella erminea* (Blackburn 1967b; CSN 19 [Suppl.], 26, 28); adults and young sometimes killed by Cats (Sorensen 1964; Bergquist 1986; Oliver); eggs and young possibly killed by rats (Sibson 1967; Oliver; *contra* Blackburn 1965, 1967b). Numbers on Red Mercury I. declined temporarily after poison air-dropped to eradicate rats, but this apparent change in numbers probably caused by natural seasonal movement (Robertson *et al.* 1993). Reduction in population in Hunua Ras blamed on Common Mynas, which sometimes take eggs (McKenzie 1979); Mynas also compete with Tui for food, and sometimes attack and kill, or at least displace Tui, at food source (CSN 24, 42); Tui sometimes also attacked and killed by Common Blackbirds and Common Starlings (Oliver); also said to have been adversely affected by competition for food with Common Starlings, Eastern Rosellas *Platycercus eximius* and Common Chaffinches *Fringilla coelebs*,

and sometimes driven away by Australian Magpies *Gymnorhina tibicen* (CSN 19 [Suppl.]). Very occasionally blamed for damage to peaches in orchards (CSN 19 [Suppl.]). Formerly hunted by Maori, using one of seven methods of capture: a skilful fowler could catch up to 100 in a day by calling birds in with an imitation and then hitting them with a long flexible stick; also speared and snared; easily captured on frosty nights, when ‘their claws were contracted by the cold, and they could not fly’ (Hutton & Drummond 1904; Turbott 1967). Formerly shot by explorers and early settlers for food: they were ‘delicate eating’ and ‘made many delicious pasties’ (Hutton & Drummond 1904; Medway 1976); Maori preserved them in their own fat in calabashes, to be consumed at feasts (Turbott 1967). Tui skins formerly illegally exported for ornamentation on ladies’ hats; one dealer in Wellington sent up to 500 skins to London (Turbott 1967). Often kept as pets by early settlers and, sometimes, Maori (Hutton & Drummond 1904; Turbott 1967). Sometimes collide with windows (McEwan 1977).

MOVEMENTS Various considered resident (Stidolph 1923; Moncrieff 1929; Bull 1959) or migratory (Wilson *et al.* 1988; Oliver), and to have seasonal patterns of occurrence (Edgar 1978; Owen & Sell 1985; Guest & Guest 1993). Movements said to be associated with availability of food, with larger numbers occurring in areas when food abundant (McCann 1952; St Paul 1975; Onley 1980; Stewart 1980; Dilks *et al.* Undated; CSN). Sometimes move between habitats, inhabiting dense ‘bush’ during winter and more open country during spring (McLean 1912).

Described as resident in Wairarapa (Stidolph 1923), Taita (Bull 1959) and near Toko (Moncrieff 1929). Present throughout year on Kermadec Is (Iredale 1910), Parua Bay (Moncrieff 1929), Whangarei Harbour (Devonshire 1979), Little Barrier I. (Gravatt 1970), Wenderholm (CSN 37), Tauranga district (Hodgkins 1949), Te Puke (CSN 39, 41), Minginui (CSN 9) and Wanganui (CSN 41). Recorded in all seasons in Orongorongo Valley (Gibb 1996).

Seasonal patterns also found. During winter, move into urban areas round Tauranga (Edgar 1978), Wellington (Stidolph 1926), Waimea Inlet (Owen & Sell 1985), Leith Valley (CSN 19), Cashmere Hills, Christchurch (CSN 1), Palmerston (Guest & Guest 1993) and in Southland (CSN 19 [Suppl.]). Disperse during summer, from Fletcher Ck into hill-country forests, returning in Apr. to winter in low-terrace forest of Fletcher Ck and hill-country forests of Reefton Saddle and Te Wharau (Dawson *et al.* 1978). Visit Greyouth during spring (CSN 36) and autumn (CSN 19 [Suppl.]). Population at Tihoi increases during winter, birds possibly coming from round Minginui (St Paul 1975), where greatest numbers occur during summer and autumn (CSN 6, 9). Migrate from Ohikanui Valley to winter in forests elsewhere (Wilson *et al.* 1988). Present in Nelson, Sept.–Apr. (Moncrieff 1929); Mohi Bush in spring–summer (CSN 42); Hibernia Ck in summer, and occasionally in winter (CSN 39); leave Fiordland over winter (CSN 19 [Suppl.]); at Parua Bay, many move inland from coast over winter (Moncrieff 1929). In Whangarei District, many winter on inland slopes of Tangihua Mts and Takakowai and Kuhumui Hills; disperse from these areas in spring; and widespread in summer (CSN 1). Local movements recorded on some islands: on Hen I., congregate in N, with few remaining in S or W, but disperse throughout island during Nov.–Jan. (Skegg 1964); on Little Barrier I., congregate at flowering Pohutukawa *Metrosideros excelsa* round coast during summer, but more widespread over winter (McKenzie 1948); on Stewart I., move towards coast in spring to breed (Oliver).

On South East I., Chatham Is, 164 birds banded Oct. 1996 to Feb. 1997: some were resighted close to banding site after 2.5 years, indicating some site-fidelity. Most breeding birds wintered on nearby Pitt I., returning to South East I. in spring to breed; birds often moved between South East and Pitt Is during spring before breeding, probably to feed, and males and non-breeders continued to do so over summer (Dilks *et al.* Undated; D.J. Onley).

On Tiritiri Matangi I., 84 birds banded 1977–78: 49 (58.3%) returned to island in following season, though believed to be an underestimation, as whole island not surveyed. Birds leave breeding areas, then island, after breeding, with a gradual decline in numbers and activity noted. Adults appear to leave island before juveniles, which move once their flight has improved. Pattern of movement throughout year varies, though often regular for individuals. Some briefly return to island during winter, others present only for breeding season. Many birds return to same home-ranges each breeding season, often in or near natal area. Move little during breeding season (Stewart 1980).

Banding Of 327 banded to 1974, 40 recoveries (12.2%). An adult banded at Orongorongo, 31 Jan. 1969, recovered at banding place over 3 years 11 months after banding (Robertson 1975).

FOOD Nectar, fruit and insects; occasionally seeds and pollen. **Behaviour** Mainly arboreal. Mostly forage in canopy and subcanopy; occasionally search for insects on forest floor (CSN 19; Oliver). Mainly feed on nectar, but also take insects or fruit when nectar not available (McCann 1952; Stewart 1980; Gaze & Clout 1983; O'Donnell & Dilks 1994). **DETAILED STUDIES:** On Hen I. (Merton 1966); Little Barrier I. (Gravatt 1969, 1971); South East I., Chatham Grp (O'Donnell & Dilks 1993); three sites on SI, one at Mt Richmond SF and two at Golden Downs SF (Gaze & Clout 1983); and in Windbag Valley, s. Westland (O'Donnell & Dilks 1994). **SIZE OF FEEDING FLOCKS:** Forage singly or in pairs, sometimes in small family groups (Heather & Robertson 1997; D.J. Onley); also seen foraging in flocks, especially at abundant sources of food, e.g. hundreds seen feeding together on seeds of Kahikatea *Dacrycarpus dacrydioides* (St Paul 1975; CSN 19, 28); on Chatham I., large flocks feed on flowering New Zealand Flax *Phormium tenax* (Dilks *et al.* Undated); and on Kapiti I., flocks of up to c. 200 birds feed on flowering flax (Wilkinson & Wilkinson 1952). **TERRITORIES:** Establish and defend feeding territories (see Social Organization for details). **FEEDING HEIGHTS, SITES:** On Hen I. (n=93 feeding obs.): 65% of observations at flowers; 25% in foliage; 3% on twigs; 5% on bark of tree branches and trunks; 1% on fruit; and 1% in air. On Little Barrier I. (n=203 feeding obs.): 47.8% of observations in canopy, 28.1% in subcanopy, 7.4% in upper understorey, 16.3% in mid-understorey, and none in lower understorey or on ground; heights at which these observations recorded: on ground and up to 1.5 m above ground (0% of obs.), 1.6–3.0 m (2.9%), 3.1–4.5 m (7.8%), 4.6–6.0 m (13.7%), 6.1–7.5 m (9.8%), 7.6–9 m (27.5%), 9.1–10.5 m (11.8%), 10.6–12.0 m (13.2%), 12.1–13.5 m (7.4%), 13.6–15 m (3.4%), and >15 m above ground (2.5%). When feeding on insects (n=27 feeding obs.): 40.7% gleaned from foliage; 25.9% from twigs; 18.5% from branches; and 7.4% from trunks of trees. On South East I. (n=29 feeding obs.): 17.2% of observations in lower canopy, 69.0% in mid-canopy and 13.8% in upper canopy; feeding from twigs (62.1%) and small branches (37.9%); heights at which these foraging observations recorded: 1–3 m (24.2% of obs.); 3–5 m (31.0%), 5–7 m (34.5%)

and >8 m (10.3%). In Windbag Valley (n=695 feeding obs.): c. 10% of observations were in lower understorey, c. 22% in upper understorey, c. 22% in shaded canopy, c. 35% in unshaded canopy, c. 8% in emergent leaves, and c. 3% above canopy. In n. SI, fewer birds foraged in conifer plantations than in adjacent native forests, but birds most abundant in areas where honeydew most plentiful; birds used plantation forests more during summer than winter, when mostly seen foraging in or adjacent to native forests (Clout & Gaze 1984). **FOOD SOURCES:** On Little Barrier I., fed mainly on nectar for most of year; fruit was seasonal component of diet, being of greatest importance Feb.–July; of 66 feeding observations in spring (Aug.–Oct.), 64 in summer, 29 in autumn, and 26 in winter: fed on nectar in 98.4% of observations in spring, 76.6% in summer, 55.2% in autumn, and 76.9% in winter; insects, 1.6%, 23.4%, 17.2%, 11.6%; and fruit –%, –%, 27.6%, and 11.6%, respectively. During autumn on South East I. (29 feeding obs.), fed in five species of trees in forest, mostly on fruit (86.2%) but also insects (13.8%); mostly fed in Ngaio *Myoporum laetum* (62.1%), but also Chatham I. Ribbonwood *Plagianthus regius* (13.8%), Chatham I. Mahoe *Melycitus chathamicus* (3.5%), Chatham I. Matipo *Myrsine chathamica* (3.5%), and Kawakawa *Macropiper excelsa* (17.2%). In Windbag Valley, obtained food from many species of plants (summarized in Table 1). Sources of food varied seasonally: fed on nectar throughout year, but proportion increased from c. 10% in Apr. and June to 32% in Aug., peaked at 73% in Oct., 54% in Dec. and 28% in Feb. Honeydew was taken in most months, and comprised up to 13% of diet in midwinter. Proportion of fruit in diet peaked during Apr., when comprised c. 50% of items. More than half of all observations of feeding on insects

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

PLANT SPECIES	FOOD ITEMS			
	General (695 obs.)	Nectar (287 obs.)	Fruit (98 obs.)	Invertebrates (27obs.)
CANOPY SPECIES				
<i>Dacrydium cupressinum</i>	17.7	–	63.3	–
<i>Dacrycarpus dacrydioides</i>	2.3	–	4.1	5.4
<i>Lagarostrobos colensoi</i>	0.1	–	–	–
<i>Metrosideros umbellata</i>	16.0	32.8	–	–
<i>Nothofagus menziesii</i>	13.2	–	–	29.7
<i>Podocarpus hallii</i>	0.4	–	–	2.7
<i>Podocarpus totara</i>	0.6	–	–	–
<i>Prumnopitys ferruginea</i>	0.7	–	2.0	–
<i>Weinmannia racemosa</i>	11.8	3.8	–	8.1
SHRUB HARDWOODS				
<i>Aristolotelia serrata</i>	0.4	–	–	–
<i>Carpodetus serratus</i>	2.7	–	17.4	–
<i>Coprosma lucida</i>	0.7	–	5.1	–
<i>Coriaria arborea</i>	1.4	3.5	–	–
<i>Fuchsia excorticata</i>	16.7	40.4	–	–
<i>Hedycarya arborea</i>	0.3	0.4	–	–
<i>Myrsine australis</i>	0.1	–	1.0	–
<i>Pseudopanax crassifolius</i>	0.1	2.1	–	–
<i>Pseudopanax edgerleyi</i>	1.0	–	4.1	–
<i>Pseudopanax simplex</i>	0.6	–	–	–
<i>Schefflera digitata</i>	0.1	–	1.0	–
OTHER PLANTS				
Ferns	0.3	–	–	–
<i>Metrosideros</i>	6.3	13.9	–	–
<i>Muehlenbeckia australis</i>	0.1	–	–	–
<i>Paraxilla</i>	1.2	2.8	–	–
<i>Ripogonum scandens</i>	0.3	–	2.0	–
GROUND OR AERIAL FEEDING	4.6	–	–	54.0

were of prey taken from air; invertebrates were most important in Aug., comprising c. 60% of diet. Diet of population on Tiritiri Matangi I. varied with season and sex of bird. Nectar was major component of diet throughout year, with proportion of arthropods highest during summer and autumn, and fruit highest during autumn. Significant difference in composition of diet between sexes during spring and autumn, when males took more nectar and females took more arthropods. Difference in diet between sexes in spring occurred despite both sexes foraging in same patches of *Sophora tetraptera*: males fed on nectar while females gleaned insects from trunks and foliage; during autumn, males and females did not feed together as often; each sex fed at different locations in winter. Dominance of males at resources probably responsible for differences in diet and feeding between sexes during autumn (Bergquist 1985b). In study at three sites on SI (n=1029 5-s obs. periods throughout year), 51% of total time was spent foraging; 36% of total time feeding was on honeydew secreted by scale insects (Coccidae: *Ultracoelostoma assimile*), 7% on insects and 8% on other food, including nectar (Gaze & Clout 1983). Honeydew is a major food source in majority of SI forest habitats because, except in Windbag Valley, these are dominated by beech trees that are usually infested with scale insects (P.D. Gaze). On Little Barrier I., appeared to prefer feeding at those plants categorized as providing the greatest reward, with flowers that are both rich in nectar and grow in dense patches, i.e. Pohutukawa *Metrosideros excelsa*, *Knightia excelsa* and *Pittosporum umbellatum* (Rasch 1985). Sometimes fly long distances to feed on seasonally flowering trees, such as *Sophora tetraptera* and Pohutukawa (Gravatt 1971; Moon 1992), and visit city parks to feed in nectar-bearing trees (Moon & Lockley 1982). FEEDING METHODS: Feed on nectar by directly probing flowers; insects usually gleaned from leaves, branches and trunks of trees or caught aerially by sallying (St Paul 1975; Stewart 1980; Oliver, CSN 19). In Windbag Valley (n=27 feeding obs.), most insects collected by gleaning (c. 80%) with rest caught by sallying, mostly in air. When eating large insects (up to 10 cm long, e.g. mantids), insect grabbed round middle of body and quickly passed through bill from end to end, then swallowed whole, head-first (CSN 1, 5; Oliver). When feeding on fruit, usually eat sarcocarp and leave seeds (St Paul 1975). When feeding on honeydew, hop up trunks of trees, often in spirals (Gaze & Clout 1983). When feeding from flowers of *Sophora microphylla*, bird perches above flowers and lifts each flower by probing deep into flower with bill; at same time, stigma is brought into contact with bird's forehead, depositing pollen; other flowers then pollinated when visited later. Flowers of Puriri *Vitex lucens* stand out on stiff penduncles and pedicels, and birds appear to have difficulty in getting access to nectar; birds must reach out to them from branches to obtain nectar, and may be seen holding on to branches at all possible angles, including hanging upside-down. When feeding on New Zealand Flax, sit on branches above flowers, and probe them deeply (McCann 1952). ADAPTATIONS: Tongue brush-like; tip composed of four finely attenuated arms, each with very fine bristles and a large blood vessel. Main body of tongue is deeply canaliculated, enabling nectar to flow towards gullet (McCann 1952, 1964).

Detailed studies ON HEN I. (67 feeding obs.; Merton 1966): **Plants** MONOCOTYLEDONS: Smilacaceae: *Rhipogonum scandens* nectar 1.5%. DICOTYLEDONS: Araliaceae: *Pseudopanax lessonii* fru. 1.5; Corynocarpaceae: *Corynocarpus laevigata* nectar 1.5; Meliaceae: *Dysoxylum spectabile* nectar 29.8; Verbenaceae: *Vitex lucens* nectar 64.2; Tiliaceae: *Entelea arborescens* sap 1.5. **Animals** INSECTS: Diptera 1.5.

On LITTLE BARRIER I. (150 birds observed feeding on nectar over 12 months; Gravatt 1969, 1970): **Plants** MONOCOTYLEDONS: Agavaceae: *Phormium tenax* 2 birds observed feeding (Nov.). DICOTYLEDONS: Araliaceae: *Neopanax arboreum* 1 (Sept.); Meliaceae: *Dysoxylum spectabile* 1 (June); Myrtaceae: *Metrosideros excelsa* 25 (Nov.–Jan.); *M. fulgens* 11 (Mar.–July); *M. robusta* 19 (Dec.–Jan.); Pittosporaceae: *Pittosporum tenuifolium* 2 (Oct.); *P. umbellatum* 35 (Aug.–Sept.); Proteaceae: *Knightia excelsa* 18 (Sept., Nov.); *Persoonia toru* 1 (Nov.); Verbenaceae: *Vitex lucens* 56 (Feb.–Nov.).

On KAPITI I., Aug. 1991–Aug. 1994 (obs. of plants frequently visited for nectar whenever flower available; Castro & Robertson 1997): **Plants** MONOCOTYLEDONS: Agavaceae: *Phormium tenax*. DICOTYLEDONS: Araliaceae: *Pseudopanax arboreous*; Cornaceae: *Griselinia littoralis*; Cunoniaceae: *Weinmannia racemosa*; Elaeocarpaceae: *Elaeocarpus dentatus*; Loganiaceae: *Geniostoma rupestre*; Meliaceae: *Dysoxylum spectabile*; Myrtaceae: *Metrosideros excelsa*; *M. fulgens*; *M. robusta*; Onagraceae: *Fuchsia excorticata*; Pittosporaceae: *Pittosporum crassifolium*; *P. eugenioides*; *P. tenuifolium*; *P. umbellatum*; Proteaceae: *Knightia excelsa*; Verbenaceae: *Vitex lucens*.

At DUNEDIN, July 1992–Dec. 1997 (direct obs. of feeding on fruit and nectar, and number of days birds recorded feeding on each; Baker 1999): **Plants** GYMNOSPERMS: Podocarpaceae: *Podocarpus totara* fru., 1. MONOCOTYLEDONS: Agavaceae: *Phormium* nectar, 18. DICOTYLEDONS: Araliaceae: *Pseudopanax* fru., 1, nectar, 35; Cornaceae: *Corokia* fru., 6; *Griselinia littoralis* fru., 2; Elaeocarpaceae: *Aristotelia serrata* fru., 9; Fabaceae: *Sophora* nectar, 65; Icacinaceae: *Pennantia corymbosa* fru., 3; Lorantheaceae: *Ileostylis micranthus* fru., 1; *Tupeia antarctica* fru., 2; Malvaceae: *Hoheria* nectar, 2; Moraceae: *Streblus heterophyllus* fru., 2; Myoporaceae: *Myoporum laetum* fru., 1; Myrsinaceae: *Myrsine australis* fru., 4; *M. salicina* fru., 7; Myrtaceae: *Lophomyrtus bullata* fru., 4; *L. obcordata* fru., 2; *Metrosideros excelsa* nectar, 2; *M. umbellata* nectar, 6; Onagraceae: *Fuchsia excorticata* nectar, 23; Pittosporaceae: *Pittosporum umbellatum* nectar, 5; Polygonaceae: *Muehlenbeckia australis* fru., 6; Proteaceae: *Knightia excelsa* nectar, 2; Rubiaceae: *Coprosma areolata* fru., 2; *C. crassifolia* fru., 1; *C. linariifolia* fru., 4; *C. lucida* fru., 6; *C. propinqua* fru., 1; *C. robusta* fru., 6; *C. rotundifolia* fru., 1; Verbenaceae: *Vitex lucens* nectar, 9.

Other records **Plants** (Nectar unless stated.) Fruit^{2,13,28,30}, pollen²³. GYMNOSPERMS: Podocarpaceae: *Dacrycarpus dacrydioides*^{34,36}, fru.^{18,23,38,39,55}, sds⁴⁰; *Podocarpus* fru.²⁷; *P. spicatus* fru.²³; *P. totara* fru.^{20,37}, sds¹⁹; *Prumnopitys ferruginea* fru.^{18,23,39}; *P. taxifolia* fru.^{18,38,39}. MONOCOTYLEDONS: Agavaceae: *Cordyline australis* fru.²³; *Phormium colensoi*¹⁴; *P. tenax*^{3,5,6,13,20,21,23,29,30,34,40}; Aquifoliaceae: *Ilex verticillata* fru.⁴¹; Iridaceae: *Freesia*³³; Liliaceae: *Aloe ciliaris*^{8,23}; *Kniphofia*²³; Pandanaceae: *Freycinetia banksii* fru.^{13,20,30}; Smilacaceae: *Rhipogonum scandens* fru.^{18,20,30,38,53}. DICOTYLEDONS: Amaryllidaceae: *Bomarea*⁸; Apocynaceae: *Parsonia heterophylla*²³; Araliaceae: *Neopanax arboreum*³⁹; *Pseudopanax*^{27,57}, fru.²⁷; *P. arborea* fru.^{23,26}; *P. chathamica*^{7,29}; *P. colensoi*⁵⁰; *P. lessonii* fru.^{21,26,54}; Caprifoliaceae: *Alseuosmia macrophylla*^{23,54}; Corynocarpaceae: *Corynocarpus laevigatus* fru.^{20,23,30}; Cunoniaceae: *Weinmannia racemosa*⁵¹; Elaeocarpaceae: *Aristotelia serrata*³⁴, fru.^{14,20}; Epacridaceae: *Dracophyllum longifolium*⁵; Ericaceae: *Azalea*³³; *Rhododendron*⁵⁶; Escalloniaceae: *Carpodetus serratus*³⁶, fru.^{38,39,57}; *Ixerba brexioides*¹⁴; *Quintinia*⁵¹; Fabaceae: *Clianthus puniceus*⁵; *Erythrina*²¹; *Sophora microphylla*^{5,8,13,18,20,21,23,28,38,39,51,52,56,57}; *Trifolium repens*⁴⁰; Fagaceae: *Nothofagus*²³; Flacourtiaceae: *Idesia* fru.^{56,60}; Icacinaceae: *Pennatia corymbosa* fru.^{38,42}; Lorantheaceae: *Elytranthe colensoi*⁵; *Tupeia antarctica* fru.²⁷; Lauraceae: *Bielschmiedia tarairi*²³; Malvaceae:

*Hibiscus*²³; Meliaceae: *Dysoxylum spectabile*^{6,10,23,26}; Melianthaceae: *Melianthus major*¹⁷; Mimosaceae: *Acacia*^{13,44}; pollen⁴²; Moraceae: *Ficus* fru.¹⁵; *Streblus heterophyllus* fru.²⁷; Myoporaceae: *Myoporum laetum* fru.^{23,27,29}; Myrsinaceae: *Myrsine* fru.²⁷; *M. australis* fru.^{24,47,48}; *M. chathamica*²⁹; *M. salicina*⁴⁹; Myrtaceae: *Acmena*⁴⁰; *Callistemon*^{8,40}; *Eucalyptus*^{23,40,50,55}; *E. globulus*¹³; *E. leucoxylon*²¹; *Kunzea ericoides*²⁷; *Leptospermum*²³; *Lophomyrtus bullata* fru.²⁷; *Metrosideros excelsa*^{1,9,12,20,21,23,28,33,45,57,59}; *M. fulgens*²⁴; *M. robusta*^{3,6,20,30,55,57,61}; *M. umbellata*^{14,23}; Oleaceae: *Ligustrum vulgare*⁴⁰, fru.⁴⁶; *Nestegis* fru.^{18,30}; *Olea*³⁹; Onagraceae: *Fuchsia*^{30,36,38,39,48,57}, fru.³⁹; *F. excorticata*^{5,23,27,33}, fru.¹⁴; Phytolaccaceae: *Phytolacca octandra*⁴⁰; Piperaceae: *Macropiper excelsum* fru.²⁹; Pittosporaceae: *Hymenosporum flavum*²³; *Pittosporum crassifolium*^{14,26,27,32,54,56,57}; Polygonaceae: *Muehlenbeckia* fru.^{29,43}; *Muehlenbeckia australis*²⁷; Proteaceae: *Banksia*⁵⁷; *Grevillea rosmarinifolia*⁴⁰; *Knightia excelsa*^{20,23,30,52,54}; Rosaceae: *Crataegus* fru.^{34,36}; *Malus sylvestris* fru.^{41,51,55}; *Prunus*^{40,57}; *P. campanulata*²¹; *P. persica*²¹, fru.⁴⁰; Rutaceae: *Citrus* fru.^{12,15,16}; Rubiaceae: *Coprosma* fru.^{20,23,30}; *C. arborea* fru.⁵⁵; *C. chathamica* fru.²⁹; *C. grandifolia* fru.⁵⁹; *C. robusta* fru.^{32,57,60}; Santalaceae: *Mida salicifolia* fru.²³; Saxifragaceae: *Ribes*³⁶, fru.³⁸; Solanaceae: *Nicotiana*⁴³; Sterculiaceae: *Brachychiton acerifolius*²³; Tiliaceae: *Entelea arborescens* fru.^{26,38}; Verbenaceae: *Vitex lucens*^{20,21,23,24,27,33,40,55}; Violaceae: *Melicytus ramiflorus* fru.^{11,20,23,27,30,55}; Vitaceae: *Vitis vinifera* fru.¹⁵; Winteraceae: *Pseudowintera axillaris* fru.²². **ANIMALS CRUSTACEANS:** Sandhoppers²⁵. **INSECTS**^{12,13,16,23,24,28,30,39,40}: Hemiptera: Honeydew^{43,58}; Cicadidae^{35,36,38,39}; Coccidae²³; Mantodea^{23,30,32,35}; Phasmatoidea^{28,31}. **Other records** Sugar water^{6,23,33}; honey²³; milk⁴.

REFERENCES: ¹ Sibson 1947; ² Dawson & Cresswell 1949; ³ Duncley 1949; ⁴ Potter 1949; ⁵ McCann 1952; ⁶ Wilkinson & Wilkinson 1952; ⁷ Bell 1955; ⁸ Prickett 1959; ⁹ Edgar 1962; ¹⁰ Bell & Brathwaite 1963; ¹¹ Blackburn 1963; ¹² Edgar *et al.* 1965; ¹³ Turbott 1967; Gravatt 14 1969, ¹⁵ 1970; ¹⁶ Merton 1970; ¹⁷ Simpson 1973; ¹⁸ St Paul 1975; ¹⁹ McEwan 1977; ²⁰ Falla *et al.* 1978; ²¹ Devonshire 1979; ²² Norton 1980; ²³ Stewart 1980; ²⁴ Gaze & Fitzgerald 1982; ²⁵ Daniel 1982; ²⁶ Cunningham & Moors 1985; ²⁷ Baker 1992; ²⁸ Moon 1992; ²⁹ Dilks *et al.* Undated; ³⁰ Oliver; ³¹ NZRD; CSN ³² 1, ³³ 2, ³⁴ 3, ³⁵ 5, ³⁶ 6, ³⁷ 7, ³⁸ 8, ³⁹ 9, ⁴⁰ 19, ⁴¹ 20, ⁴² 21, ⁴³ 22, ⁴⁴ 23, ⁴⁵ 24, ⁴⁶ 25, ⁴⁷ 28, ⁴⁸ 29, ⁴⁹ 30, ⁵⁰ 32, ⁵¹ 33, ⁵² 34, ⁵³ 35, ⁵⁴ 37, ⁵⁵ 38, ⁵⁶ 39, ⁵⁷ 41, ⁵⁸ 42, ⁵⁹ 43, ⁶⁰ 44, ⁶¹ 45.

Young Mainly fed by female (Merton 1970), but sometimes by both parents, especially after fledging (Stewart 1980). Fed on nectar and insects for first few days after hatching, then subsequently on fruit and larger insects (Moon & Lockley 1982). When young fed on liquid nectar, two methods used: (1) parent holds bill horizontally and young take nectar from tip of bill; (2) parent perches above young and vigorously regurgitates with pumping action, pointing bill vertically downward (Blackburn 1963). On Tiritiri Matangi I., young fed mainly on insects; in 41 h of observations at seven nests, 96% of feeds comprised insects, 4% nectar, fed mostly to older nestlings (Stewart 1980).

Plants Nectar (Blackburn 1963; Merton 1970), fruit (Moon & Lockley 1982). **GYMNOSPERMS:** Podocarpaceae: *Podocarpus totara* fru. (CSN 7). **DICOTYLEDONS:** Onagraceae: *Fuchsia* fru. (Guthrie-Smith 1910); Rubiaceae: *Coprosma* fru. (Merton 1970); Violaceae: *Melicytus ramiflorus* fru. (Blackburn 1963). **Animals** **INSECTS** (Blackburn 1963; Moon & Lockley 1982): Coleoptera (Stewart 1980); Diptera: Tipulidae (Stewart 1980); Hemiptera (Stewart 1980): Cicadidae (Blackburn 1963; Merton 1970); Hymenoptera: wasps (Stewart 1980; Moon & Lockley 1982); Lepidoptera: larv. (Merton 1970); Phasmatoidea (Merton 1970; Moon & Lockley 1982). **Other matter** Sugar water (CSN 4).

Intake On Kapiti I., energy intake (kJ/min) for birds feeding on nectar from five species of plants ranged between 0.1 and 1.3 kJ/min; estimated energetic requirements (0.25 kJ/min) could only be satisfied when feeding from flowers of *Dysoxylum spectabile* and *Pittosporum crassifolium*, or when feeding selectively on flowers of *Pseudopanax arboreus*; feeding on flowers of *Geniostoma rupestre* or early flowers of *D. spectabile* did not satisfy energy requirements and, in such cases, birds could have been foraging for pollen or small insects. Average number of flowers visited by individual Tui while foraging at various plant species: *G. rupestre* 72.4 fl./min (12.6; 10.2 min); *D. spectabile* (early flowering) 41.3 (8.49; 2.6 min), late flowering 43.1 (5.11; 12.7); *P. arboreus* (male fl.) 79.1 (5.97; 3.8); *P. crassifolium* 38.0 (9.08; 25.3) (Castro & Robertson 1997).

SOCIAL ORGANIZATION Based on contribution by E. Marks; most information from studies on islands where Tui rather concentrated and often free of predators, particularly 2-year study of social organization and foraging ecology on Tiritiri Matangi I. and Whangaparaoa Pen. (Stewart 1980); 2-year study of behaviour, social interactions and song at North Shore, Auckland, NI, including at artificial feeding stations (Bergquist & Craig 1988); study of movement of groups in breeding and non-breeding areas at North Shore (Bergquist 1985a); and study of hierarchy, aggression and noises made with wings (Craig 1984); some other information in Stewart & Craig (1985) and Bergquist (1985b). Throughout year, often seen singly or in pairs, but gather where food is concentrated, e.g. patches of flowering kowhai *Sophora tetraptera* (Bergquist & Craig 1988). Social organization flexible; maintain breeding territories and may hold feeding territories or form hierarchies at any time of year at feeding sites (Stewart 1980). Towards end of breeding season, Jan.–Apr., recorded in discrete feeding groups consisting of: neighbouring families; parents with two broods of current season; or parents with young of both current and previous seasons; groups of 3–15 birds occurring at rich sources of food during winter (Bergquist 1985a). Said that some birds continue to visit their territories throughout year (NZRD). However, Stewart (1980) found that pairs tended to separate after nesting, and no evidence that they associated together over winter, though siblings were sometimes seen together. Birds within flocks individually compete for food (Stewart 1980). In autumn and winter, males dominated females at feeding station made up of several feeding sites: in autumn, birds of pair fed together less often than during breeding season, and in winter, fed apart (Bergquist 1985b). Pair-bonds re-established during Sept., at start of each breeding season. During breeding season, pairs hold breeding territories, with male and female often feeding together before young fledge (Bergquist 1985a,b). Members of family flocks that have been together over winter often nest near each other (see below).

Bonds Monogamous (*contra* NZRD). Pair-bond maintained during breeding season. Some pairs remained stable over several years (Stewart 1980), though nature of pair-bond during non-breeding season not known. Females able to breed when 1 year old (Bergquist 1985a). In one breeding area on Tiritiri Matangi I., sex-ratio apparently skewed, with 67% of banded birds in area female (Stewart 1980). **Parental care** Only female builds nest, but male remains nearby; only female incubates; during incubation, male defends breeding territory and nest, spending >50% of time inside territory, either singing or guarding, and usually present when female leaves to forage. Female does most feeding of, and all brooding of, nestlings; only female defends immediate area round nestlings. Males that are

dominant at sources of nectar near breeding territories tend to feed chicks less often than lower ranking males, but may indirectly help females by maintaining access to resources (Stewart 1980). Both sexes feed fledgelings (Stewart 1980; Dिल्ks *et al.* Undated), though said to be mainly carried out by female (Blackburn 1963). However, if female lays second clutch, male may take over feeding (Stewart 1980). Young usually independent after 8–12 days or c. 2 weeks after fledging (Blackburn 1963; Stewart 1980; Bergquist 1985a), but may take up to 3 weeks (Stewart 1980), or several weeks (Wilkinson & Wilkinson 1952). Independent young may continue to beg for food, but are usually ignored (Stewart 1980). Form family groups after fledging (Dिल्ks *et al.* Undated). At first, young stay together near nest-site, then groups gradually move to rich feeding areas but avoid food-bearing trees, as they are often chased by adults. Family groups tend to gather at abundant food, and site-related hierarchies appear to develop (Stewart 1980). Once, parents dived at and gave threat postures to their brood <1 week after fledging, though parents possibly trying to keep group together for safety or feeding (Blackburn 1963). Stewart (1980) suggested that some siblings separated 3–4 weeks after fledging, or in some cases even earlier, though later work found some families stay together over winter and longer (see above).

Breeding dispersion Nest solitarily; average distance between nests of neighbouring pairs not known; female builds several nests, usually close together, before laying in one; see Breeding. On Tiritiri Matangi I., >100 birds present in 200 ha during breeding season (Stewart & Craig 1985). Immatures (yearlings) return to natal areas ($n=7$) (Stewart & Craig 1985). In one study, two birds nested within a few metres of natal sites (Stewart 1980). In another study, two male yearlings each defended food sources 100 m from parents' nest; after pairing, one nested 1 km from parents' nest, the other 1.5 km. Three females each nested within 150 m of parents' nest. Females have higher degree of philopatry than males (Bergquist 1985a). **Territories** BREEDING TERRITORIES: During breeding season on Tiritiri Matangi I., each pair establishes territory where they nest and spend much time, though occasionally leave to feed at rich sources of food. Thought to defend air-space above territory. Only males defend breeding territory, excluding conspecifics and some other species (Stewart 1980). When defending territory during early stages of nesting, male overtly aggressive, but by nestling stage, much time spent in Song-bouts and guarding from song-posts or other vantage points (Stewart 1980); for discussion of territorial behaviour, see Social behaviour: Agonistic Behaviour. At one nest, male more aggressive after hatching, chasing of Common Blackbirds, Song Thrushes *Turdus philomelos*, Common Mynas, House Sparrows *Passer domesticus* and Silvereyes, but not Goldfinches *Carduelis carduelis* or Grey Fantails *Rhipidura fuliginosa* (Blackburn 1963). Male spends average of 70% of time in defence and advertisement when territory being established and during nesting, mostly by Song (Stewart 1980). Female defends area round nest-site (Stewart 1980) but mostly only when nestlings present, and in response to predators rather than conspecifics; see Social Behaviour: Parental anti-predator strategies. Each year, birds establish breeding territories in similar areas (Bergquist 1985a); of seven males on territories, five returned to nest in similar area in following season (Stewart 1980; Stewart & Craig 1985). On Tiritiri Matangi I., age of birds and order of flowering or fruiting vegetation in the area influence establishment of territories: older males defended areas near supplies of nectar, whereas younger males were farther away; earliest nests were built by

birds defending territories near supplies of nectar. Early establishment of a territory in an area ensured priority of access to specific resources, though males that established territories early at Tiritiri Matangi I. still travelled 4.5 km to forage at kowhai *Sophora microphylla* till blossom declined; birds of pair usually left territory together, and joined small flocks before travelling, but did not always return together; when trees bloomed within male's territory, he stopped moving from site, though mate continued to feed elsewhere. As season progressed, size of territories decreased as more birds moved into area (Stewart 1980). Birds defended territory round nest-site till young mobile, then defended mobile areas round young with Song and aggressive defence, and defence of nest-site decreased unless female re-nested. FEEDING TERRITORIES, HIERARCHIES: Throughout year, males establish feeding territories at sites where food abundant, especially with constant supplies of food, such as at artificial feeders (Stewart 1980). Not known whether females defend independent feeding territories (Craig 1984). When many birds present at site, pressure from intruders can be so great that exclusive ownership breaks down and site-specific hierarchies form. Dominance among males mostly determined by age, with older birds dominant (Stewart 1980). In addition, males are dominant over females, and adults are dominant over juveniles (Stewart 1980; Craig 1984). At feeding sites, Tui apparently dominant over Bellbirds and Stitchbirds (Craig 1984; Rasch 1985). OUTSIDE BREEDING SEASON: During winter, where food abundant, males establish territories in association with social hierarchies, chasing intruders from core-area round resource, but rarely any farther. Conspecifics and other species, especially Bellbirds, are excluded (Stewart 1980). Territories much smaller than during breeding season; one male defended c. 1000 m² in winter and 24,750 m² in breeding season. In social hierarchies, males are most aggressive. Around artificial feeder: largest and most dominant males defended trees nearest the feeder, and least dominant males had territories farthest away. Highest-ranking birds fed alone; middle-ranking birds fed alone after high-ranking birds had left. Hierarchy unstable (Stewart 1980). Birds sometimes return to same feeding areas each year: banded birds regularly returned to same feeding station during May–July and same patches of kowhai during Aug.–Oct. (Bergquist 1985a); one male defended same winter territory in successive years (Stewart 1980). DURING BREEDING SEASON (Nov.–Feb.): On Tiritiri Matangi I., similar hierarchies form at some sources of nectar. Nectar from *Metrosideros* often only source available, and levels of aggression high within these trees; no bird able to exclude all other Tui from tree. Social hierarchy formed was based on proximity of resource to each male's territory, i.e. male that nested closest to tree was most dominant, followed by his mate and then his nearest neighbours; though influence of sex of birds was secondary (Craig 1984). Paired female appeared to have similar rank as mate, was involved in few interactions, and often foraged undisturbed. Subordinate birds feed when more dominant birds absent. Once young of year arrived at feeding areas, hierarchies were unstable and older juveniles (those from earlier nests) appeared more dominant than younger ones (Stewart 1980). ROUND ARTIFICIAL FEEDING STATION: Birds rarely interacted at feeders. During breeding season, for 3–4 weeks before young brought to feeders, pairs came in and each male defended feeder while mate fed; later, pairs brought dependent fledgelings and male continued defence. Once young feeding independently, family group moved to other sources of food, often returning 1–2 weeks later, but not defending a feeder unless visit by a second brood was imminent. As nesting

asynchronous, a sequence of resident pairs appeared at station over breeding season, each using feeders heavily for 5–7 weeks. When there was overlapping use of station by three females (25 Dec.–17 Jan.), on only four occasions in 358 visits were two Tui at the same feeder at the same time. Thus, during breeding, use of feeders was temporally and spatially partitioned. In winter, resident (those with breeding areas within 1 km of artificial feeding station) or local (those breeding 1–5 km away) maintained more frequent daily access to feeders than outsiders (those breeding farther away). In same area, just before breeding season, in patches of flowering kowhai *Sophora tetraptera*, agonistic interactions increased when large numbers of birds congregated, and pairs of birds vigorously defended trees or parts of trees; single males excluded other males but allowed females to feed. At one such site, of 17 banded Tui, 12 were adults defending kowhai trees, while five did not defend trees but fed within the site wherever they could; four of these were juveniles that could feed without aggression only in their parents' patch. Status of an individual at feeding station or natural source depended on its competitive abilities and status within its group (e.g. males dominant over females), and status of group to which it belonged (e.g. resident groups dominant over outsiders) (Bergquist & Craig 1988). **Home-range** During winter, forage over large areas; foraging ranges of 51 banded individuals (38 males; 13 females) were 1–30 km, five males travelling up to 30 km; regularly returned to same feeding sites (Bergquist 1985a). During breeding season, males ranged over smaller distances than at other times of year, though early in season some nesting birds travelled 8 km each day to feeding sites (Stewart 1980). At North Shore, Auckland, foraging range of nesting birds was restricted to c. 0.5 km because of need to defend of nest, incubate and attend chicks (Bergquist 1985a). After fledging, families stay near nest for c. 2 weeks (Dilks *et al.* Undated).

Roosting Roost at night. Once recorded roosting in mangroves (CSN 31). Females brood nestlings at night (Stewart 1980). Fledgelings roosted in Karaka tree *Corynocarpus laevigatus*; when newly fledged, roosted as a group but later did not (Blackburn 1963). Sing at roost first thing in morning; sometimes sing after dusk, particularly on moonlit nights (D. Brunton). When breeding on Tiritiri Matangi I., return from feeding areas on mainland in mid-afternoon (Stewart 1980). Forage and rest during daylight (Bergquist & Craig 1988).

SOCIAL BEHAVIOUR Based on contribution prepared by E. Marks; studies as for Social Organization, with addition of Craig (1984, 1985), who compared social behaviour of NZ honeyeaters. **Flock behaviour** When flying from breeding areas on Tiritiri Matangi I. to feed on mainland for day, small flocks first gathered in forest, made a few high-altitude flights in direction of destination but returned to forest, then eventually flew off (Stewart 1980). Early in breeding season, activities performed by males are associated with territories and maintenance of pair-bonds, including: Song-bouts from song-posts; pair-bond vocalizations; and diving and chasing sequences. Activities most intense at dawn and dusk (Stewart 1980; see below).

Agonistic behaviour Feathers of primaries are modified, with slots in wings that produce sounds during displays and chases; sounds thought to be mainly aggressive in function, but also heard in courtship display. Slots in wings are largest in males; smaller in females, which are typically subordinate to males, and smallest in juveniles (see Fig. 1); possible that variations in size of slots produces different sounds and that

these differences are used as signals in aggressive situations, e.g. juveniles may sound different from adults and so avoid confrontation (Craig 1984). **SINGING:** During breeding season on Tiritiri Matangi I., territorial males sing from song-posts above canopy, where able to survey range. Period when territory is being established characterized by frequent, intense Song-bouts from emergent trees round territory (Stewart 1980). At feeding sites, loud Song used by birds to announce their presence and determine hierarchies. At artificial feeding station made up of several feeders at North Shore, Auckland, Song encouraged avoidance rather than aggression, and few agonistic interactions were observed. Throughout year, dominant individuals (of both sexes) and groups sang before and when using feeder, signalling to subordinate birds to avoid feeder. Often dominant individuals, usually resident males and their offspring, sang from high posts near feeding station. When resident pair arrived at feeder, they duetted before feeding (Bergquist & Craig 1988). Elsewhere noted that during non-breeding season, Song, similar to that given during breeding season, was given in feeding territories in flowering or fruiting trees; song-posts were used and counter-singing occurred between birds, but both occurred much less often than during breeding season (Stewart 1980). Playback of Song in winter resulted in prolonged aggressive attacks (Bergquist & Craig 1988). **OTHER POSSIBLE TERRITORIAL DISPLAYS:** From when territory being established till start of incubation, Song-flights above and below canopy, and Dive Displays occur. **SONG-FLIGHT** involves near-vertical dive by male from great height, ending just above canopy; sometimes accompanied by calls. Females sometimes perform Song-flights below canopy, ending just above ground. Assumed to be an advertising display directed at both neighbours and mate (Stewart 1980). In **DIVE DISPLAY**, male dives below canopy, using a more undulating flight. Sometimes seen away from territories, and thought also to function in advertisement (Stewart 1980). Said that some advertising dives by male involve loud rustling of wings, whirring and singing (NZRD). **CORROBOREES:** Communal display where 5–7 birds (males sometimes accompanied by their mates) gathered on branches 1–2 m from ground at intersection of several territories, with males singing vigorously; usually 2–3 birds faced each other <1 m apart and sang, while others watched silently; groups stayed together for up to 10 min, during which time those not singing left. Only seen during initial stages of breeding, and thought to function in maintenance of territories. Similar to Corroborees observed in Aust. honeyeaters. Neither aerial displays nor Corroborees seen at feeding territories (Stewart 1980). **CHASES:** In confrontations, intruders chased from territories (Stewart 1980). When mated pair of residents fed at artificial feeder, male defended feeder, chasing intruders using wing-claps and noisy flight. Long chases often performed by dominant birds at sources of nectar (Bergquist & Craig 1988). Said that male clicks bill and rustles wings much when chasing intruders from breeding territory (NZRD). Aggressive postures also include partial opening of wings (J.L. Craig). Persistently mob Long-tailed Cuckoo *Eudynamys taitensis* (NZRD).

Sexual behaviour On Tiritiri Matangi I., courtship consisted of violent chasing beneath canopy, and frequent singing by both partners. **PRE-COPULATORY DISPLAY** seen twice: facing female, male perched in horizontal posture, slowly rotating body in semicircle, and singing; copulation or a chasing sequence followed. During incubation, male occasionally fed female (Stewart 1980). Said that: advertising for mate mainly involves male singing and performing aerial displays; courtship

involves chasing round nesting area after male had fed female; and duets. Also said that during incubation, male sings from nearby trees and performs aerial displays, and that female sometimes sings from nest (NZRD).

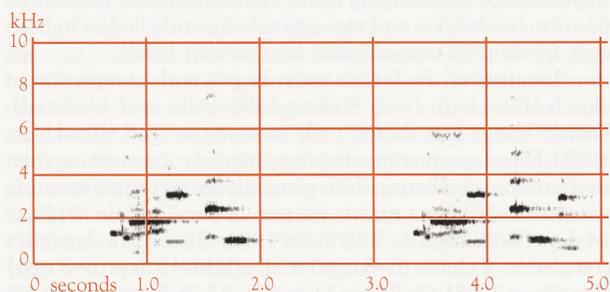
Relations within family groups If nest intact, fledgelings may return to nest for shelter, but when nest almost disintegrated, fledgelings will not return to nest-site but stay together nearby (Stewart 1980). Less than 1 week after fledging, young made first attempt to sing (Blackburn 1963). **Parental anti-predator strategies** When with nestlings, female does most defence of area round nest. When people intrude, female gives Distraction Display, vigorously calling as she does so; male normally sings from nearby tree (Stewart 1980). Similar details given in NZRD, but adds, in response to person, female flies in tight circles close by; may land and perform Broken-wing Distraction Display, clacking bill and giving loud Alarm Calls.

VOICE Quite well known, mainly from anecdotal information. Study of social organization and foraging ecology on Tiritiri Matangi I. and Whangaparaoa Pen., NI, by Stewart (1980) includes some observations on voice. Study by Craig (1984) on wing-noise, includes sonagram. Andersen (1909, 1911, 1913, 1915, 1917, 1918, 1926) at different times and locations recorded >100 calls in musical notation. Mclean (1912) also gives calls in musical notation. Has been classed as one of the seven best songsters of the world (Hartshorne 1973). Notes are varied, rich and pleasing, and especially melodious during spring and summer (Mclean 1912). Song given throughout year (St Paul 1975). Some calls said to be ventriloquial (Andersen 1909, 1926). Among the first species to be heard at dawn, and can be heard at any time of day; in the evening, sing at intervals while moving from tree to tree around roosting area (Mclean 1912). Singing by moonlight not uncommon (St Paul 1975). Sing at rest, on the nest and on the wing (Andersen 1926). On arrival from wintering areas, males begin to establish territories with frequent intense bouts of Song; Dive Displays, which may be accompanied by vocalizations, and Song-flights (see Social Behaviour) occur most often from this time until start of incubation (Stewart 1980). Once females return to breeding areas there are frequent bouts of Song by both partners (Stewart 1980). When a person approaches a nest, female gives a Distraction Display with vigorous calling, and male normally Sings from a nearby tree (Stewart 1980). Males give vigorous bouts of Song during Corroborees (see Social Behaviour) (St Paul 1975; Stewart 1980). When travelling long distances between feeding sites said to wheel upward calling others, before proceeding in small loose flocks (Heather & Robertson 1997). Both sexes sing loud and complex Songs in all seasons; the male is more vociferous (Buller 1888; Andersen 1923; Bergquist & Craig 1988; NZRD). Duets may be sung, with the birds singing together or alternating (Andersen 1913, 1926). When a great number of birds are singing at one time they appear to segregate into small groups, the Song of each group being in time and tune, while not always harmonizing with the others; such choruses are rare in the evening (Andersen 1918, 1926). Duets are given by pairs (Buller 1888; Bergquist & Craig 1988). Calls said to be useful to distinguish between the sexes (Stewart 1980). Females appear not to defend feeding territories and do not sing at sources of food (Stewart 1980). Song conveys individual, group and locality information, which should permit birds to identify conspecifics by their Songs (Bergquist & Craig 1988). The Song of an individual is distinctive, permitting its identification; one bird gave a Song that varied little over some weeks; at most locations, although the

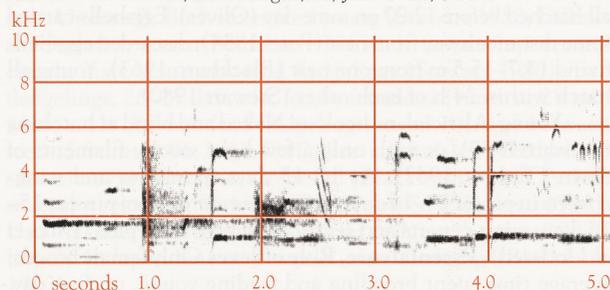
birds may each be uttering somewhat different sets of notes, there appears to be one set that is probably common to all, though at some locations (e.g. Stewart I.) no common set was discerned; one new Song appeared within a week to be in use by nearly every bird of the few at that location (Mclean 1912). Themes sung are so varied that repertoire of an individual may include scores or even hundreds of themes (Andersen 1926). Song varies from month to month and from place to place (St Paul 1975; Oliver). **GEOGRAPHICAL VARIATIONS:** On Raoul I., Kermadec Is, Song variously reported as slightly different from that on mainland (Cheeseman 1888, 1891), very different (Iredale 1910, 1913), 'quite different' and not as raucous except for warning or distress calls (Ward 1969), and similar, although rather subdued (Merton 1970); it seems to have periods of relative silence, varying in timing from year to year (Ward 1969); and there is singing at night all year round on moonlit nights (Iredale 1910; Merton 1970). On Stewart I., Song richer and more varied in tone than on mainland (Mclean 1912). Voice of subspecies *chathamensis* similar to nominate but Song is shorter, simpler and less varied; Song at said to be little used, but there is much mimicry (Oliver). **INTERSPECIFIC COMPARISONS:** Some notes indistinguishable from those of Bellbird, 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 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 1984; NZRD). A duet between Tui and Bellbird has been reported, both birds being in view in same tree (Andersen 1911, 1915, 1926). **RESPONSE TO PLAYBACK:** Song associated with nesting territories elicits an aggressive response when played back in feeding territories (Stewart 1980). During winter, birds reacted aggressively to playback of Song (Bergquist & Craig 1988). On Chatham Is, birds reacted strongly to replay tapes, but only when breeding (Dilks *et al.* Undated). **MIMICRY:** Mimic, often with its own embellishments, almost every bird species, and when domesticated, imitates almost every noise it hears (Andersen 1926). Probably mimics Bellbird, and bell-like notes in Song are said to be rare in those parts of range where Bellbirds absent (Oliver 1922; NZRD). During a brief visit to Raoul I., Kermadec Is, chatter of Red-crowned Parakeet *Cyanoramphus novaezelandiae* was mimicked, as part of Song, by all birds heard to give full Song; this had not been reported by earlier observers and assumed to be a new component of the repertoire (Robertson 1996). Captive birds were much prized by the Maori for their ability to imitate, and were taught sentences of welcome, platitudes, and insults; a compliment to a good orator was *me he korokoro tui*—'how eloquent he is; he has the throat of a Tui' (Buller 1888; Andersen 1926). Because of their imitative ability they were also taken to Sydney as caged birds (Bennett 1860). **NON-VOCAL SOUNDS:** Flight can be particularly noisy; the species can be identified from loud whirring or *whurru* of wings, even if not seen (Buller 1888; Andersen 1909; Mclean 1912; St Paul 1975; Oliver). This earned for them the name among sealers of 'Breaksea devils', Breaksea Sound being a resort of sealing gangs (Oliver). During courtship there are very rapid noisy aerial chases in tight circles around home-range or territory (Stewart 1980). Wing-noise includes a wide range of frequencies, with major components in the lower frequencies, particularly <1000 Hz, and is heard in flight during chases and displays, most conspicuously during aggressive interactions, but also during courtship displays. However, at other times birds appear to fly without making

audible sounds with wings. Sonagrams show that gaps occur in wing-noise and that it ends abruptly, thus suggesting that birds control its production (Craig 1984). It appears to be produced by slots in wing formed by notches in eighth primary; these slots are larger in males than females, and are absent or extremely small in young birds (Craig 1984, 1985). Said to click bills during chases and Distraction Displays (NZRD).

Adult SONG: Song is composed of rich and varied mellifluous notes (sonagrams **A** and **B**); including sweet, soft, liquid warbling notes; notes 'like a touch on a high key of an organ'; deep bell-like *bongs*; chimes; sighs; sobs; cries; coughs; laughs; gurglings; sneezes; and sounds like the shattering of a pane of glass, or the drawing of a cork from a bottle (Buller 1888;



A L.B. McPherson; Invercargill, SI, Jan. 1984; P107



B J. Kendrick; P100

Andersen 1926; Ward 1969; Oliver). On Raoul I., Kermadec Is, dawn Song started with whistles, coughs, gurgles, wheezes and liquid notes (Ward 1969). Song is given during breeding season by males from song-posts and by both partners in frequent bouts of Song (Stewart 1980). One afternoon Song lasted >30 min (Andersen 1926). At time of establishment of breeding territories on Tiritiri Matangi I., some birds commuted to Whangaparaoa Pen., where they defended food sources with intense and frequent Song; counter-singing between males in different trees occurred with great regularity, and birds seldom used song-posts but remained at the food source to sing (Stewart 1980). Outside breeding season, Song generally similar to that occurring during breeding; used to defend feeding territories, and normally given from within canopy of food tree; song-posts are used and counter-singing occurs, but each occurs far less often than during breeding season (Stewart 1980). When person approaches nest, male sings from nearby tree (Stewart 1980). **WHISPER-SONG** is sung softly in throat, so faintly that it is not always heard by an observer, and is interspersed with normal Songs (Andersen 1926). Suggestion that Song contains frequencies inaudible to humans (Oliver; Falla *et al.* 1979; NZRD) probably comes from observers seeing birds utter Whisper-song, but from too far away for it to be audible (T. Howard). May be used during courtship (Andersen 1926). **ALARM CALL:** Petulant whine given on appearance of New Zealand Falcon

Falco novaeseelandiae, or on any unusual happening (McLean 1912). High-pitched plaintive *ke-e-e-e*, said to be an alarm note (Falla *et al.* 1979), may be same call. **DISTRESS CALL:** Loud piercing cry or shriek, which attracts other Tui, may be given when nest with nestlings approached by person, or when young handled (Wilkinson 1927; Moncrieff 1928; Ward 1969). **Other calls** High-pitched call given by male during Pre-copulatory Display (see Social Behaviour: Sexual behaviour) (Stewart 1980). When people approached nests, females scolded and gave Distraction Displays, with vigorous calling or guttural squawks (Murray 1947; Stewart 1980). Great din, chortling and jabbering from birds drunk on nectar (St Paul 1975).

Young Until 3 weeks after hatching utter feeble *cheep*. This strengthens with development, becoming an almost incessant plaintive note when fledged, sometimes changing to an impatient scream when parent approaches with food (Buller 1888; Moncrieff 1928; Blackburn 1963). A bird just able to flutter gave a high-pitched distress call when handled (Ward 1969). Six days after leaving nest, one bird gave several clear sweet single notes, the first attempt at Song (Blackburn 1963). Alarm Call *ke-e-e-e* said to be acquired after leaving nest but before any attempt at Song (Buller 1888).

BREEDING Reasonably well known; study of nominate *novaeseelandiae* over two seasons on Tiritiri Matangi I. (Stewart 1980); some information for subspecies *chathamensis* on South East I., Chatham Is, during 1996–97 season (Dilks *et al.* Undated). Sometimes raise two broods in a season (Potts 1884; Turbott 1967; Oliver).

Season **NOMINATE NOVAESEELANDIAE:** Kermadec Is: Breed, Sept.–Nov.; eggs, late Sept.; young, Nov.; fledgelings, early Oct. to early Nov. (Iredale 1910; Sorensen 1964; Merton 1970). NI: Eggs, Oct. to mid-Jan.; young, Dec.–Jan.; fledgelings, Nov., Dec., early Feb. and Mar. (Guthrie-Smith 1910; Mclean 1912; Stidolph 1923; Moncrieff 1928; Murray 1947; Blackburn 1963; Stewart 1980; CSN 26, 30, 34); also, nesting recorded in Aug., and young, Mar.–May (Turbott 1967). On Tiritiri Matangi I., nest-building coincided with earliest availability of nectar from New Zealand Flax *Phormium tenax* and Rewarewa *Knightia excelsa*; earliest nests constructed by birds defending home-ranges near available sources of nectar; eggs, Nov.–Dec. (Stewart 1980). **SUBSPECIES CHATHAMENSIS:** Eggs, mid-Nov., early Dec.; young, late Nov. to late Dec.; fledgelings, late Dec. to late Jan.; onset of breeding likely to be influenced by flowering of flax (Dilks *et al.* Undated).

Site Usually in fork of shrub, top of sapling, in or under canopy of tree; sometimes in or under vines *Rubus*, and beneath crown of tree-fern; usually sheltered, though sometimes in open site; nests in small trees placed in fork of branch and main stem; those in larger trees built in fork near end of branch (Potts 1884; Guthrie-Smith 1910; Iredale 1910; Moncrieff 1928; Blackburn 1963; Turbott 1967; Stewart 1980; Dilks *et al.* Undated; Oliver). On Tiritiri Matangi I., of 59 nests (not all active): 20 (33.8%) in Kohekohe *Dysoxylum spectabile*, 18 (30.5%) in tree-fern, 11 (18.6%) in Mapou *Myrsine australis*, three (5.1%) in *Leptospermum*, three (5.1%) in Pohutukawa *Metrosideros excelsa*, two (3.4%) in Mahoe *Melicactus ramiflorus*, and two (3.4%) in Raurekau *Coprosma australis* (Stewart 1980). On Solomon I., near Stewart I., where petrels return to nests at night, Tui nests placed in sites protected by small branch or cluster of twigs sufficiently robust to fend off descending petrel (Oliver). On Kermadec Is, usually nest in fork of *Metrosideros kermadecensis* (Oliver). **MEASUREMENTS (m):** **NOMINATE NOVAESEELANDIAE:** Height of nest: NI, 6.0 (4.47; 1.8–14.6; 9) (Wilkinson 1924;

Moncrieff 1928; Murray 1947; Blackburn 1963; CSN 28); Kapiti I., 1.5–7.6, mostly 3.0–3.7 (Wilkinson 1927; Wilkinson & Wilkinson 1952); Minginui area, 2.4–24.4 (St Paul 1975); Kermadec Is, many nests c. 9 m (Iredale 1910). Heights of 59 nests on Tiritiri Matangi I.: 19 (32.2%) at 1.5–3.0 m; 23 (39.0%) 3.0–4.5 m; ten (16.9%) 4.5–6.0 m; two (3.7%) 6.0–7.5 m; two (3.7%) 7.5–9.0 m; three (5.1%) >10.5 m (Stewart 1980). On Tiritiri Matangi I., nests built within c. 180 m of nectar sources; of 18 active nests: eight (44.4%) within 15 m of source of nectar; six (33.3%), 15–45 m; single (5.6%), 45–75 m; two (11.1%), 75–105 m; single (5.6%), 135–165 m (Stewart 1980). **SUBSPECIES CHATHAMENSIS:** Height of nest, including three approximations, 3.2 (1.44; 1.5–6; 7) (Dilks *et al.* Undated).

Nest, Materials Large, untidy nest with shallow cup-shaped cavity, loosely secured to site; composed of twigs, leaves, plant stems, grass, straw, rootlets, sometimes with moss, lichen, scales from tree-fern and wool. Lined with finer twigs, grass, fine roots, ferns, lichen and sometimes feathers and hair-like fibres from tree-fern; two nests contained scales of young tree-fern fronds, one nest with goat hair, another, a piece of wool (Potts 1884; Iredale 1910; Wilkinson 1924, 1927; Moncrieff 1928; Wilkinson & Wilkinson 1952; Murray 1947; Turbott 1967; Stewart 1980; Dilks *et al.* Undated; Oliver). Twigs in one nest held together with spider web (Moncrieff 1928). One nest composed almost entirely of twigs of *Leptospermum*, with largest twigs at base of nest, and smaller towards top; cavity lined with brown hair from tree-fern, interlaced with a few blades of grass (Turbott 1967). One nest a shallow cup of twigs, lined with moss (Iredale 1910); another had foundation c. 30 cm thick built from stout twigs (Iredale 1910; Oliver). Both sexes build but female does most (Wilkinson & Wilkinson 1952); probably only female builds (Stewart 1980); female seen collecting and carrying material (Blackburn 1963; Dilks *et al.* Undated). Completed and incomplete nests deserted if disturbed by observer (Guthrie-Smith 1910); may complete a nest then abandon it before laying and build new nest nearby (Iredale 1910); one active nest had a complete but unlined nest on other side of same tree (Murray 1947). **MEASUREMENTS** (cm; includes some approximations): External diameter, 25.2 (4.85; 20.3–30; 3); external depth, 19.5 (12.2; 7.6–30; 4); internal diameter, 8.3 (2.77; 6.0–11.4; 3); internal depth, 6.2 (1.07; 5.1–7.6; 4) (Iredale 1910; Wilkinson 1924, 1927; Moncrieff 1928; Wilkinson & Wilkinson 1952; Turbott 1967); external diameter, 17.8–25.4 (no N given) (Wilkinson & Wilkinson 1952).

Eggs Oval to elongated oval; some eggs described as glossy, others as having rough texture (Potts 1884; Oliver). Pinkish, sometimes white, usually with spots and blotches of pale dull red, mostly at larger end, with smaller end sometimes nearly white and devoid of markings; others entirely devoid of markings (Potts 1884; Wilkinson 1927; Wilkinson & Wilkinson 1952; Oliver); sometimes yellowish red or brownish red, mostly at larger end; markings sometimes form indistinct zone round larger end (Potts 1884); usually white, sometimes suffused with pinkish brown, with red-brown markings at larger end; one clutch light brown, with dark-brown streaks (Iredale 1910). **MEASUREMENTS:** Nominate *novaeseelandiae*: Kermadec Is, 27.5 (2.55; 24–30; 4) × 20.3 (1.19; 19–21.5) (Oliver); a clutch of four, 28.1 (27.5–28.5) × 20 (20–20.25) (Merton 1970); Kapiti I., mean, c. 34 × 22 (Wilkinson & Wilkinson 1952); SI, two eggs, 30.5 × 22 and 30.6 × 22 (Oliver); Adams I., 32 × 23 (Oliver). Subspecies *chathamensis*: three eggs, 32.9 × 22.2, 31.5 × 22.3 and 30.5 × 22.1. (Dilks *et al.* Undated). Ten eggs in NMNZ, from unknown location, 30.7 (1.97; 28.7–34.6) × 21.0

(0.41; 20.4–21.6). **WEIGHT:** Subspecies *chathamensis*: three eggs, 8.5, 8.6 and 8.3 (Dilks *et al.* Undated).

Clutch-size Nominate *novaeseelandiae*: Kermadec Is, usually four, sometimes three, once five (Iredale 1910); Kapiti I., two or three, sometimes four (Wilkinson & Wilkinson 1952); Tiritiri Matangi I., three (2–4; 9); first year females laid more two- and four-egg clutches than older birds (Stewart 1980). Subspecies *chathamensis*: C/4 × 1 (Dilks *et al.* Undated).

Laying Eggs laid on consecutive days (Blackburn 1963; Stewart 1980; Oliver). Sometimes lay replacement clutch after failure of eggs or young; one female laid second clutch within 14 days of losing young (Stewart 1980). One instance of laying two clutches in same nest: nest in crown of tree-fern had contents tipped out by an emerging frond; nest returned to its original position by observer and two eggs subsequently laid in it; both eggs appeared in nest on same day (Stewart 1980).

Incubation By female only; begins with completion of clutch (Blackburn 1963; Stewart 1980; Dilks *et al.* Undated). Female leaves nest during early morning to feed (Blackburn 1963). Females sometimes incubate more during morning than in afternoon; incubation shifts generally longer during morning (Stewart 1980). **INCUBATION PERIOD:** 14 days (Iredale 1910); c. 14 days (Wilkinson & Wilkinson 1952; Oliver); 14 days after completion of clutch (n=3 eggs) (Oliver); 14–15 days (n=3 eggs) (Blackburn 1963). On Tiritiri Matangi I., 13.25 days (0.96; 12–14; 4); 12 days × 1, 13 days × 1, 14 days × 2 (Stewart 1980). Three eggs all hatched before 12:00 on same day (Oliver). Eggshells carried some distance away from nest (Potts 1884); discarded eggshells found 13.7–15.5 m from one nest (Blackburn 1963). Young all hatch within 24 h of each other (Stewart 1980).

Young Altricial, nidicolous. Naked and blind at hatching (Stewart 1980), or with only a few light woolly filaments of down (Turbott 1967). At 12–13 days, primaries and wing-coverts in pin; at 14–15 days, primaries emerge from pins; at 15–16 days, wing-coverts and rectrices emerge from pins (Dilks *et al.* Undated). **Parental care, Role of sexes** Only female broods; average time spent brooding and feeding young, on first day, 82% (78–84; no N); on third day, 37% (16–47; no N); from 8 days, young brooded only at night (Stewart 1980). Both sexes, but mostly female, feed young, and male infrequently feeds female at nest (Stewart 1980); both sexes feed young (Dilks *et al.* Undated), contrary to Blackburn's (1963) statement that female alone feeds young. Three young, 16–19 days old, fed 5 times in 8 min; mean interval between feeds, 2.0 min (1.63; 0–4; 4) (Dilks *et al.* Undated). Feeding rates (minutes between feeds) for young in four nests: during first week after hatching, 19.5 ± 4.4 min; >1 week after hatching, 10.6 ± 5.4; at 8–11 days, proportion of time spent feeding young, 5–10% for female, 2–5% for male (Stewart 1980). **Growth** At hatching, mean dry weight 6.9 ± 0.3 g; length of tarsus, 9.9 ± 1.6 mm; length of head and bill, 19.3 ± 4.1 mm. Gain of weight of two young from different broods: Day 1, 6.5 and 7.0; Day 7, 36.5 and 30.0; Day 9, 50.0 and 40.0; Day 15, 78.0 and 68.0; for increase in length of wing for a brood of three young, and increase in length of tarsus of males and females, see Table 2. Fastest growth occurs in broods raised by parents at least 3 years old; slowest growth in broods raised by first-year parents (Stewart 1980). Both sexes remove faecal sacs, often eating them, though female removes most; larger young defecate over edge of nest (Stewart 1980). Nest, branches of nest-plant and ground below nest can become spattered with excreta (Wilkinson 1927; Moncrieff 1928).

Fledging to independence **FLEDGING PERIOD:** Appears to vary greatly. Mean, c. 14 days (no N) (Wilkinson & Wilkinson 1952); 15.5 days (14–23; 8 nests), though at another nest,

Table 2. Length of wing for a brood of three, and length of tarsus; measurements in mm (Stewart 1980).

AGE (DAYS)	WING	TARSUS OF MALES	TARSUS OF FEMALES
2	19.4 (1.31; 18.0–20.6)	18.7 (18.6–18.8; 2)	16.6 (n=1)
4	30.3 (1.72; 28.4–31.7)	23.4 (21.6–25.2; 2)	22.7 (n=1)
6	41.7 (4.19; 38.3–46.4)	30.3 (1.15; 29.2–31.5; 3)	28.6 (0.31; 28.3–28.9; 3)
8	58.0 (5.77; 52.8–64.2)	36.0 (1.12; 35.0–37.6; 4)	33.7 (0.81; 33.0–34.6; 3)
10	69.6 (3.44; 66.7–73.4)	37.4 (36.9–37.9; 2)	34.7 (n=1)
12	73.7 (5.65; 70.0–80.2)	38.4 (37.4–39.4; 2)	36.0 (n=1)
14	83.9 (4.31; 79.4–88.0)	38.8 (38.0–39.5; 2)	36.2 (n=1)
15	91.2 (8.75; 83.0–100.4)	39.2 (38.9–39.5; 2)	–

single chick left nest after only 11 days (Stewart 1980); once 14–15 days (Murray 1947); 21 days (n=3 young) (Oliver); two young fledged at 21–22 days, though a third left nest at 17–18 days but later returned to nest (Blackburn 1963); 17–20 days (n=2); two chicks still in nest at 18–21 days old but gone from nest 3 days later; three young, 15–16 days old, leapt from nest after being disturbed by observer (Dilks *et al.* Undated). One 10-day-old chick that fell out of nest and was replaced by observer leapt out immediately and scrambled under nearby bracken, but chick had climbed back into nest by next morning (Wilkinson & Wilkinson 1952). Three young fledged between 10:00 and 14:00 (Blackburn 1963); two chicks fledged between 16:00 and 09:15 next day (Dilks *et al.* Undated). Form family groups after fledging and remain near nest for c. 2 weeks (Dilks *et al.* Undated). Both sexes feed young (Stewart 1980; Dilks *et al.* Undated; *contra* Blackburn 1963). If female lays second clutch, male alone may feed fledgelings (Stewart 1980). Two fledgelings, 26–27 days old, fed by female six times in 29 min while male did not feed fledgelings; mean interval between feeds, 5.8 min (3.96; 2–11; 5) (Dilks *et al.* Undated). Fledgelings sometimes return to nest to be fed (Blackburn 1963). Fed for several weeks after fledging (Wilkinson & Wilkinson 1952). Usually independent 8–12 days after fledging (Stewart 1980); largely independent c. 2 weeks after fledging (Blackburn 1963).

Success From eight eggs in four nests, four (50%) hatched, three (37.5%) fledged; young from only one of the four nests fledging (Wilkinson 1927; Murray 1947; Blackburn 1963). On Tiritiri Matangi I., mean of three young fledged per successful nest (no N); no correlation between success and distance from nest-site to nectar source, or between early and late nests (Stewart 1980). Nests occasionally blown down during strong winds (McLean 1912). If disturbed by observer, likely to desert a newly laid clutch but not a well-incubated clutch (Guthrie-Smith 1910). Eggs taken by Stoats *Mustella erminea* (CSN 19 [Suppl.]) and Common Mynas (McKenzie 1979); young taken by Stoats (CSN 26); two young taken by Kiore *Rattus exulans* after falling from nest (Stewart 1980). On Chatham Is, mean minimum number of fledgelings per family group, 2.25 (n=41 family groups); of four nests, one nest successful; two nests with eggs deserted, one immediately after being found; one nest with eggs failed after period of strong wind (Dilks *et al.* Undated).

PLUMAGES Prepared by A.M. Dunn. Fledge in juvenile plumage. Partial post-juvenile (first pre-basic) moult to first immature occurs shortly after fledging. Immature plumage resembles adult. Complete first immature post-breeding (second pre-basic) moult from immature to adult plumage occurs at end of first year. Thereafter, complete post-breeding (pre-basic) moults each cycle produce successive adult plumages without change in appearance. Sexes similar in plumage. Two subspecies; nominate described below. Descriptions of nominate based

on examination of skins of 116 adults, 14 juveniles and 17 immatures.

Adult (Definitive basic). Much of plumage strongly iridescent, giving slightly different colour from different angles. **HEAD AND NECK:** Feathers of forehead, crown, nape, ear-coverts, chin and throat, strongly iridescent with black (89) bases to feathers; appearance of feathers changes from dark green (c162A) to dark olive (c49), depending on angle of view; sometimes have straw-yellow (c56) sheen. Feathers of hindneck and sides of neck narrow and elongated, with some reduction in barbules, and tend to curl to one side, particularly on sides of neck; appear strongly iridescent dark green as feathers of head, but with distinct white shaft-streaks. Lores and eye-ring, black (89). Very narrow indistinct moustachial stripe formed by white shaft-streaks on single line of small iridescent dark-green feathers. Modified feathers at sides of throat elongated, with narrow iridescent dark-green bases and broad white distal halves; distal half of feather has reduced barbules and curls in upon itself. These modified feathers clump and curl together forming white ball-like ornament on each side of throat, each formed from c. 20 feathers. **UPPERPARTS:** Feathers of upper mantle similar to those of hindneck, but iridescence often appears dark blue (c74) or dark violet (c72). Lower mantle, back, scapulars and rump, black-brown (c119) with iridescence to tips of feathers; iridescence weaker than on head and neck and mostly appears straw-yellow (c56), but can appear slightly dark blue (c74) or dark violet (c72) from some angles, especially on scapulars. Uppertail-coverts strongly iridescent, with black (89) bases to feathers; iridescence of centre of each feather can change from green (c63) to green-blue (c65) in appearance depending on angle of view, and appearance of fringe can change from dark blue (c74) to dark violet (c72). **UNDERPARTS:** Feathers of breast as those of forehead: strongly iridescent with black (89) bases to feathers; appearance of feathers changes from dark green (c162A) to dark olive (c49) depending on angle of view; sometimes have straw-yellow (c56) sheen, and sometimes have paler, brownish (ne) shafts. Feathers of upper belly, black (89) with iridescence to tips of feathers; iridescence weaker than on breast and varies from dark green (c162A) to dark blue (c74) or dark violet (c72). Feathers of lower belly and vent lack iridescence; mostly black-brown (119), but often have light-brown (c223C) tips, especially on feathers closer to flanks. Thighs, black-brown (c119). Feathers of flanks, dark grey (c83) and mostly concealed by wings and longer feathers of breast and belly. Undertail-coverts, iridescent with black (89) bases to feathers; iridescence varies from dark green (c162A) to dark blue (c74). **UPPERTAIL:** Rectrices, black (89) with strong dark-green iridescence; iridescence strongest on outer webs and rather weak on inner webs, and changes from dark green (c162A) to dark olive (c49), depending on angle of view; sometimes have straw-yellow (c56) sheen or dark-blue (c74) sheen. **UNDERTAIL:** Black (89); no iridescence.

UPPERWING: Smaller marginal secondary coverts, black-brown (119) with strong iridescent tips to feathers; iridescence varies from dark green (c162A) to dark blue (c74). Large marginal secondary coverts and median secondary coverts, mostly white with black-brown (119) bases to feathers; bases have slight dark-green (c162A) to dark-blue (c74) iridescence. Greater secondary coverts, all primary coverts, alula, primaries and secondaries, black (89) with strong iridescent sheen to outer webs; iridescence varies from dark green (c162A) to dark blue (c74). P8 has notch in middle of inner web (see Ageing). Small number of individuals have small white spots to tips of outer webs of some inner greater secondary coverts. Tertiaries as other remiges, but with iridescent sheen to both inner and outer webs. **UNDERWING:** Marginal coverts, black-brown (119) with strong iridescent tips to feathers; iridescence varies from dark green (c162A) to dark blue (c74). Rest of coverts, dark grey (c121). Remiges, black-brown (119).

Nestling Hatch naked (Stewart 1980).

Juvenile Much duller than adult, with little or no iridescence to body-plumage. **HEAD AND NECK:** Forehead, crown, nape, hindneck and sides of neck, dark brown (121) to black-brown (119), usually with very fine cream (c92) shaft-streaks to feathers, but shaft-streaks absent or very faint in some. Loes and eye-ring, black (89). Ear-coverts, black-brown (119). Chin and throat mostly grey-black (82); sometimes lower throat slightly paler dark grey (83). **UPPERPARTS:** Mostly black-brown (119), usually with very fine cream (c92) shaft-streaks to feathers. Scapulars and uppertail-coverts often have very weak iridescence to tips of feathers; iridescence, dark green (c162A), to dark blue (c74), depending on angle of view. **UNDERPARTS:** Grey-black (c82) to black-brown (c119), often with very fine cream (92) shaft-streaks to feathers of breast. **TAIL:** Similar to adult, but with less iridescence on rectrices. **UPPERWING:** Smaller marginal secondary coverts, black-brown (119); either lack iridescence of adult or iridescence very faint. Large marginal secondary coverts and median secondary coverts, mostly off-white (ne) with black-brown (119) bases to feathers; bases lack iridescence. Greater secondary coverts similar to adult but with much weaker iridescence. Primary coverts, alula and remiges similar to adult but with slightly less iridescence. P8 different shape from adult (see Ageing, Fig. 1). **UNDERWING:** As underwing of adult, but marginal coverts lack iridescence.

First immature (First basic). Similar to adult in plumage, but retain juvenile greater coverts, alula, remiges and rectrices; these feathers show much more wear than those of adult at same time of year. Juvenile p8 readily distinguished from that of adult on shape (see Ageing, Fig. 1).

Aberrant plumages Partially or wholly leucistic individuals have been reported at several locations (Oliver). Other aberrant plumages have been reported, but all appear to involve a reduction in amount of melanin in all or part of plumage. Individuals have been reported with varying amounts of cream, fawn, umber, brown or smoky-brown plumage (Oliver).

BARE PARTS Based on photos (Williams 1963; Brathwaite 1974; Moon 1979, 1992; Moon & Lockley 1982; Barnett 1985; Chambers 1989; Williams & Karl 1997; NZRD). Sexes similar. **Adult** Bill, black (89) or black-brown (119). Gape, dark brown (c22). Tongue, light grey-brown (c27). Inside of mouth, pink (c7). Iris, black-brown (c119). Orbital ring, grey-black (82) or black-brown (82). Legs and feet, black (89) or grey-black (82) or dark brown (223); usually paler grey on rear of tarsus (D.J. Onley). Soles, yellowish brown (D.J. Onley). **Nestling** Very young nestlings (photo: Moon 1979): bill, gape and inside of

mouth, orange-yellow (18); bare skin on head, dull pink (c5). At c. 2.5 weeks (photo: Moon & Lockley 1982): bill, orange-buff (153) to orange-yellow (18) with black (89) suffusion near tip and around nostrils; gape, orange-yellow (18); iris, black (89); orbital ring, yellow-brown (c24); unfeathered skin on face, pink (c7). Gape, yellow, fading to cream by about 4 weeks (Blackburn 1963). At 5 weeks, bill, dark grey to black with pale-yellow lines extending to tip (Blackburn 1963). **Juvenile** No information. **First immature** No information; probably as adult.

MOULTS Based on examination of skins of 106 adults and 26 juveniles and immatures (CM, NMNZ) and published information (Onley 1986). **Adult post-breeding** (Pre-basic). Complete; primaries outward. Few birds sampled were actively moulting. Of skins, only three had active moult of primaries; two of three collected in Mar. were moulting primaries, with PMS of 7 and 29; one of four collected in May was moulting primaries, with PMS of 43. Moult of primaries probably completed rapidly; of three with active moult of primaries, the two with more advanced moult had four growing primaries in each wing. Only one, in Mar., was recorded with active moult of tail and active moult of body; no other specimens had active moult of either tail or body. Onley (1986) examined skins from four museums and concluded that most moult occurred in Feb. and Mar. **Post-juvenile** (First pre-basic). Few data. Partial; replace body-plumage and coverts, but retain remiges and rectrices (Onley 1986; this study). One bird in mostly juvenile plumage in Feb. had active moult of feathers of underparts. Another, from Jan., had active moult in most tracts of body-plumage and had attained c. 70% of immature (first basic) plumage. **First immature post-breeding** (Second pre-basic). Few data. Probably complete; timing probably similar to adult post-breeding. One was starting moult of head, neck and upperpart feathers in Dec. No further information.

MEASUREMENTS **NOMINATE NOVAESEELANDIAE:** (1–3) NI, SI, Kermadec Is and Auckland I., skins (CM, MV, NMNZ): (1) Adults; (2) Juveniles; (3) First immatures. (4–6) NI and SI, skins (Onley 1986): (4) Adults; (5) Juveniles; (6) First immatures. (7–9) Adults (and probably first immatures), live: (7) Tiritiri Matangi I. and Arklles Bay, Whangaparaoa Pen. (Stewart 1980); (8) Orongorongo Valley, Wellington (Robertson *et al.* 1983); (9) Tiritiri Matangi I. and Whangaparaoa Pen. (Craig *et al.* 1981a,b).

	MALES	FEMALES
WING	(1) 154.5 (3.57; 147–161; 51)	136.0 (5.63; 128–151; 29) **
	(2) 132, 146	134.2 (8.77; 128–147; 4)
	(3) 141.5 (8.73; 129–149; 6)	128.3 (4.00; 123–136; 11) **
	(4) 154.3 (3.1; 149–163; 79)	138.4 (3.8; 130–146; 27) **
	(5) 145.0 (4.1; 141–150; 5)	131, 133
	(6) 147.7 (2.0; 145–151; 12)	130.6 (1.9; 127–134; 14) **
	(7) 144.7 (137–155.0; 21)	129.0 (121.0–133.3; 15)
	(8) 152.2 (4.67; 142–163; 78)	133.2 (4.98; 125–142; 46) **
	(9) 144.2 (5.10; 13)	129.3 (2.58; 9) **
TAIL	(1) 119.9 (3.72; 112–128; 54)	109.4 (5.19; 98–122; 29) **
	(2) 110, 112	105.0 (6.67; 98–115; 5)
	(3) 112.3 (7.58; 100–119; 6)	104.4 (6.25; 96–116; 11) *
	(4) 123.2 (3.5; 115–133; 76)	112.8 (4.1; 105–125; 27) **
	(5) 114.6 (0.5; 114–115; 5)	104, 106
	(6) 117.9 (3.6; 112–122; 11)	107.1 (3.6; 102–113; 14) **
	(7) 116.8 (111.9–121.3; 21)	107.0 (100.7–111.2; 15)
	(8) 122.3 (4.66; 104–134; 61)	108.8 (4.78; 100–117; 32) **
	(9) 116.9 (3.00; 12)	107.0 (3.18; 9) **
BILLS	(1) 33.5 (1.28; 30.3–36.1; 53)	30.1 (1.68; 27.5–35.4; 27) **

	(2)	31.1 (2.52; 28.4–34.1; 5)	31.3 (1.88; 30.0–34.6; 5)	ns
	(3)	33.0 (3.02; 27.7–35.3; 5)	29.3 (1.62; 27.3–31.2; 11)	**
BILL F	(4)	24.5 (2.6; 22.9–27.7; 79)	22.4 (1.3; 20.4–26.0; 27)	**
	(5)	23.0 (1.8; 21.2–25.8; 5)	23.0, 23.2	
	(6)	24.8 (1.2; 22.4–26.6; 12)	22.0 (0.9; 20.7–23.2; 11)	**
	(8)	26.2 (1.70; 22–30; 61)	23.4 (1.33; 21–26; 32)	**
THL	(7)	63.3 (61.1–65.0; 21)	57.1 (57.0–59.0; 15)	
TARSUS	(1)	38.3 (1.20; 35.7–41.2; 54)	34.7 (1.69; 31.3–39.5; 29)	**
	(2)	37.0 (1.15; 35.1–38.1; 5)	36.0 (1.80; 34.6–39.1; 5)	ns
	(3)	37.4 (2.45; 34.0–40.6; 6)	34.4 (0.76; 32.7–35.7; 11)	**
	(4)	40.3 (1.4; 37.0–42.8; 79)	36.5 (1.7; 34.1–41.2; 27)	**
	(5)	40.6 (1.6; 39.1–42.5; 5)	36.0, 36.4	
	(6)	39.7 (0.5; 39.0–40.7; 12)	35.8 (1.2; 34.0–38.3; 14)	**
	(7)	39.4 (38.0–41.0; 21)	35.9 (35.4–37.0; 15)	
	(8)	40.7 (1.06; 38–44; 58)	37.0 (1.43; 32–40; 29)	**
TOE	(8)	34.9 (1.95; 29–39; 61)	31.1 (1.50; 29–37; 32)	**

(10) Live birds from Tiritiri Matangi I. and skins from unspecified locations; Min P8 = Minimum width of eighth primary (Craig 1984).

		ADULT MALES	ADULT FEMALES	JUVENILES
MIN P8	(10)	3.8 (1.05; 38)	4.7 (1.19; 18)	6.4 (0.50; 10)

Size of notch (or slot) on inner edge of p8 differs between sexes in adults and between adults and juveniles (see Ageing). An indication of depth of notch on p8 can be gained by measuring minimum width of p8; those with deeper notches have narrower minimum width of p8. Minimum width of p8 was significantly less in adult males than in adult females ($P < 0.01$), and was significantly greater in juveniles than in either adult males or adult females ($P < 0.01$). See Craig (1984) for another estimate of relative size of notch (or slot).

SUBSPECIES CHATHAMENSIS: (11) Chatham Is, adults, skins (CM, NMNZ). (12–14) South East I., live (Dilks *et al.* Undated): (12) Adults; (13) Juveniles; (14) Immatures.

		MALES	FEMALES	
WING	(11)	154, 166, 166	144, 144	
	(12)	159.7 (5.47; 138–171; 46)	141.8 (3.00; 135–149; 69)	**
	(13)	152.2 (3.92; 141–157; 21)	136.7 (2.70; 132–141; 19)	**
	(14)	152.8 (2.48; 148–156; 7)	136.7 (4.55; 131–146; 16)	**
TAIL	(11)	128.5 (2.65; 126–132; 4)	116, 121	
	(12)	132.4 (6.41; 114–155; 46)	119.1 (4.41; 111–132; 67)	**
	(13)	126.7 (5.40; 108–137; 21)	115.0 (4.03; 109–122; 19)	**
	(14)	128.5 (8.02; 118–136; 6)	117.1 (6.81; 109–130; 14)	**
BILL S	(11)	33.3, 33.8, 37.2	30.2, 32.9	
BILL F	(12)	26.1 (1.18; 24.6–29.3; 15)	23.5 (1.30; 20.4–26.3; 26)	**
	(13)	23.5 (0.77; 21.8–24.5; 12)	21.4 (0.78; 19.7–22.0; 8)	**
	(14)	25.1 (1.13; 24.0–26.5; 4)	23.0 (1.27; 21.0–24.7; 6)	*
BILL W	(12)	9.0 (0.96; 7.0–12.6; 37)	8.9 (1.27; 6.7–12.4; 53)	ns
	(13)	8.5 (0.97; 6.6–10.5; 17)	7.6 (0.73; 6.2–8.6; 13)	**
	(14)	9.4 (0.93; 7.9–10.8; 7)	9.0 (1.16; 7.8–11.8; 16)	ns
BILL D	(12)	7.9 (0.55; 6.5–9.2; 44)	7.2 (0.58; 5.2–8.1; 59)	**
	(13)	7.4 (0.46; 6.4–8.1; 21)	6.6 (0.96; 5.0–9.4; 19)	**
	(14)	7.8 (0.46; 7.3–8.4; 7)	6.9 (0.36; 6.3–7.6; 17)	**
THL	(12)	65.7 (1.56; 59.1–69.0; 46)	59.5 (1.18; 57.3–65.6; 69)	**
	(13)	63.6 (1.56; 61.3–66.7; 21)	57.6 (1.35; 54.6–60.2; 19)	**
	(14)	66.1 (2.06; 63.3–68.7; 7)	59.0 (1.43; 55.9–61.7; 17)	**
TARSUS	(11)	42.0 (1.03; 40.7–43.1; 4)	37.5, 38.6	
	(12)	44.7 (1.53; 39.3–48.9; 46)	40.5 (1.60; 38.7–48.8; 68)	**
	(13)	43.9 (1.20; 41.4–46.2; 21)	39.8 (1.32; 25.8–41.3; 19)	**
	(14)	45.1 (1.29; 43.5–46.5; 7)	39.9 (1.10; 37.7–41.3; 17)	**

WEIGHTS NOMINATE NOVAESEELANDIAE: (1–3) NI, SI, Kermadec Is and Auckland I., from museum labels (CM, MV,

NMNZ): (1) Adults; (2) Juveniles; (3) First immatures. (4–5) Adults (and probably first immatures), live: (4) Orongorongo Valley, Wellington (Robertson *et al.* 1983); (5) Tiritiri Matangi I. and Whangaparaoa Pen. (Craig *et al.* 1981a,b). (6) Little Barrier I., adults and immatures, live (Gill & Veitch 1990). **SUBSPECIES CHATHAMENSIS:** (7–11) South East I., live (Dilks *et al.* Undated): (7) Adults (all months); (8) Juveniles; (9) First immatures; (10) Adults caught Jan. 1995; (11) Adults caught Jan. 1997.

		MALES	FEMALES	
	(1)	110.3 (17.67; 62–148; 45)	76.8 (12.33; 57.7–100.3; 18)	**
	(2)	100.1 (36.80; 45.5–125.0; 4)	50.0, 69.2, 75.2	
	(3)	102.0, 120.0	70.7 (9.22; 54.0–80.3; 7)	
	(4)	124.9 (10.02; 97–150; 75)	89.6 (6.54; 70–105; 46)	**
	(5)	121.2 (5.74; 19)	87.0 (5.09; 12)**	
	(6)	111, 125, 145	79	
	(7)	162.8 (21.50; 89–240; 46)	112.2 (12.22; 89–170; 67)	**
	(8)	134.4 (11.92; 108–162; 21)	97.9 (8.07; 86–112; 19)	**
	(9)	149.1 (15.3; 121–168; 7)	108.1 (17.49; 87–159; 17)	**
	(10)	154.7 (n=11)	107.9 (n=22)	
	(11)	174.9 (n=14)	110.7 (n=24)	

Adult males were significantly heavier in Jan. 1997 than in Jan. 1995 ($P < 0.01$); there was no significant difference between females in these years (Dilks *et al.* Undated). Dilks *et al.* (Undated) suggested that difference between years in weight of males may be result of differences in timing of breeding in the two years. Breeding started earlier in 1996–97 breeding season, and as a result males may have been released from parental duties by Jan.

STRUCTURE Wing rather long and broad. Ten primaries: p6 longest; p10 58–62 mm shorter, p9 19–23, p8 8–12, p7 1–3, p5 0–2, p4 3–9, p3 16–23, p2 23–26, p1 28–33. P4–p8 emarginated on outer web; p5–p8 on inner web. In adults, p8 also has a notch about halfway down edge of inner web (see Ageing, Fig. 1). Nine secondaries, including about three tertials; tips of longest tertials fall short of secondaries on folded wing. Tail long and square at tip; 12 rectrices. Bill moderately long and rather sturdy; about half length of head. Culmen has downward curve to pointed tip. Lower mandible much straighter than upper mandible, but has slight downward curve. Tarsus long and thick; scaling scutellate in front (partly fused), fused to rear. Tibia fully feathered. Middle toe with claw, 29.4 (2.14; 27.0–32.2; 6). Outer toe 77–86% of middle, inner 74–81%, hindtoe 96–107%.

AGEING Adults have a notch on edge of inner web of p8; rounded notch is c. 2 mm deep in centre, 12–20 mm long and positioned 4–5 cm from tip (see Fig. 1). Juveniles lack this notch on p8. First immatures retain juvenile primaries.

GEOGRAPHICAL VARIATION Two subspecies: nominate *novaeseelandiae* on mainland and some islands, including Kermadec and Auckland Is; and subspecies *chathamensis* on Chatham Is. Little variation within nominate in either size or plumage. Nominata described fully above.

SUBSPECIES CHATHAMENSIS: Larger than *novaeseelandiae* (see Measurements), and the two subspecies differ slightly in plumage. Descriptions of *chathamensis* based on examination of skins of six adults, one juvenile and three immatures. **Adult** Very similar to *novaeseelandiae* in plumage, and only separable in direct comparison. Iridescence on feathers tends to be slightly

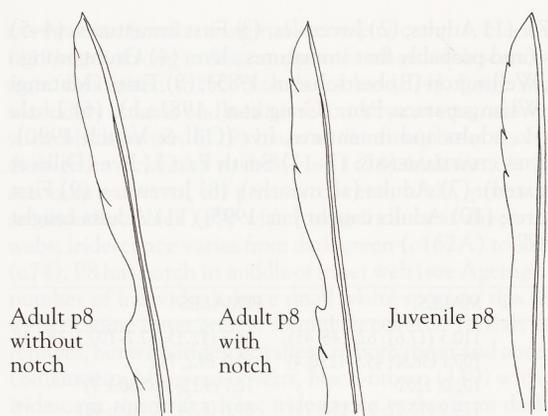


Figure 1 P8 of adult and juvenile (Source: Onley 1986)

bluer than that of nominate. **HEAD AND NECK:** Strong iridescent sheen to feathers of forehead, crown, nape, hindneck, sides of neck, ear-coverts, chin and throat, slightly bluer than nominate; appearance changes from dark green (c162A) to dark green-blue (dark 64) depending on angle of view; none has straw-yellow sheen. Rest as in nominate. **UPPERPARTS:** Mostly as nominate but iridescent sheen to uppertail-coverts bluer than nominate; green-blue (c65) to blue (c168), depending on angle of view; fringe has similar appearance to nominate. **UNDERPARTS:** Strong iridescent sheen to feathers of breast slightly bluer than nominate; dark green (c162A) to dark green-blue (dark 64) depending on angle of view; never has straw-yellow sheen; feathers of lower breast sometimes dark violet (c72). Rest of underparts as in nominate. **UPPERTAIL:** Strong iridescent sheen to rectrices slightly bluer than nominate; dark green (c162A) to dark green-blue (dark 64) or dark blue (74) depending on angle of view. **UNDERTAIL:** As nominate. **UPPERWING:** As nominate, or with slightly bluer iridescence to feathers. **UNDERWING:** As nominate. **Juvenile** Probably not separable from nominate; possibly have slightly bluer iridescence to remiges and rectrices. **First immature** (First basic). Differences from adult, same as those between adult and first immature 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