Order **PASSERIFORMES**

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

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

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

The Passeriformes divide into two main groups:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Family CALLAEIDAE[1]   New Zealand wattlebirds

A small but morphologically rather diverse family of three species of small-medium to medium-large passerines, endemic to NZ. Two species, Saddleback *Philesturnus carunculatus* and Kokako *Callaeas cinerea*, extant but threatened; the third, Huia *Heteralocha acutirostris*, is extinct (Oliver; Peters; NZCL). Taxonomic affinities of the family have been subject to some debate. Garrod (1872) suggested that the Huia was related to the families Icteridae (New World orioles, grackles and allies) and Sturnidae (starlings), but this was later rejected by Mayr & Amadon (1951), who placed the New Zealand wattlebirds between the Grallinidae (*Grallina*, *Corcorax* and *Struthidea*) and the Cracticidae (butcherbirds and allies). Sharpe (1877) placed them in the Corvidae between *Picathartes* (rockfowls and rock-jumpers) and *Falculea* (vangas). Based largely on pterylography and osteology (summarized below), Stonor (1942) concluded that all three species of New Zealand wattlebirds are from the same stock that gave rise to the Sturnidae and their immediate allies. Again, Mayr & Amadon (1951) rejected the hypothesis that Callaeidae and Sturnidae are allied. Oliver combined Saddleback and Huia in the family Philesturnidae, and placed Kokako in a separate but closely allied family Callaeadidae. Williams (1976) did not give an opinion concerning the affinities of the group. Sibley & Ahlquist (1985, 1990) lacked DNA samples of the three species and were thus unable to conduct DNA–DNA hybridization analysis with other passerines; consequently these authors combined them as the family Callaeatidae and placed them between the Corvidae and Picathartidae.

Species range in size from medium-small (Saddleback: length *c.* 20 cm, weight *c.* 80 g) to large (Huia: length *c.* 53 cm, *c.* 400 g). Morphological and osteological characteristics shared by the three species are (Stonor 1942; Williams 1976; Oliver): Wings rather short and rounded at tips. Ten primaries; p10 rather long. Nine secondaries, including three tertials. Tail long and rounded at tip; 12 rectrices. Bill varies between species: rather short and robust with decurved upper mandible in Kokako; long and straight with compressed ridge along culmen in Saddleback; and, in Huia, very long and sickle-shaped in adult female, shorter and only slightly decurved in adult male. Tongue morphology varies: lanceolate and shallowly bifid at tip in Saddleback, oblong and truncated at tip in Kokako (McCann 1964). Tarsus rather long; scaling laminiplantar. Feet rather large and strong. Hindclaw fairly long. All species have distinct and brightly coloured fleshy wattle on each side of gape. All species have weak keel to sternum and large nasal depressions. Kokako has following cranial features: distinct 'bridge' on upper edge of nasal; large lachrymals with thickened basal portion abutting jugal bar; large post-orbital processes; deep temporal fossae; two small unfused sesamoid bones, larger of which separates articulation of lower mandible from quadrate; maxillo-palatines expanded below vomer into pointed head; and palatines thickened and trans-palatine processes extend posteriorly to acute tip. Huia has similar palate structure and post-orbital processes to Kokako, but also has: articulation of lower mandible extends greatly backward; smaller lachrymals; distinct occipital crest; lacks deep temporal fossae; and lacks sesamoid bones. See Buller (1888) for more details on osteology of the Huia. Little known about osteological characters of Saddleback, but said to be similar to Huia, particularly in having distinct extension of articulation of lower mandible.

Plumage varies: mostly bluish grey in Kokako; blackish with distinct rufous band across upperparts in Saddleback; black with white tip to tail in Huia. Juvenile Kokako and Saddlebacks superficially resemble adults, but have softer and more loosely textured feathers of head and body. Kokako hatch with well-developed natal down (Gill 1993). Undergo a partial post-juvenile (first pre-basic) moult to adult-like first immature (first basic) plumage. Acquire adult plumage in complete first immature post-breeding (second pre-basic) moult, probably when *c.* 1 year old. After acquiring adult plumage, a complete post-breeding (pre-basic) moult each cycle produces successive adult (basic) plumages with no change in appearance. Sexes alike in plumage. Primaries moult outward, starting at p1; in Kokako, up to three primaries grow at once. Moult of tail and body not well known; timing probably much as moult of primaries.

Inhabit native forests, from lowlands to higher altitudes of mountain ranges. In NI, Kokako found mainly in structurally complex lowland forests, preferring tall mature hardwood forest dominated by Tawa *Beilschmiedia tawa* with emergent podocarps; in SI, occur in higher-altitude forests dominated by beech *Nothofagus*. Only survive in habitat free of most exotic predatory mammals. Saddleback occupies evergreen coastal and mixed lowland broadleaf forests, especially seral forests and secondary growth with high turnover of dead wood and numerous fruiting shrubs; also in coastal and montane shrublands. Translocated populations of Saddleback also occur in range of other habitats, such as lowland beech forest, mixed evergreen podocarp–hardwood forest and in exotic pines and wattles. Huia mainly inhabited montane and lowland hardwood–podocarp forests with dense understorey, occasionally beech forest (I. Flux; J.G. Innes; T.G. Lovegrove; see species accounts).

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[1] For discussion of correct spelling of family name, see Peters.

In Saddleback and Kokako, breeding adults sedentary and territorial throughout year and from year to year, though, in Saddleback, adults known to traverse neighbouring territories to forage and drink. In Kokako, young disperse, sometimes >20 km, before settling into territories close to natal territories (see species accounts).

Omnivorous, but main components of diet vary with species: Kokako eats mainly fruit and leaves and, less often, flowers, moss, buds, nectar and invertebrates; Saddleback eats mainly insects and berries, as well as other invertebrates and nectar and occasionally buds; Huia considered a specialist predator of Huhu beetle *Prionoplus reticularis* larvae, but also ate other invertebrates and fruit. Forage at all levels in forests: on soil, in leaf-litter and decaying timber on ground; and among branches and live and dead foliage of trees and shrubs from near ground to canopy. Forage mostly by probing, tearing and gleaning; probe bark of trees, dead and decaying wood of branches, trunks, stumps and logs, and often tear off chunks of bark or wood from trees, exposing insects beneath. Sometimes lift fronds, leaves, lichens or moss, and sometimes toss leaves like a Common Blackbird *Turdus merula*. Bills long and strong, and forage with them either open or closed; upper mandible sometimes used as skewer; also use bill to zirkeln. Male and female Huia had markedly different bills: males had strong, slightly decurved, moderately long bills and well-developed cranial musculature, allowing them to break up rotten wood by chiselling and gaping; while females had longer, slender and more decurved bills, suited to probing holes and crevices. Use feet to manipulate and hold food. Kokako and Saddleback forage throughout day; and usually forage singly or in pairs, very occasionally in larger groups. Saddlebacks often seen foraging with Grey Fantails *Rhipidura fuliginosa* (see species accounts).

Social organization of the family appears to be rather uniform. None appear to be particularly gregarious, with birds usually seen singly or in pairs, but sometimes form small family groups after breeding (see species accounts). All species monogamous and form long-term pair-bonds, possibly remaining paired for life. Where known, both parents feed nestlings and fledgelings, but only female incubates or broods. All species thought to nest solitarily and defend an all-purpose territory throughout the year. Territories maintained mostly by vocalizations, but threat displays, chasing and even physical fighting have been recorded during territorial disputes. Both extant species perform Archangel Displays (see species accounts) and courtship feeding as part of pair-formation and pair-bond maintenance. Vocalizations also play a major role in all sexual activities and all other aspects of social behaviour.

Vocalizations are varied, but all produce melodious piping or flute-like vocalizations. Other vocalizations include organ-like notes, and harsher chattering or churring vocalizations. Much variation between different locations in the vocalizations heard, and components of song can often be categorized to local dialects. All respond strongly to imitation or playback of their vocalizations. Both extant species often perform duets, and both also sometimes counter-sing with neighbours.

Solitary nesters. Typically, female alone constructs nest, incubates and broods, while being fed by the male. However, young usually fed by both parents. A variety of nesting sites used, but Kokakos nest mostly among branches of trees and shrubs, 2–32 m above ground, mostly ≤10 m, while Saddlebacks usually nest in hollows in trees or epiphytes at low levels, including on ground. Huias nested on ground to high in canopy. Build large, cup-shaped nests, consisting of loosely constructed base mostly of sticks and twigs, with inner layer and lining of finer material. Eggs oval, though also elliptical-ovate in Kokako. Ground-colour pale, usually shades of pale to darker pinkish or purplish grey, but also white and very pale browns; marked with spots and blotches, sometimes streaks or lines, of shades of brown and purple, usually concentrated at large end. Clutch-size usually two or three, occasionally one or four; Huias said to have often laid clutches of four, but clutch-size variously claimed to be from one to five. Normally raise one or two broods per season. Incubation period from 16 to 28 days; fledging period, from 25 to 37 days. Breeding failures largely result of predation, mostly by small introduced mammals, such as rats *Rattus* and Common Brushtail Possums *Trichosurus vulpecula*, which are able to attack the low and easily accessible nests, but also by predatory birds such as Swamp Harriers *Circus approximans*, Southern Boobooks *Ninox novaeseelandiae* and Wekas *Gallirallus australis* (see species accounts).

All members of family globally threatened: Kokako is endangered; Saddleback near threatened; and Huia extinct (Stattersfield & Capper 2000; Fuller 2002; NZCL; for details see species accounts). Ranges of Saddleback and Kokako much reduced, but both increasing with translocations to offshore islands and protected mainland sites (particularly Saddleback). Main threat is predation by introduced mammalian predators; Kokako also probably adversely affected by competition from introduced omnivores and herbivores, which eat foods also eaten by Kokako and have altered pattern of regeneration of forests. Historically, all three species adversely affected by loss or fragmentation of habitat, through logging (both clear-felling and selective logging, and subsequent degradation) and large-scale clearing and burning of native vegetation, and to some extent, hunting. Predation by introduced mammals may also have contributed to extinction of Huia.

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Callaeas cinerea **Kokako**

COLOUR PLATE FACING PAGE 992

Glaucopis cinerea Gmelin, 1788, *Syst. Nat.* 1(1): 363 — Queen Charlotte Sound, South Island, New Zealand.

The generic name refers to the orange-and-blue wattles at the base of the bill (Greek κάλλαιον, a cock's wattles). The specific epithet is based on Latham's (1781; *Gen. Synop. Birds*, **I**, p. 364, pl. xiv) 'Cinereous Wattle-bird' from Latin *cinereus*, ash-grey.

OTHER ENGLISH NAMES North Island, South Island or Orange-wattled Kokako; Wattled, Blue-wattled or Orange-wattled Crow; Wattlebird or Cinereous Wattlebird; Gillbird or Blue Gill; Organ-bird.

MAORI NAMES Hokako; Honga; Honge; Onga; Onge; Pakara; Werewere.

POLYTYPIC Nominate *cinerea*, throughout forested parts of the SI and Stewart I., now probably extinct; *wilsoni* Bonaparte, 1850, formerly widespread in NI, now restricted to 14 managed populations N of line between East C. and Taranaki; reintroduced to wild in Hawkes Bay and Wellington in 2004 and successfully introduced to Little Barrier, Tiritiri Matangi and Kapiti Is.

FIELD IDENTIFICATION Length *c.* 38 cm; wingspan not known; weight: males 233 g, females 218 g. Distinctive, medium-large forest bird, with: short, thick downcurved bill; short, broad and rounded wings, tips of which reach just past uppertail-coverts when wing folded; long, broad tail, with rounded tip, and which curves downward; and long, sturdy legs. Much larger than Saddleback *Philesturnus carunculatus*, with much shorter and decurved bill (fairly straight in Saddleback), larger and more rounded wattle (smaller and narrower in Saddleback), and longer rounded tail (shorter, square-tipped in Saddleback). Sexes alike (though females slightly smaller); and no seasonal variation. Adults largely blue-grey, with black mask, brownish lower underbody, and large, rounded wattles at base of bill, and which lie flat against throat (not pendulous). Two subspecies that differ most obviously in colour of wattles: bright blue in subspecies *wilsoni* from NI; and bright orange (with blue lower edge) in nominate *cinerea* from SI, which almost certainly extinct. Only NI Kokako (*wilsoni*) described below; for details of SI Kokako (nominate), see Plumages and related matters. Juvenile differs from adult by smaller and pink wattle, and brownish-grey plumage. Immature like juvenile but with more bluish-grey mantle, and gradual development of adult bare parts; differs from adult mainly by pinkish wattle, at least till *c.* 3 months old, and retained juvenile plumage of tail and much of wing. **Adult** Nearly wholly blue-grey, with: starkly contrasting black mask from lower forehead and lores to behind eyes and anterior ear-coverts, and which is bordered by pale-grey, further emphasizing mask; black chin; and olive-brown lower underbody (rear-flanks, centre of lower belly, thighs, vent and undertail-coverts). Tail, blackish brown with broad olive-brown edges to feathers. Folded wing largely blue-grey; remiges, olive-brown with, in most, bluish-grey wash to outer edges. Underwing: coverts, bluish grey; remiges, dark brown. Bill, black. Iris, dark brown. Orbital ring, black. Large, rounded bright-blue wattles extend from gape at base of bill, over cheeks, and either overlap or nearly overlap under throat; wattles flush with throat not pendulous (as some writers and artists depict), and are larger when breeding. Rarely, NI birds with orange wattles reported, and assumed to be colour variants of *wilsoni* (see Bare Parts). Legs and feet, black. **Juvenile** Similar to adult but without blue tinge to plumage, and with much more loosely textured plumage; held for only very short time after fledging, and some complete most of post-juvenile moult to immature plumage even before fledging. Almost wholly grey with brownish tinge, contrasting little with olive-brown lower underbody (which as adult) with small and diffuse blackish mask (confined to lores and round eye) with narrow and indistinct pale-grey border to rear edge; wings and tail largely brown. Outer primaries slightly broader than in adult and with rounded tips (tips pointed in adult); and rectrices narrower with much more pointed tips (rectrices broad with rounded tips in adult). Bill, black with pink gape and base to lower mandible. Wattle, pink and roughly half size of that of adult. Orbital ring, dark grey. **Immature** Very like juvenile but with bluish-grey mantle (brownish grey in juvenile) and without loosely textured feathering; at first wattles as juvenile but soon change (see below). Differ from adult in more brownish-grey upperparts and fore-underbody, lacking bluish tinge except for bluish-grey mantle; also retain juvenile remiges and rectrices, which dark brown and with rounded tips to outer primaries and narrower rectrices with more pointed tips (as juvenile). Wattles as juvenile at first; soon develop bluish edge and turn purplish pink, then pinkish blue. Some develop large blue wattle, like that of adult, by 3 months after fledging, but some still have remnants of pink after 9 months; at 1 year after fledging, wattles as adult. Rest of bare parts as juvenile at first; not known when attain full adult coloration.

Similar species At a glance, **Tui** *Prosthemadera novaeseelandiae* may be briefly confused, but Tui much smaller, with longer and more slender bill, and white plumes on throat and hindneck; Tui a much more adept flier, with more rapid wing-beats and flight can be noisy; habits of the two also very different.

Rare and localized, but not uncommon in some managed areas; confined to a few scattered, heavily forested areas in NZ. Mainly seen in pairs or singly, sometimes in small family groups, of adults and up to three young; occasionally in small groups of non-territorial subadults and adults, of two or, exceptionally, 12. Individuals and pairs can maintain territories for many years. Usually located by call. Highly mobile despite weak flight, usually moving about by hopping, running or bounding on powerful legs through vegetation or over ground; move about in trees either by rapidly laddering upward, bounding vertically from branch to branch using legs alone, or rapidly squirrelling by running adeptly through interlocking branches of canopy (see Movements). Struggle to gain height by flying, but traverse territory readily with short, powerful

leaps and small flights between branches, and longer gliding flights (to 200 m) from high launch points; fly noisily on short but broadly rounded wings, with primaries and tail spread. Mostly eat fruit and leaves, as well as other vegetable matter and invertebrates; feed parrot-like, grasping food with one foot, while balancing on perch. Song loud and beautiful, and given for long periods, with singing birds flapping wings and holding head vertically with throat puffed out; pairs duet with organ- or flute-like calls interspersed with short clucks and buzzes (see Voice for detail).

HABITAT   Based on contribution by J.G. Innes and I. Flux. Well known in NI, from detailed research associated with indigenous logging controversies in 1978–81 (Hay 1981; Leathwick 1981), 1981–82 (Powlesland 1987) and 1982–84 (Best & Bellingham 1991), and other studies in managed areas (e.g. Overdyck 1999). On NI, found mainly in structurally complex lowland forests, below 750 m asl (Crook et al. 1971, 1972; Lavers 1978; Clout & Hay 1981; Hay 1981; Leathwick 1981; MacMillan & McClure 1990; Best & Bellingham 1991; Hudson 1994; Heather & Robertson 1997; Overdyck 1999), preferring tall mature hardwood forest dominated by Tawa *Beilschmiedia tawa* with emergent podocarps (Hay 1981; Leathwick 1981; O'Donnell 1984; Best & Bellingham 1991); recorded close to 900 m asl (Hudson 1994). In dissected terrain, territories mainly on ridge-tops or side-spurs (Williams 1990; Jones et al. 1999). Sing from highest emergent trees; most travel is through canopy or subcanopy but rarely on ground; most foraging in subcanopy or gully shrub-hardwoods. On SI, formerly found in forested habitats, including beech *Nothofagus* and podocarp–hardwood forests and forest edges from coast to >900 m asl (Potts 1873; Reischek 1885b; Smith 1888; Fulton 1907).

   NI   Mainly in Tawa–podocarp forest (St Paul & McKenzie 1974; Leathwick et al. 1983; Powlesland 1987; MacMillan & McClure 1990; Greene 1995; Ravine 2004); with canopy dominated by Tawa, sometimes with associated Kohekohe *Dysoxylum spectabile*, Mangeao *Litsea calicaris*, Rewarewa *Knightia excelsa*, Kamahi *Weinmannia racemosa* or Hinau *Elaeocarpus dentatus*, and occasional emergent Rimu *Dacrydium cupressinum*, Totara *Podocarpus totara*, Miro *Prumnopitys ferruginea*, Matai *Prumnopitys taxifolia* and Northern Rata *Metrosideros robusta* (Leathwick 1981; Leathwick et al. 1983; O'Donnell 1984; Overdyck 1999; Ravine 2004). Also in mixed broadleaf forests, such as in Northland, mature forest dominated on ridges by Kauri *Agathis australis* and Totara (Powlesland 1987; Best & Bellingham 1991). At higher altitude (e.g. Te Urewera NP), canopy may include Tawheowheo *Quintinia serrata* and Hard Beech *Nothofagus truncata* (Ravine 2004). Typically, understorey and gully vegetation of habitats diverse, and includes food plants Putaputaweta *Carpodetus serratus*, Raurekau *Coprosma grandifolia*, Hangehange *Geniostoma rupestre*, Pigeonwood *Hedycarya arborea*, Mahoe *Melicytus ramiflorus*, and Five-Finger *Pseudopanax arboreus*; and canopy commonly with lianes and epiphytes used as food (including lianes Kareao Supplejack *Ripogonum scandens*, Bush Lawyer *Rubus cissoides* and White Rata *Metrosideros diffusa*) and epiphytes (including kahakaha *Collospermum*, Weeping Spleenwort *Asplenium flaccidum*, filmy ferns *Hymenophyllum*, orchids *Dendrobium cunninghamii* and *Earina*) (Hay et al. 1985a; Powlesland 1987; Best & Bellingham 1991; Corson 1997; see Food). Occasionally in shrublands and regenerating seral forest adjacent to Tawa–podocarp forest (MacMillan & McClure 1990; Innes & Flux 1999), including low (2–4 m) stands of Manuka *Leptospermum scoparium* (Williams 1990).

   Regularly use mature exotic forests adjacent to territories, for feeding on insects. One established territory in 37-year-old Slash Pine *Pinus elliottii* in Rotoehu Forest, Bay of Plenty, in 1987 (Calder & Innes 1987). Successful translocation to Tiritiri Matangi I. with substantial planted shrubland, grassland and some exotic canopy trees suggests considerable adaptability to new habitats (Jones 2000).

   SI   Occupied a variety of forest habitats, and scrubby forest clearings or margins, from coast to near tree-line, and including forests dominated by beech *Nothofagus* and by podocarp–hardwood associations, such as Southern Rata *Metrosideros umbellata*, Kamahi and Rimu. Among these forests the shrub-hardwood understorey species are likely to have been key determinants of habitat quality, and included species of small-leaved *Coprosma*, Kotukutuku *Fuchsia excorticata*, tutu *Coriaria*, Putaputaweta; Mahoe; Hangehange, Broadleaf *Griselinia littoralis*, Mountain Ribbonwood *Hoheria glabrata*, Horoeka *Pseudopanax crassifolius* and Stinkwood *Coprosma foetidissima* (Potts 1873; Travers 1871; Reischek 1885b; Smith 1888).

   Detailed studies   All NZ. At PIKIARIKI, PUREORA, WAIKATO (1978–81), occurred in podocarp–Tawa–mixed hardwood forest with large mature podocarps, mainly Matai, emergent over a dense diverse canopy of tree-ferns and shrub hardwoods, commonly Five-finger, Raukawa, Mahoe, Pate, Putaputaweta and *Fuchsia*, with lesser amounts of Raurekau, Broadleaf, Horopito *Pseudowintera colorata*, Kaikomako *Pennantia corymbosa* and Toro *Myrsine salicina*; and with abundant lianes and epiphytes. At WAIPAPA, PUREORA, inhabited podocarp–hardwood forest much as at Pikiariki, though Rimu dominant rather than Matai, and Tawa the most abundant hardwood (Leathwick 1981; Leathwick et al. 1983). At MAPARA, WAIKATO (1978–81), inhabited two major forest types: (1) Tawa-dominated forest predominated on ridges and podocarps were only occasionally present owing to past logging; other hardwood species present in moderate amounts included Pigeonwood, Hinau, Mahoe, Kamahi, Titoki *Alectryon excelsus* and Mapou *Myrsine australis*; epiphytes were common, in particular kahakaha, *Phymatodes diversifolium* and Bamboo Orchid *Earina mucronata*. (2) Mahoe-dominated forest occupied most plateau and gully sites; tree-ferns Wheki *Dicksonia squarrosa* and Soft Tree-fern *Cyathea smithii* were abundant, as were lianes *Tetrapathaea tetrandra*, bush lawyer *Rubus* and Kareao Supplejack (Leathwick 1981; Leathwick et al. 1983). At ROTOEHU, BAY OF PLENTY (1978–81), habitat included: (1) a climax association on ridges and plateaus in which Tawa and Kohekohe dominant, with Hinau, Mangeao and Rewarewa present; abundant epiphytes (especially *Phymatodes diversifolium* and kahakaha); and Soft Tree-fern dominant in understorey, with lesser amounts of Pigeonwood, Mahoe and Kawakawa *Macropiper excelsum*; (2) a gully–hardwood association heavily modified by logging, typically with scattered large Tawa emergent over a dense layer of Mahoe, Pigeonwood, young Rewarewa, Silver Fern *Cyathea dealbata*, Rangiora *Brachyglottis repanda*, Kawakawa and Wheki; and (3) some terri-tories also included a disturbed association, probably originating from past burning dominated by Kamahi and Rewarewa in the canopy, with Kanuka and tall Mamaku *Cyathea medullaris* present (Leathwick 1981; Leathwick et al. 1983). In PUKETI FOREST, NORTHLAND, vegetation of six territories (1982–84) was very diverse owing to varying topography and associated changes in moisture, drainage, shelter, shade and site-fertility, as well as impacts of natural and human disturbance: gully vegetation consisted mainly of Pukatea *Laurelia novae-zelandiae*, Kareao Supplejack and Kohekohe; Rimu, Taraire *Beilschmiedia tarairi* and Kohekohe dominated lower ridge-flanks; mid- to upper ridge-flanks and rolling ridge-tops were vegetated mainly with Towai *Weinmannia silvicola*, Taraire, Kohekohe and Tawa, with Totara being locally common. Ridge-top sites in the most dissected terrain were characterized by Totara with Kauri subdominant, or Kauri with Totara subdominant (Best & Bellingham 1991).

DISTRIBUTION AND POPULATION Based on contribution by J.G. Innes and I. Flux. Endemic to NZ.

NZ Formerly widespread, now much reduced (NZCL), though expanding after translocation to islands and mainland. **NI** Widespread in n. half, though at sparsely scattered sites, on Auckland Isthmus and from Hunua Ras and Coromandel Pen., S roughly to line joining East C. and C. Egmont (Innes & Flux 1999; NZ Atlas). Translocated to Lady Alice, Little Barrier, Tiritiri Matangi and Kapiti Is and, in 2004, reintroduced to Hawkes Bay and Wairarapa (see Introductions, below). For former range, see Change in range below. NORTHLAND: Occur at Puketi, Waima and Mataraua. Introduced to Lady Alice I. in 2003. AUCKLAND: Introduced on Little Barrier I. and Tiritiri Matangi. S. AUCKLAND: Occur in Hunua Ras; and an unviable remnant population on Coromandel Pen. BAY OF PLENTY, N. VOLCANIC PLAIN AND W. EAST COAST: Occur Kaimai Ra. (Opuiaki, Mokaihaha), and at Kaharoa, Rotoehu and Manawahe near Rotorua Lakes. Largest national population in Te Urewera NP, mainly in Waimana Catchment. HAWKES BAY: Reintroduced to wild at Boundary Stream in 2004 (see Introductions). WAIRARAPA: Reintroduced to wild at Pukaha–Mt Bruce in 2003 (see Introductions). WELLINGTON: Introduced on Kapiti I. (see Introductions). TARANAKI: In N, a few possibly still inhabit area between Ohura and Okau, on Waitaanga Saddle. WAIKATO: Healthy populations at Mapara, Waipapa and Mangatutu, with scattered birds elsewhere, including Herangi Ra., Pikiariki and Tihoi (Williams 1976; Lavers 1978; O'Donnell 1984; Hay et al. 1985a; MacMillan & McClure 1990; Innes & Flux 1999; Heather & Robertson 2000; NZ Atlas; NZCL; CSN; J.G. Innes & I. Flux). **SI** Probably extinct. Last recorded on mainland in 1967 round Teal Ck, in Mt Aspiring NP, near Makarora, nw. Otago (McBride 1981). Subsequent searches in same area unsuccessful (Clout & Hay 1981). Occasional later claims not verified, e.g. Paringa R., Nov. 1976 (CSN 24); Nelson Ls NP, June 1996 (Anon. 1996); and, on Stewart I., a feather found and some unconfirmed sightings in early 1987 (Buckingham 1987).

Breeding Throughout most of range except where remnant populations lack male–female pairs (i.e. at Puketi, Coromandel Ra., Taranaki, Herangi Ra.).

Introductions ISLAND TRANSLOCATIONS: Several translocations since 1981 (Merton 1983; Hay et al. 1985a; I. Flux).
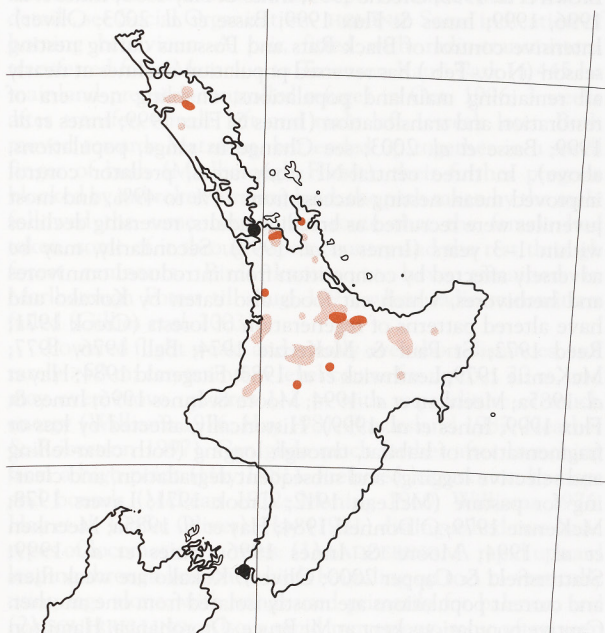
Between Oct. 1981 and Apr. 1983, 25 Kokako transferred from near Rotorua to Little Barrier I.; and another two translocated there from Great Barrier I. in 1994 (Hay et al. 1985a; Marsh 1995; Moore & Innes 1996; Innes & Flux 1999; NZCL; CSN 31, 33). Six from n. Waikato, five from Manawahe (Bay of Plenty), two from Makino (Taranaki), seven from Little Barrier I. (from translocated population), seven from Mt Bruce (captive bred from Mangatutu stock) and five from Mapara (managed population at Waikato) released on Kapiti I. between 1991 and 1996 (Moore & Innes 1996; Innes & Flux 1999; I. Flux). Two from Mapara (managed population) and four from Mt Bruce (captive bred from Mangatutu stock) released on Tiritiri Matangi I. in 1996 (Moore & Innes 1996; Innes & Flux 1999; Jones 2000; I. Flux). Two hand-reared juvenile females from Kaharoa released on Lady Alice I. (Northland) in 2003.

MAINLAND TRANSLOCATIONS: Increasing. Four unsuccessfully released at Trounson Kauri Park, NI, before 1996 (Moore & Innes 1996). Two females and one male from Mapara released at Pikiariki (Pureora, Waikato) in 1994; and four Mapara females released at Hunua Ras in 1995 to bolster remnant males. In Hunua Ras, translocated females travelled more but vocalized less than resident females; and did not breed successfully (Overdyck 1999). Five pairs taken from Otamatuna (Te Urewera) in 2001 to captivity at Boundary Stream, Hawkes Bay; two pairs bred in third season and all released to wild in 2004. At Mt Bruce–Pukaha in Wairarapa, four female and two male Mangatutu birds released during 2003; one pair formed and bred successfully in the wild in their first season. Two non-breeding captive pairs (ex-Mangatutu), together with two other wild-caught Mangatutu birds released to wild 2004; breeding recorded again in 2004–05 (I. Flux; J.D. Hudson).

IN CAPTIVITY: At Mt Bruce National Wildlife Centre (Wairarapa), Otorohanga Zoological Society, Hamilton Zoo (Waikato) and Auckland Zoo.

Change in range, populations By the 1870s, populations had become scattered, though still widespread; by 1880s, range had contracted and populations declined markedly; and regarded as rare by 1912 (McLean 1912; Medway 1968; Williams 1976; Lavers 1978; Falla et al. 1981). **NI** Formerly widespread (Lavers 1978; Innes & Flux 1999), occurring in most areas except n. Far North (N of Rangaunu Harbour), s. Volcanic Plateau, Hawkes Bay, and some parts of Wairarapa, Wellington and Manawatu (Lavers 1978; Hay et al. 1985a). Range has contracted markedly in 20th century (Medway 1968; Hay et al. 1985a) and confined to n. half of NI by 1960 (Lavers 1978). In some areas, recorded rates of decline were 50% in 3 years (Innes et al. 1999; Statterfield & Capper 2000; J.G. Innes). In Northland, where incorrectly claimed to have become extinct by 1900 (Oliver), recorded in three of six forests surveyed in 1979, but recorded in only one of these in 1993 (Pierce et al. 1993). Puketi population estimated at 87 in 1984; 32 in 1992; perhaps five single males in 2005. Attempts under way to save genes by translocating remaining males to Lady Alice I. to breed with hand-reared females from Kaharoa, Bay of Plenty. Most recently recorded in mainland Auckland in 1944 (Lavers 1978). Population on Great Barrier I. said to have been becoming rare by early 1970s (Reed 1972); estimated 12 present in 1985 (Hay et al. 1985b); and last two translocated to Little Barrier I in 1994 (Marsh 1995; Heather & Robertson 2000; see Introductions). Population in Hunua Ras has declined greatly: in early 1900s, very abundant (nearly as plentiful as New Zealand Pigeons *Hemiphaga novaeseelandiae*, which were being 'shot by the sackful') (St Paul & McKenzie 1974); in c. 1940s, considered common, though confined to a few isolated remnants of forest (St Paul & McKenzie 1974); in 1957, population estimated at 250–300 birds; declined to 60–70 birds in 1972; 40 birds in 1988; and

26–28 in 1992–94 (St Paul & McKenzie 1974; MacMillan & McClure 1990; Greene 1995). Now nine pairs and increasing (H.J. Speed). Common on Coromandel Pen. in 19th century, but populations declined greatly since; 14 records between 1900 and 1970 (Lavers 1978), and current population said to comprise single bird (Marsh 1995; Innes & Flux 1999). Formerly plentiful round Whakatane (St Paul 1977) but no longer recorded there. Marked declines recorded round Rotorua (St Paul & McKenzie 1974) but now recovering in managed populations at Rotoehu, Kaharoa and Manawahe. Similar large historic declines in Kaimai–Mamaku Ra., but populations now managed at Mokaihaha and Opuiaki. Surveys in 1990–94 revealed 625 Kokako in Te Urewera NP, scattered in seven subpopulations over a large area; 270 remained in 1992–93, and 180 in 1996. Intensive pest control, especially at Otamatuna (Waimana Catchment), has reversed decline; now estimated 550 in Te Urewera (Jones *et al.* 1999; J.G. Innes & I. Flux). Rather widespread in area bounded by Mt Ruapehu, headwaters of Rangitikei R. and headwaters of Waitotara R. in early to mid-1880s (Medway 1968) but gone by 1900 (Hay *et al.* 1985a). In Taranaki, most of the scattered populations now extinct (O'Donnell 1984), e.g. recorded in forests round Mokau R. till 1960s, but gone by 1981; present in Tangarakau Gorge in 1940s but gone by early 1980s; not recorded near Whangamomona since 1976; last confirmed record in Matemateaonga Ra. in 1974; and round Mt Egmont, last confirmed record was in 1938, in Pouakai Ras, though unconfirmed report in 1960s (MacDonald 1966; Lavers 1978; O'Donnell 1984); remaining population declined dramatically in late 1980s and early 1990s (CSN 41). One or two may remain in Waitaanga, n. Taranaki (B. Williams). In Waikato, various scattered populations have declined or become extinct by early 1980s, e.g. formerly widespread in Herangi Ra. but, by early 1980s, apparently extinct in S and populations in N were small and localized; not recorded round Te Maika, S of Kawhia Harbour, since 1962; and in Mt Karioi Forest, present till at least 1960s but gone by 1980 (MacDonald 1966; O'Donnell 1984). In Pureora Forest Park, part of the Waipapa Ecological Area that held 24 territories in 1979 (Hay 1981) held ten in 1991 (Meenken *et al.* 1994). Intensive pest control after 1995 reversed declines to yield 43 adults in 27 territories in 1999 (Speed *et al.* 1999) and 212 adults in 90 territories in 2003 (J.G. Innes & I. Flux). Similarly, part of the Mangatutu Ecological Area (n. Pureora) pest-managed since 1995 held ten pairs and nine singles in 1996, 33 pairs and nine singles in 2000, and 46 pairs and 16 singles in 2004 (Thurley *et al.* 2004). Populations in Taranaki, Whanganui, w. Waikato, Coromandel Pen. and Great Barrier I. have all declined either to extinction or to 'a handful of single birds' (Moore & Innes 1996). In Wellington, numerous before 1890s but very rare by 1892; few records in 20th century, but persisted in Tararua Ra. till 1960s (MacDonald 1966; Lavers 1978). Reintroduced to wild at Pukaha–Mt Bruce, in Wairarapa, and to Boundary Stream, in Hawkes Bay, in 2004 with subsequent successful breeding. Active management of key mammal pests (Black Rats and Common Brushtail Possums *Trichosurus vulpecula*) at selected sites reversed declines at remaining populations after 1990 (Clout & Saunders 1995; Moore & Innes 1996; Innes & Flux 1999; Innes *et al.* 1999) and enabled subsequent translocations; national total of pairs increased annually after 2001 (J.G. Innes & I. Flux). At Mapara, after 8 years of pest control, total population of Kokako trebled, the number of breeding pairs increased eightfold, and the composition of the population changed from mostly old males to mainly young birds, with roughly equal gender-ratio (Innes & Flux 1999; Innes *et al.* 1999). **SI** Former distribution patchy but included most forested regions of the SI and Stewart I.; known to have occurred on and W of S. Alps, from Marlborough and Nelson S to Fiordland and Stewart I.; also formerly occurred along some rivers draining to E from S. Alps, and, round e. coast, on Banks Pen., Otago Pen. and in the Catlins (Potts 1873; Reischek 1885b; Smith 1888; Fulton 1907). Museum skin held at Auckland said to be collected from Stephens Is, though locality of collection doubted by some (Medway 2004). In 1889, said to have been rapidly approaching extinction and, by late 19th century, had gone from many areas where formerly plentiful (Potts 1873; Smith 1888; Fulton 1907). Isolated individuals probably persisted later (McBride 1981; R. Buckingham) but now considered extinct.

Status Endangered (Stattersfield & Capper 2000).

Populations Total population in 2003 estimated at 1726, including at least 640 pairs. ISLANDS: Little Barrier I., estimated 200 pairs; Tiritiri Matangi I., three pairs, three singles; Kapiti I., 14 pairs, seven singles; Lady Alice I., two juvenile females in 2003. MAINLAND: NORTHLAND: Puketi, four singles; Mataraua, 11 pairs, ten singles; Waima, one pair, one single; S. AUCKLAND: Hunua, four pairs, ten singles; BAY OF PLENTY, N. VOLCANIC PLAIN AND E. WEST COAST: Opuiaki, ten pairs, 14 singles; Mokaihaha, eight pairs, six singles (Kaimai–Mamaku Ra.); Kaharoa–Onaia, 40 pairs, five singles; Rotoehu, 35 pairs, ten singles; Manawahe, 14 pairs, three singles (Rotorua); Ikawhenua, four pairs, 12 singles; Waimana, 146 pairs, 38 singles (Te Urewera NP); WAIKATO: Mangatutu, 33 pairs, nine singles; Waipapa, 77 pairs, 13 singles; Mapara, 40 pairs, 16 singles. Small remnants also elsewhere in Coromandel, w. Waikato, Pureora and Te Urewera; and small translocated populations at Boundary Stream (Hawkes Bay) and Pukaha–Mt Bruce (Wairarapa) (J.G. Innes & I. Flux, from Kokako Recovery Group). RECORDED DENSITY: *c.* 0.25 birds/ha, Moki SF, Taranaki (CSN 31); 0.16–0.23 birds/ha, Pikiariki and Mapara (Waikato) and Rotoehu (Bay of Plenty) (Hay 1981).

THREATS AND HUMAN INTERACTIONS Based on contribution by J.G. Innes and I. Flux. Well known, from detailed study of causes of decline since 1989, and widespread monitoring of intensive pest-control programs at most remaining populations (Innes & Flux 1999; Innes *et al.* 1999; Flux & Innes 2001a). **NI** Eggs, chicks and sitting females often taken by introduced predators, especially Black Rats and Common Brushtail Possums, which is primary limiting factor of national population; sometimes also taken by Stoats *Mustela erminea* and Swamp Harriers *Circus approximans* (Clout & Hay 1981; Brown *et al.* 1993; Greene 1995; Innes & Hay 1995; Innes *et al.* 1996, 1999; Innes & Flux 1999; Basse *et al.* 2003; Oliver). Intensive control of Black Rats and Possums during nesting season (Nov.–Feb.) has reversed population declines at nearly all remaining mainland populations, enabling new era of restoration and translocation (Innes & Flux 1999; Innes *et al.* 1999; Basse *et al.* 2003; see Change in range, populations, above). In three central-NI study areas, predator control improved mean nesting success from 14% to 49%, and most juveniles were recruited as breeding adults, reversing declines within 1–3 years (Innes *et al.* 1999). Secondarily, may be adversely affected by competition from introduced omnivores and herbivores, which eat foods also eaten by Kokako and have altered patterns of regeneration of forests (Crook 1971; Reed 1972; St Paul & McKenzie 1974; Bell 1976, 1977; McKenzie 1979; Leathwick *et al.* 1983; Fitzgerald 1984; Hay *et al.* 1985a; Meenken *et al.* 1994; Moore & Innes 1996; Innes & Flux 1999; Innes *et al.* 1999). Historically, affected by loss or fragmentation of habitat, through logging (both clear-felling and selective logging) and subsequent degradation, and clearing for pasture (McLean 1912; Crook 1971; Lavers 1978; McKenzie 1979; O'Donnell 1984; Hay *et al.* 1985a; Meenken *et al.* 1994; Moore & Innes 1996; Innes *et al.* 1999; Stattersfield & Capper 2000; Oliver). Kokako are weak fliers and current populations are mostly isolated from one another. Captive populations kept at Mt Bruce, Otorohanga, Hamilton

and Auckland primarily to perpetuate particular (Taranaki, Puketi) genotypes (Innes & Flux 1999; Heather & Robertson 2000; R. Collen). Possibly occasionally shot by people hunting New Zealand Pigeons (McLean 1912; MacMillan & McClure 1990; Pierce *et al.* 1993). Formerly, eaten very occasionally; Reischek made soup from them (Westerskov 1979), though generally said to be 'not palatable' (St Paul & McKenzie 1974) and 'unfit to eat' (McLean 1912). Not usually eaten by Maori, though they occasionally did so opportunistically, attracting birds with a call-leaf (Best 1942). Wattles worn by Maori as ornaments on cheeks (Turbott 1967). At nests show considerable tolerance to human activity (McKenzie 1951, 1953; Innes & Hay 1995; see Social Behaviour, Breeding). **SI** Agents of decline probably as for NI. Authors have variously blamed: Cats (Travers 1871); Cats and people (Reischek 1885b); forest clearance, disturbance and climate change (Potts 1873); Dogs and Cats (Smith 1888); and rats, stoats *Mustela* and collectors (Fulton 1907), the predators perhaps irrupting after beech mast (Clout & Hay 1981). Large numbers of SI Kokako were collected for sale to European museums (Oliver).

MOVEMENTS Based on contribution by J.G. Innes and I. Flux. Movements well known because most current populations include some, and often many, colour-banded birds (see Banding). Sedentary. Adults highly mobile within discrete, defended territories of up to 14 ha, which maintained year-round (Hay 1981; Powlesland 1987; Best & Bellingham 1991; Innes *et al.* 1996; I. Flux & P. Bradfield; see Social Organization). Members of a pair usually move about together, with male often leading (Flux & Innes 2001a). In Puketi, Northland, different parts of territory used in different seasons, depending on availability of food and weather; range generally smaller in summer–autumn and larger in late winter to early spring (Best & Bellingham 1991); and near Pureora described as recurring in a subsection within one territory before incubation (Innes & Hay 1995). Food plants widely dispersed so do not flock to locally abundant food sources (Hay *et al.* 1985a) but groups occasionally reported, sometimes moving about together (see Social Organization). DISPERSAL OF YOUNG: While average distance between natal territory and place of final settlement 1200–2100 m, total movements before settlement probably far greater; one radio-tagged juvenile moved at least 20.2 km between Sept. 1992 and Mar. 1993; for details, see Social Organization. HOMING: Some indication of homing behaviour: A pair, fitted with radio-transmitters, transferred from Mataraua to Trounson Kauri Park (a 445 ha mainland predator-controlled refuge) in Oct. 1996; 3 weeks after transfer, female left and male left 1 week later. Both moved towards Mataraua, but ended up together in a small finger of bush (Marlborough Forest), their further progress blocked by unbroken farming land; the path taken by the male followed the same convoluted route that the female had taken, some of it through open country and the rest through forest remnants. Birds known to have remained in Marlborough Forest till Aug. 1997, when radio-transmitters failed (Gillies *et al.* 2003).

Powered flight weak, and usually over short distances, and rarely >50 m; can maintain level course for up to c. 20 m, and may even move upwards 1–2 m with expenditure of much energy (Williams 1976; Hay 1981; Powlesland 1987; Heather & Robertson 1997). Can glide much farther after launching from a high point (Hay 1981). Preferred locomotion by hops and bounds (McLean 1912; Maning 1960; Williams 1976; Hay *et al.* 1985a; Oliver). Hay (1981) distinguished two basic types of locomotion in trees: (1) LADDERING: A rapid upward leaping through branches, birds bounding up to 1 m vertically using legs alone, with wings used primarily for balance; and (2) SQUIRRELLING: Also a rapid movement, most often seen in areas of even canopy-height; birds run with considerable agility through the interlocking branches of canopy at a pace close to that of a human walk. Once, party of seven described, in May 1906, working through bush with 'short flights and great bounds', through tops of Manuka trees on a spur, till reaching a feeding ground and launching themselves down, and using long legs to 'actually swing from branch to branch at times', very rarely using wings for locomotion (McLean 1912).

Banding Extensive. Most extant populations have some colour-banded birds, and recent detailed research sites have many, e.g. 234 banded at Mapara 1990–2001 (I. Flux & P. Bradfield) and 109 banded at Rotoehu 1989–97 (P. Jansen & J.G. Innes), cf. six banded by Hay (1981) and none by Powlesland (1987). Translocated birds always colour-banded. Most movement data (above) revealed by banding. LONGEVITY: Long-lived, possibly to 25 years old. One female banded as adult in 1989 at Rotoehu still alive in 2004 (J.G. Innes; L.E. Molles).

FOOD Based on contribution by J.G. Innes and I. Flux. Mainly eat fruit and leaves and, less often, flowers, moss (foliage and capsules), buds, nectar and invertebrates (see Table 1, also see below). Described as sequential specialist (Hay 1981); eat many species of plant and invertebrate, importance of each varying between seasons, years and territories. In 1978–81 in Waikato–Bay of Plenty: at Pikiariki, known to eat 44 plant and three invertebrate species; at Rotoehu, known to eat 25 plant species, and at Mapara, known to eat 35 plant and five invertebrate species (Hay 1981). At Puketi in 1981–82, ate 68 different foods, but only eight contributed >5% to diet in any season (Powlesland 1987); at Puketi in 1982–84, ate 85 species of plant and invertebrate but mostly in small amounts, with only 24 contributing >1% of overall diet seasonally, and ten species made up half diet (Best & Bellingham 1991). **Behaviour** Access foods by gliding between trees, 'laddering' and 'squirrelling' (see Movements) rapidly between branches, then smaller movements to branch tips if required. Often, intense feeding spells of 10–30 min interspersed with quiet roosting and preening, or singing. Quiet when foraging (McLean 1912; *contra* NZRD). Pairs usually forage near each other, and maintain contact with soft vocalizations. Forage throughout day. At Hunua, time spent foraging generally increased from morning to afternoon, possibly because singing occurred mostly in mornings (Overdyck 1999). At Puketi, fed most commonly in middle part of the day (Best & Bellingham 1991). Marked differences in diet between different territories in the same season, reflecting variation in abundance of food between territories. Mapara females translocated to Hunua Ras initially selected different foods compared to resident females but diets became nearly identical over time (Overdyck 1999). In general, Kokako in the wild did not investigate non-toxic pellet baits used in aerial pest control operations (Innes & Williams 1990), though one of four captive birds did (Spurr 1993). By Feb. 2005, at least 393 Kokako (including six juveniles) had been monitored through aerial 1080 poisoning operations since 1986; five disappeared, consistent with poisoning, and one was verified with 1080 present, suggesting maximum mortality estimate of 1.3% with 5% chance it will exceed 4% (Flux & Innes 2001a). On Kapiti I., two of 13 (15%) monitored Kokako were probably killed during aerial poisoning with brodifacoum for rodent eradication, perhaps because no cinnamon (a repellent) was included in baits (Empson & Miskelly 1999). DETAILED STUDIES: Well known in NI, from research projects associated with controversies over logging of indigenous forests: at Pikiariki and Mapara, in Waikato, and Rotoehu in Bay of Plenty, 1978–81 (Hay 1981; Leathwick 1981); and at Puketi, Northland, 1981–82 (Powlesland

1987) and 1982–84 (Best & Bellingham 1991); as well as other ongoing studies in managed areas (e.g. Overdyck 1999). FORAGING ASSOCIATIONS: Forage in pairs, singly (McLean 1912; HJNC 1975; CSN 28, 31) or in family groups, though a group of seven were once reported foraging together (McLean 1912). FORAGING HEIGHTS AND SITES: Forage at all levels of vegetation, but mainly below canopy where crowns of shrub hardwoods, most foliage of tree hardwoods and epiphytes found (McLean 1912; McKenzie 1949, 1951; Hay 1981; Best & Bellingham 1991; Heather & Robertson 1997; Overdyck 1999; CSN 31). Rarely feed on ground or among leaf-litter (McLean 1912; McKenzie 1951; HJNC 1975; Clout & Hay 1981; CSN 28). At Pikiariki, in 1978–81, most foraging on shrub hardwoods (41% of foraging obs.) with rest on podocarps (17.8%), invertebrates (15.9%), epiphytes (12.2%), lianes (7.1%), tree hardwoods (4.3%), Tawa *Beilschmiedia tawa* (1.2%) and tree-ferns (0.2%); shrub hardwoods, epiphytes and lianes used for food at greater frequencies than their abundance in the habitat, while podocarps, Tawa and tree-ferns used less. However, importance of podocarps and Tawa as food sources increases when epiphytes and lianes are included with their host trees. Only 0.2% of movement observations on ground (Hay 1981). At Puketi in 1982–84, foraged mostly from shrub hardwoods (34.5%) and epiphytes (28.4%) with rest on tree hardwoods (11.8%), podocarps (10.0%), lianes (5.9%) and Nikau Palm *Rhopalostylis sapida* (5.9%). Importance of tree hardwoods increases greatly when records for epiphyte, liane, and invertebrate species are placed with their hosts; 70% of epiphyte foods were from tree hardwoods, and 19% from podocarps, with only 5% from shrub hardwoods. Most liane (59%) and invertebrate (79%) foods were taken from tree hardwoods, especially Kohekohe *Dysoxylum spectabile* (20%), Towai *Weinmannia silvicola* (15%) and Taraire *Beilschmiedia tarairi* (11%) for lianes, and Towai (38%), Taraire (21%) and Tawa (16%) for invertebrates. Foraging on ground occurred in winter and spring (0.1–3.9% of foraging obs./season) and (0.5%) in early and mid- to late summer 1982–84; more frequent (4.8% in one territory) in winter 1983 after unripe fruits shaken from canopy in storm. However, median foraging heights were lowest in summer, when much of diet came from lianes and shrub hardwoods, and were highest in winter 1984 when feeding on epiphytes in emergents (Best & Bellingham 1991). FORAGING METHODS AND FOOD-HANDLING: Insects gleaned from bark or foliage (McLean 1912; Moorhouse 1996). In one 20-min bout at Pureora, pair removed 60 compound leaves of Pate *Schefflera digitata* from one tree to glean Sixpenny Scale Insect *Ctenochiton viridis* (Clout & Hay 1989). Often observed probing moss, either to obtain food (e.g. moss capsules, insects, *Polypodium* rhizomes) or water, or possibly both (McLean 1912; McKenzie 1951; St Paul 1966; St Paul & McKenzie 1974). Rarely, turn leaf-litter with feet or bill (McLean 1912; HJNC 1975). Often forage by holding food in one foot, parrot-fashion, resting that leg on a branch and bending the head down to foot to eat (McKenzie 1949; Turbott 1967; Hay 1981; Powlesland 1987; Oliver); this requires a stable feeding platform, explaining why branches used more than twigs as eating perches, even though more food obtained from twigs (Powlesland 1987). Eat Casemoths (*Liothula*) by holding in one foot and squeezing down case with bill, like toothpaste (Hay et al. 1985a). Strip pericarp off fruits >1 cm in diameter (e.g. Tawa, Puriri *Vitex lucens*, Taraire) but swallow smaller fruits (including Kareao Supplejack *Ripogonum scandens*, Pigeonwood *Hedycarya arborea*) whole (Clout & Hay 1989). SEASONAL AND ANNUAL VARIATION: Types and species of food eaten, and frequency with which food obtained from different classes of vegetation, vary markedly annually, seasonally, and between different territories in same season and year (Best & Bellingham 1991). Reliance on leaf material highest in

winter and spring, while fruit dominates diet when available in autumn and early winter. Insects taken primarily in late spring and summer, especially when feeding young (St Paul 1966; Hay 1981; Hay et al. 1985a; Powlesland 1987; Best & Bellingham 1991; Heather & Robertson 1997). Large differences in importance of all food groups from year to year, e.g. Matai *Prumnopitys taxifolia* comprised 18% of foliage in Pikiariki study area but ranged from 1% to 80% of foraging observations in different years (Hay 1981; Hay et al. 1985a). At Puketi in 1982–84, foraging activity greatest in colder parts of year (38–47% of activities in June–Sept., when air temperatures low, daylight hours restricted, and available foods limited) and least in summer (16–21%) (Best & Bellingham 1991). At Hunua, mean diurnal time allocated to foraging by breeding males 6.4% in summer and 27.4% winter; and by breeding females 12.3% summer and 33.5% winter (Overdyck 1999). FORAGING ADAPTATIONS: Bill rather thick with two ridges separated by a deep groove, with a rough, file-like surface for grasping leaves and berries (McCann 1964); ridges probably also used for chewing leaves, particularly finely ground leaf that is fed to chicks (I. Flux). DRINKING: Drink in typical passerine fashion from drops adhering to foliage, or by ripping holes in the bases of leaves of Kahakaha *Collospermum hastatum* to release trapped water (Best & Bellingham 1991). May probe mosses to obtain water (McKenzie 1951; St Paul 1966; St Paul & McKenzie 1974).

Table 1. Proportion of main components of diet at Pikiariki, Rotoehu and Mapara, Waikato–Bay of Plenty (Hay 1981); and at Puketi, Northland, 1981–82 (Powlesland 1987). (Powlesland separated epiphytes from other sources of leaves and fruit, whereas Hay aggregated them in these data.)

Years	Pikiariki 1978–81	Rotoehu 1978–81	Mapara 1978–81	Puketi 1981–82
N (total feeding obs)	2616	749	1598	1586
MAIN COMPONENTS OF DIET				
Plant material				
Fruit	38	36	43	44
Leaves	37	19	25	15
Flowers	1	3	1	1
Buds	1	1	1	2
Epiphytes	–	–	–	11
Nectar	–	–	–	1
Invertebrates	13	7	8	8
Unknown	10	34	22	18

Detailed studies At PIKIARIKI, PUREORA, 1978–81 (2616 direct obs. of feeding, undertaken by sampling behaviour at 1-min intervals; therefore, total obs. equals total feeding time [2616 min]; presented data only for 14, of 81, foods that contributed >10% of diet obs. in any season; other foods [<10% obs.] in Other records below; Hay 1981): **Plants** FILICOPHYTES: Aspleniaceae: *Asplenium flaccidum* lvs 2.6% total foraging time; Polypodiaceae: *Polypodium (Phymatodes) diversifolium* lvs 2.9. GYMNOSPERMS: Podocarpaceae *Prumnopitys taxifolia* lvs 4.1, fru. 6.5; *Dacrydium cupressinum* lvs 2.9. DICOTYLEDONS: Araliaceae: *Pseudopanax arboreus* fru. 8.1; *P. crassifolius* fru 1.5; *P. edgerleyi* fru 4.6; Grossulariaceae: *Carpodetus serratus* lvs 3.2; Icacinaceae: *Pennantia corymbosa* lvs 1.9; Oleaceae: *Nestegis cunninghamii* fru. 1.3; Polygonaceae: *Muehlenbeckia* lvs 1.4; Ripogonaceae: *Ripogonum scandens* fru. 1.6. **Animals** INSECTS: Coccidae: *Ctenochiton viridis* 13.7.

At ROTOEHU, BAY OF PLENTY, 1978–81 (749 direct obs. of feeding, undertaken by sampling behaviour at 1-min intervals; therefore, total obs equals total feeding time [749 min]; presented data for 15, of 42, foods that contributed >10% of diet

obs. in any season; other foods [<10% obs.] in Other records below; Hay 1981): **Plants** BRYOPHYTES: Moss 3.1% of total foraging time. FILICOPHYTES: Polypodiaceae: *Polypodium (Phymatodes) diversifolium* lvs 3.2. DICOTYLEDONS: Cornaceae: *Griselinia littoralis* fru. 3.8; Lauraceae: *Beilschmiedia tawa* fru. 11.5; *Laurelia novae-zelandiae* lvs 1.6; Meliaceae: *Dysoxylum spectabile* buds 1.4, fru. 1.9; Monimiaceae: *Hedycarya arborea* fru 1.5; Piperaceae: *Macropiper excelsum* fru. 4.5; Proteaceae: *Knightia excelsa* fl. 4.4, fru 2.8; Ripogonaceae: *Ripogonum scandens* lvs 1.8; Violaceae: *Melicytus ramiflorus* fru. 3.2. **Animals** INSECTS: Hemiptera: Coccidae: *Ctenochiton viridis* 2.1; Lepidoptera: Psychidae: *Liothula omnivora* 3.7.

At MAPARA, WAIKATO, 1978–81 (1598 direct obs. of feeding, undertaken by sampling behaviour at 1-min intervals; therefore, total obs. equals total feeding time [1598 min]; presented data for ten, of 54 foods that contributed >10% of diet obs. in any season; other foods [<10% obs.] in Other records below; Hay 1981): **Plants** BRYOPHYTES: Moss 3.1% of total foraging time. FILICOPHYTES: Polypodiaceae: *Polypodium (Phymatodes) diversifolium* lvs 3.2. DICOTYLEDONS: Cornaceae: Lauraceae: *Beilschmiedia tawa* fru. 8.5; Monimiaceae: *Hedycarya arborea* fru 7.7, lvs 2.0; Passifloraceae: *Tetrapathaea tetrandra* lvs 3.4; Ripogonaceae: *Ripogonum scandens* lvs 6.4, fru. 14.6; Violaceae: *Melicytus ramiflorus* lvs 3.5, fl. 1.2, fru. 2.4. **Animals** INSECTS: Lepidoptera: Psychidae: *Liothula omnivora* 3.7.

At PUKETI, NORTHLAND, 1982–84 (7428 foraging obs. [from 23,236 obs. activity] undertaken at 1-min intervals as above, i.e. for 7428 min; presented data for 15, of 85, species that contributed >2% to diet overall; other foods [<2% of obs.] in Other records below; Best & Bellingham 1991): **Plants** BRYOPHYTES: Moss lvs, capsules 3.5% of total foraging time. FILICOPHYTES: Aspleniaceae: *Asplenium flaccidum* lvs 6.6; Polypodiaceae: *Polypodium (Phymatodes) diversifolium* lvs 4.3. GYMNOSPERMS: Podocarpaceae: *Podocarpus hallii* fru., leaf buds 6. DICOTYLEDONS: Araliaceae: *Pseudopanax arboreus* fru., flower, lvs, bark 4.6; Arecaceae: *Rhopalostylis sapida* fru., lvs 5.9; Asteraceae: *Olearia rani* fru., fl. buds, lvs, petiole, leaf buds 7.3; Cornaceae: *Griselinia lucida* fru., fl. buds, lvs, leaf buds 5.3; Loganiaceae: *Geniostoma rupestre* var. *ligustrifolium* fru., fl., fl. buds, lvs, leaf buds 2.3; Myrsinaceae: *Myrsine australis* fru., fl. buds, lvs 2.4; Pittosporaceae: *Pittosporum tenuifolium* fru., lvs 2.6; Ripogonaceae: *Ripogonum scandens* fru., fl., fl. bud, lvs 3.9; Rubiaceae: *Coprosma grandifolia* fru., fl., lvs, leaf buds, bark, dead material, exudate 5.3; Verbenaceae: *Vitex lucens* fru., fl., nectar 5.7. **Animals** INSECTS: Lepidoptera: Psychidae: *Liothula omnivora* 2.4.

At HUNUA (S. AUCKLAND), 1997–98 (4038 obs. foraging; obs. made at 30-sec intervals cf. 1 min above; nine, of 69, foods [some species aggregated] that contributed >4% of diet overall; other foods [<4% obs.] included in Other records below; Overdyck 1999): **Plants** FILICOPHYTES: Hymenophyllaceae: *Hymenophyllum* and *Trichomanes* 4.1. DICOTYLEDONS: Araliaceae: *Schefflera digitata* 4.3; Cornaceae: *Griselinia* 4.7; Lauraceae: *Beilschmiedia tawa* fru. 10.0; Grossulariaceae: *Carpodetus serratus* 7.1; Monimiaceae: *Hedycarya arborea* 9.9; Myrsinaceae: *Myrsine salicina* 5.8; Rubiaceae: *Coprosma grandifolia* 18.4; Ripogonaceae: *Ripogonum scandens* 6.8.

Other records (All NI) **Plants** (Where type of plant material [e.g. lvs, fru.] not given, source listed plant species as food without stating what was eaten.) Leaves, fruit, buds, flowers, nectar, ferns, moss, lichens[7,9,11,12,14,16]. LICHENS[9,12,16]. BRYOPHYTES[5,11,18], including moss capsules[24]. FERNS: Leaves[17,21]; Aspleniaceae: *Asplenium*[16]; *Asplenium falcatum*[9]; *A. bulbiferum* lvs[12]; *A. flaccidum* lvs[11,21]; *A. oblongifolium* lvs[12]; *A. polyodon*[12]; Blechnaceae: *Blechnum*[9,12]; *B. filiforme* lvs[12]; Cyatheaceae: *Cyathea*[16]; *C. dealbata* lvs[9]; *C. smithii* lvs[9]; Dicksoniaceae: *Dicksonia*[16]; Grammitidaceae: *Ctenopteris heterophylla* lvs[12]; Hymenophyllaceae: *Hymenophyllum*[9,12,16]; *Trichomanes*[16];

Lycopodiaceae: *Lycopodium varium* lvs[12]; Polypodiaceae: *Anarthropteris lanceolata* lvs[12]; *Microsorium*[16]; *Phymatosorus pustulatus*[18]; *Polypodium (Phymatodes) diversifolium*[11], rhizomes[5]; *Pyrrosia eleagnifolia* lvs[12]; *P. serpens*[9]; Schizaeaceae: *Lygodium articulatum* lvs[12], sporangia[5]. GYMNOSPERMS: Podocarpaceae: *Dacrydium cupressinum*[16], lvs[9], fru.[12]; *Dacrycarpus dacrydioides* fru.[11,12], lvs.[9]; *Phyllocladus trichomanoides* fru.[11,12]; *Podocarpus* fru.[11]; *P. ferrugineus*[16], fru.[5,9,11]; *P. totara*[16], fru., lvs[9,12]; *Prumnopitys taxifolia*[16], buds, cones[9,12]. MONOCOTYLEDONS: Arecaceae: *Rhopalostylis sapida*[13,16], lvs, fru.[11]; Asteliaceae: *Astelia solandri*[16], fru., fl., lvs, petioles[12]; Cyperaceae: *Gahnia pauciflora*[12]; *Uncinia*[12], lvs[12]; Liliaceae: *Collospermum hastatum*[16], fru.[9,11,12], lvs[12]; *Cordyline banksii* fru.[11]; Orchidaceae: *Bulbophyllum*[9]; *B. pygmaeum* lvs[12]; *Dendrobium cunninghamii*[16], fl.[11], fl. buds, stems[12], lvs[11,12]; *Drymoanthus adversus* lvs[12]; *Earina autumnalis* lvs, fru.[9,11,12], fl., petioles, stems[12]; *E. mucronata*[16], lvs[9,11,12], buds[11], fl.[9,12], fl. buds, stems[12]; Pandanaceae: *Freycinetia baueriana*[16], fru.[11], fl.[11,12], lvs, stems, bark, dead material[12]. DICOTYLEDONS: 'Thistles'[6,17]; Alseuosmiaceae: *Alseuosmia macrophylla* fru.[11], lvs[11,12]; *A. pusilla*[16]; Apocynaceae: *Parsonsia albiflora* fru.[6]; *P. heterophylla* fru.[17], lvs, fl.[9]; Araliaceae: *Pseudopanax arboreus*[13,16], lvs[9,11], fl.[9]; *P. crassifolius*[16], fru.[2,11,12,14], lvs[12]; *P. edgerleyi*[16], lvs[9,11,12], buds[11], fl.[9], fl. buds[12], fru.[11,12]; *Schefflera digitata*[13,16], lvs, fru.[9,11,12], fl. buds, bark[12]; Asteraceae: *Brachyglottis repanda*[16], dead material[12]; *B. kirkii* lvs[12]; *Olearia*[16]; *O. rani*[13], lvs[11]; Chloranthaceae: *Ascarina lucida*[16]; Coriariaceae: *Coriaria arborea* fru.[17]; Cornaceae: *Griselinia littoralis*[16], lvs, buds[9]; *G. lucida* lvs[1,5,9,11], buds[11], fl.[9]; Cruciferae: *Brassica oleracea* lvs[6]; Cunoniaceae: *Ackama rosaefolia* fl.[12]; *Weinmannia* lvs[5]; *W. sylvicola* lvs[3,12], fl., fl. buds, petioles, leaf buds[12]; *W. racemosa* lvs, fru.[9]; Elaeocarpaceae: *Aristotelia serrata*[16], fru.[5,14], lvs[9,12]; *Elaeocarpus dentatus*[16], fl.[12], fru.[1,9,11,12], lvs[9,11,23]; Epacridaceae: *Cyathodes fasciculata* buds[11], fru.[11,12], lvs[12]; *Dracophyllum latifolium*[16], bark[12]; Escalloniaceae: *Carpodetus serratus* fru.[14]; *Quintinia serrata*[16]; *Ixerba brexioides* fl.[12]; Fabaceae[5,19]; Grossulariaceae: *Carpodetus serratus*[5,16], lvs[11], fl.[11], fru.[9]; Icacinaceae: *Pennantia corymbosa* fru.[9]; Lauraceae: *Beilschmiedia tawa*[13,16], fru.[2,11,12,24], lvs[4,5,9,12], fl.[9,12], dead material[12]; *B. tarairi*[16], buds[11,12], fru., fl., lvs[12]; *Laurelia novae-zelandiae* lvs[16]; *Litsea calicaris* lvs, fru.[9,12]; Loganiaceae: *Geniostoma rupestre* var. *ligustrifolium*[16], fru.[9]; Meliaceae: *Dysoxylum spectabile*[24], lvs[9,12], fru.[11,12], fl., petiole[12]; Monimiaceae: *Hedycarya arborea*[13,16], lvs[9,12], fru.[5,9,12], leaf buds[12]; Myrsinaceae: *Myrsine australis*[13], lvs[5,11], fru.[9,11]; *M. salicina*, lvs[5,12], fru.[11,12]; Myrtaceae: *Lophomyrtus bullata*[16], fru.[12]; *Metrosideros*[16]; *M. diffusa* lvs[9,12]; *M. perforata* lvs[5,12], fl.[13]; *M. robusta* fl.[12]; Oleaceae: *Nestegis cunninghamii* lvs[9]; *N. lanceolata* lvs, leaf buds[12]; *N. montana* lvs[12]; Onagraceae: *Fuchsia excorticata* fru.[6,8,9,12], lvs[3,9,12], fl.[9,12], buds[9]; Passifloraceae: *Tetrapathaea tetrandra*[16], fru.[9]; Piperaceae: *Macropiper excelsum*[16], fru.[9]; Pittosporaceae: *Pittosporum colensoi* fru., lvs[9]; *P. cornifolium* fru.[11,12], fl., lvs[12]; *P. eugenioides* fru.[2,9]; *P. tenuifolium* lvs, fru.[11]; *P. virgatum* lvs[12]; Proteaceae: *Knightia excelsa*[13,16], fru.[12], fl.[11,12], lvs[9], nectar[11]; *Toronia toru* fl., fru.[12]; Ranunculaceae: *Clematis*[16], lvs[9]; *C. indivisa* fl.[6]; *C. paniculata* lvs[9,11,12], fru., fl., fl. buds, petioles[12]; Smilacaceae: *Ripogonum scandens*[13,16], fru.[1,5,6,8,11,14,22,24], lvs[11], fl.[9]; Rosaceae: *Rubus* lvs, fru.[9,16]; *R. australis*[6], fru., lvs[12]; *R. cissoides*[14], fru.[8,12,17]; Rubiaceae: *Coprosma* lvs[8]; *C. arborea* fru., lvs[12]; *C. grandifolia*[13,16], fru.[1,5,9,11,20], lvs[5,9,11], buds[11], fl.[9,11]; *C. lucida* lvs[1]; *C. parviflora* lvs[12]; *C. spathulata* fru.[11], lvs[12]; *Nertera depressa*[16]; Santalaceae: *Mida salicifolia* fru.[11], lvs[12]; Sapindaceae: *Alectryon excelsus* lvs, fru.[9]; Scrophulariaceae: *Hebe stricta*[16]; Verbenaceae: *Vitex lucens*[16], nectar[11], fl.[9], fru.[9,11]; Violaceae: *Melicytus lanceolatus*[21], lvs[3], fru.[20]; *M. macrophyllus* lvs, fru.[11,12]; *M. micranthus* lvs[12]; *M. ramiflorus*[16], lvs[11,12], fru.[12], buds[9]; Winteraceae: *Pseudowintera axillaris*[16]; *P. colorata*[10], fru.[9]. **Animals** MOLLUSCS: Slugs[9]. SPIDERS: Spider eggs[12]. INSECTS[1,6,8,12,14,15,17]: Hemiptera: Cicadidae[7]: *Amphipsalta zealandica*[9]; Coccidae[14]: *Ctenochiton*

viridis[11]; Lepidoptera: Psychidae: *Liothula omnivora*[11]; Mantodea: Praying mantis[9]; Tortricidae[11]; Orthoptera: Stenopelmatidae: *Deinacrida megacephala*[1]; unident. cocoon[12]; unident. larv.[12].

REFERENCES: [1] McLean 1912; [2] McKenzie 1949; [3] Hamerton 1959; [4] St Paul 1963, [5] St Paul 1966; [6] Turbott 1967; [7] HJNC 1975; [8] Falla *et al.* 1981; [9] Hay 1981; [10] Norton 1982; Powlesland [11] 1987; [12] Best & Bellingham 1991; [13] Greene 1995; [14] Innes & Hay 1995; [15] Heather & Robertson 1997; [16] Overdyck 1999; [17] Oliver; [18] NZRD; CSN [19] 4, [20] 24, [21] 25, [22] 26, [23] 29, [24] 31; [25] I. Flux & P. Bradfield.

Young Nestlings and fledgelings fed by both parents; parents come to nest alone or together (see Breeding: Young, Fledging to independence, and below). NESTLINGS: Claim that female regurgitates food on nest (HJNC 1975) needs confirmation, as previously unreported for passerines. Food carried in bill and upper throat or crop, with a prominent bulge often apparent (McKenzie 1951; HJNC 1975; Innes & Hay 1995); food loads usually comprise 2–4 berries, often supplemented with chewed leaves or insects, but can consist entirely of berries or chewed leaf (McKenzie 1951; Innes & Hay 1995). Food may be delivered to a single chick or divided among brood (McKenzie 1951; Innes & Hay 1995; Oliver); and chicks fed more per hour and day as they approached fledging (Innes & Hay 1995). At MAPARA, throughout incubation and early brooding periods (Weeks 1–3 of nesting period [starting from laying first egg]) male made only brief visits, lasting seconds, to feed female at or near nest, interspersed with absences of 32 min (2–82; 34); in Weeks 4–5, males visited more often, feeding both female and nestlings, with mean interval between visits of 18 min (n=40), and females spent progressively more time off nest. Late in nesting cycle (Week 6 onwards), parents tended to forage and return to nest together, with mean interval between visits 21 min (n=34) for males and 24 min (n=21) for females (I. Flux & P. Bradfield). At a single nest at PUREORA, first chick-feeding visit by female to be followed by leaving nest rather than staying to brood occurred 5 days after hatching; thereafter, mean rate at which female visited to feed chicks increased rapidly and peaked 5 days before chicks fledged at mean 3.7 visits per hour; visiting rate of male remained constant throughout, at mean interval of 37 min, or 1.6 visits/h (0.7–2.2; 24); in month before fledging 25% (7–54%) of feeding visits were by both parents together (Innes & Hay 1995: see Fig. 3). At COROMANDEL, 9 days before fledging, adults made mean 3.75 visits to nest per h with a mean visit duration of 16 min (1–35; 35); by 5 days before fledging, number of visits increased to 4.1/h and mean duration decreased to 14.7 min (1–46; 58) (Innes & Hay 1995). At a single nest in MOUMOUKAI RAS, E of Auckland, interval between feeds decreased from a mean of 32 min (15–40) 9 days before fledging, to 11 min (1–26) on day chicks first left nest; overall, chicks fed every 25–30 min, with feeding rates fastest in morning and slowing considerably in afternoon before increasing again in evening; in final days of observation, when intervals short, much food collected from within a few metres of nest (McKenzie 1951). For details of interval between visits to nest and brooding by females, see Breeding (Young: Brooding). FLEDGELINGS: Also fed by both parents; at first, almost all food provided by parents and fledgelings often return to nest to be fed; young gradually move farther away from nest as they get older (Hay *et al.* 1985a; I. Flux & P. Bradfield; also see Breeding: Fledging to independence). Fledgelings sample a variety of foods and non-foods (dead twigs, unripe fruit, etc.), holding them in their bills before accepting or rejecting item. Timing of foraging independence little known but appears to vary greatly; said usually to forage independently 3 weeks after fledging (Hay *et al.* 1985a; I. Flux & P. Bradfield). Independently foraging

juveniles may however remain in parents' territory for some months (Hay 1981; Innes & Flux 1999; Flux & Innes 2001a; I. Flux & P. Bradfield). May also continue to receive some food from adults for up to 1 year or young may be ejected from natal territories immediately after fledging, and presumably forage independently at this age (Hay 1981; Innes & Hay 1995; Heather & Robertson 1997; Innes & Flux 1999; Flux & Innes 2001a; I. Flux & P. Bradfield).

No detailed studies. **Plants** Unident. fruit[2,4], unident. leaves[4], unident. rhizomes[1]. MOSS: Unident.[4,6]. FERNS: Unident.[6]; Dicksoniaceae: *Dicksonia*[4,6]; Lycopodiaceae: rhizomes[1]. DICOTYLEDONS: Araliaceae: *Pseudopanax edgerleyi* lvs[5]; Coriariaceae: *Coriaria* fru.[1]; Monimiaceae: *Hedycarya arborea* fru., lvs[1]; Myrsinaceae: *Myrsine salicina* lvs[5]; Ripogonaceae: *Ripogonum scandens* fru.[1]; Rubiaceae: *Coprosma grandifolia* fru.[1]; Violaceae: *Melicytus ramiflorus* lvs[5]. **Animals** SPIDERS[4]. INSECTS: Coccidae: *Ctenochiton viridis*[3,4]; Coleoptera: Curculionidae: unident. larv.[4]; weevils[4]; Hemiptera: Cicadidae: cicada[4]; Diptera: fly larv.[4]; Lepidoptera: unident. larv.[4]; Psychidae: Bag Moth[4].

REFERENCES: [1] McKenzie 1951; [2] HJNC 1975; [3] Powlesland 1987; [4] Innes & Hay 1995; [5] CSN 2; [6] I. Flux.

SOCIAL ORGANIZATION Based on contribution by J.G. Innes and I. Flux. Subspecies *wilsoni* of NI well known, nominate of SI very poorly known; detailed studies of territoriality, in central NI (Hay 1981) and, with banded birds, at most remaining populations on mainland, especially Mapara, Waikato (I. Flux & P. Bradfield; also Innes *et al.* 1996; McLeod 1998; Jones *et al.* 1999; Overdyck 1999) and on islands (Jones 2000; Rowe 2001; Brown *et al.* 2004). Roosting studied in Rotoehu SF, near Rotorua, using six birds fitted with radio-transmitters (Shorten & Brown 1992). Following from NI unless stated. Both pairs and singles defend exclusive territories year-round. Young (up to three) may remain with parents for up to 1 year, and non-territorial subadults and adults sometimes gather and move in small groups and interact with unrelated territorial adults (I. Flux & P. Bradfield), e.g. at Mapara, groups of 2–7 (I. Flux & P. Bradfield) and parties of 4–7 in Apr.–May 1906 in Mangamaia Valley, East Coast (McLean 1912). The meeting of two such groups probably explains rare reports of parties of up to 15 (McLean 1912; McKenzie 1949; Hatch 1979; CSN 3, 9), e.g. 15 near Rerepahupahu Falls, Taranaki–Wanganui, May 1955, and 12 near Motu, Raukumara Ra., 1959 (MacDonald 1966). On SI, said usually in pairs (Travers 1871; Potts 1873; Reischek 1885b). Food plants widely dispersed, so do not flock to locally abundant food sources (Hay *et al.* 1985a), but groups occasionally reported (see Social Organization)

Bonds Apparently monogamous; pair-bonds maintained throughout year and sometimes for several years, though tenacity of pairing varies individually. Members of pair usually found close to each other, often feeding together and duetting (Williams 1976; Hay *et al.* 1985a; Shorten & Brown 1992; Innes & Hay 1995). Do not pair for life, as sometimes suggested in older literature (e.g. Williams 1976). Courtship behaviour, including allopreening and courtship feeding, occurs throughout year (I. Flux & P. Bradfield; see Social Behaviour). DURATION OF PAIR-BOND, AND DIVORCE: At Mapara, between 1990 and 2000, 7.4% of pairs split each year for reasons other than death of previous partner; from detailed observations of many colour-banded birds, 1989–2001, lowest fidelity shown by one female that paired with four males in 5 years. New pairs formed in the previous territory of either male or female (I. Flux & P. Bradfield). Over 4 years at Rotoehu, 1989–93, 21 (48%) of pairs monitored in any breeding season were intact the following year, and 19 (43%) had split; no pair remained intact for duration of the study. Both

males and females either moved to new mate or disappeared; and no females were left as singles, though males were on seven occasions, suggesting overall male excess (Innes *et al.* 1996). In Te Urewera, no known banded pair stayed together for >3 years; in one season, one female had three partners (J.D. Hudson). Pair-bonds often break when pairs translocated to off-shore islands (I. Flux & P. Bradfield). Adults from different source populations, with different Song dialects, translocated to Kapiti I. initially formed pairs with mates singing same dialect (Brown *et al.* 2004). However, females bred on Kapiti did not choose mates with syllable repertoires similar to their father's, indicating that female Song-preference develops during transient months after fledging. Males born on Kapiti learn their syllable repertoires from neighbours after establishment of territory. This suggests that same-source mating will not continue after juvenile recruitment (Rowe 2001; also see Voice). MALE–MALE PAIRS: Most common in declining, unmanaged populations with strongly male-biased sex-ratio, e.g. in Mapara population, when pest control began in 1989, only four of 15 territorial pairs were male–female (Innes *et al.* 1999). However, some Kokako form male–male pairs even in presence of females (Innes & Flux 1999). Male–female pairs, male–male pairs perform Archangel Display and duets, courtship-feed, build nests and, rarely, sit (McLeod 1998; Flux & Innes 2001a; I. Flux & P. Bradfield). Male–male pairs at Mapara seen to build two nests; one was normally constructed, and pair sat on completed nest for several days after its completion, though sittings brief (<10 min) and erratic (I. Flux & P. Bradfield). In Hunua Ras, 1998–99, male–male pairs tended to duet for longer than male–female pairs (Overdyck 1999). AGE OF FIRST BREEDING: At Mapara, of 17 female recruits for which age at first breeding is known, ten (59%) bred aged 1 year and the remaining seven (41%) bred at 2 yrs (Basse *et al.* 2003). **Parental care** Only females brood, though both parents feed and attend nestlings, and remove faecal sacs (see Food, Breeding for details). Fledgelings also fed by both parents, with almost all food provided by parents at first. Timing of foraging independence and natal dispersal little known and appear to vary greatly; dispersal from natal territories ranges from 1–3 weeks after fledging up to 1 year; young seem to forage independently by *c.* 3 weeks, presumably earlier if natal dispersal is earlier (see Food: Young, Breeding: Fledging to independence; see below). DISPERSAL OF YOUNG: Fledged young typically remain in parental territories for several months, usually 4 (Hay *et al.* 1985a; Meenken *et al.* 1994; Heather & Robertson 1997; Innes & Flux 1999; Innes *et al.* 1999). However, young may be ejected from parental territory immediately after fledging (within 1 week) (Innes & Flux 1999); or remain in natal territory for up to 1 year, until following breeding season (Innes & Hay 1995; Heather & Robertson 1997; Innes & Flux 1999; Oliver). In central NI, when adults raised two broods, fledgelings from first brood always left natal territories before second brood fledged (Innes *et al.* 1999). Young also reported to remain with parents till next breeding season on SI (Reischek 1885b). Average distance between nest and place of final settlement of young: at Rotoehu, 1270 m (max. 2770; n=20) (J.G. Innes); at Mapara, 2040 m (max. 5410; n=82) (I. Flux & P. Bradfield); at Otamatuna, Te Urewera NP, 1400 m (max. 4650; n=47) (J.D. Hudson, G. Jones & C. Thyne). However, total movements before settlement probably far greater than final net distances above; at Mapara, one radio-tagged juvenile moved at least 20.2 km between Sept. 1992 and Mar. 1993 (I. Flux & P. Bradfield); and at Otamatuna, subadults ranged widely before settling adjacent to existing territories of other Kokako (J.D. Hudson, G. Jones & C. Thyne). Subadult females dispersed farther than males at all sites (references as above).

Breeding dispersion Nest solitarily, within exclusive defended territories (Innes & Hay 1995; Hay *et al.* 1985a; I. Flux & P. Bradfield). **Territories** Both paired and single adults maintain type-A territories year-round, in which all resources obtained (Williams 1976; Hay *et al.* 1985a; Best & Bellingham 1991; Innes & Hay 1995; see Social Behaviour: Agonistic behaviour). Territories must therefore be large enough to contain wide diversity of food species to provide sustenance throughout the year, and more than enough food at any one time of year to accommodate irregular production of many seasonal foods, such as fruits, flowers, buds and invertebrates (Best & Bellingham 1991). Frequent switches of mates and movements between territories revealed after many Kokako banded (see Bonds). At Mapara, 1999–2000, after divorce, new pairs occupied previous territory of either male or female (I. Flux & P. Bradfield). At Rotoehu, 1989–94, pairs that stayed together for more than one season (n=13) always occupied virtually same territory each year; five pairs had territories in same location for 3 consecutive years (Innes *et al.* 1996). Unpaired territory-holders mostly male, especially in declining populations, since females are killed by predators on nests, creating male excess (Innes *et al.* 1999). At Rotoehu, 1989–94, of 13 territorial Kokako that were single for at least 30 days, 11 were definitely (by nesting behaviour) or probably (by leg measurement [Flux & Innes 2001a]) males (Innes *et al.* 1996). SIZE AND USE OF TERRITORIES: Usually 7–14 ha in area. At Rotoehu, Bay of Plenty, 9–14 ha; at Mapara, 4–12 ha (Hay 1981; Innes *et al.* 1996; Innes & Flux 1999); and at Puketi, 3.8–7.4 ha (Best & Bellingham 1991). Territories can persist for years (Hay *et al.* 1985a; Powlesland 1987; Innes & Hay 1995; Innes & Flux 1999; I. Flux & P. Bradfield). Territories may also be held by single males, male–male pairs, and briefly by single females (McLeod 1998; I. Flux & P. Bradfield). Size of territory apparently inversely related to density: in high-density populations where pests managed, such as Mapara, territories often smaller, to 4 ha (I. Flux); and in one sparse, declining population in Taranaki, territories of some unbanded birds estimated to be 80 ha (Williams 1990). In steeply dissected terrain, territories often concentrated on crests of ridges (Williams 1990; Jones *et al.* 1999). Not all parts of territories used equally; in Puketi, activity concentrated in territory centres at some territories but not others; different parts of territory used in different seasons, depending on availability of food and weather, with used area smaller in summer–autumn and larger in late winter to early spring (Best & Bellingham 1991). RESPONSE TO PLAYBACK: Territoriality and response of Kokako to playback used for surveys, which were pioneered by Crook *et al.* (1971) and later much refined (Hay 1981; Flux & Innes 2001a). 'Walk-through' surveys determine distribution and approximate density in very large forest areas, with observers traversing ridges and compass routes, playing recorded tape at intervals, and visiting each location only once. 'Territory mapping' requires repeat visits to map movements of pairs and singles in their territories. 'Roll-calls' are repeated visits (usually weekly) to a particular group of territories to verify that all occupants have survived a pest control operation, usually aerial poisoning.

Roosting Pairs roost together within territory, though site of roost may change regularly, e.g. in Rotoehu SF, Jan.–Mar. 1991, one pair roosted in at least nine different places within territory over 9 weeks (Shorten & Brown 1992). Nesting females roost at nest at night (Shorten & Brown 1992; Innes & Hay 1995; I. Flux & P. Bradfield) with male partners roosting near nest (once *c.* 50 m from nest). Adults roost close to their dependent fledgelings, usually within 20–30 m. Appear to roost near top of tall trees. Some birds were seen to move up to 50 m from night roost before starting dawn chorus (Shorten & Brown 1992). During Dec. 1973, Moumoukai, Auckland, calls first heard at 04:45 (sunrise at 04:56) with no calls heard after 07:15 (CSN 21).

SOCIAL BEHAVIOUR Based on contribution by J.G Innes and I. Flux. No focused studies of most aspects but reasonably well known from thousands of hours of field observation undertaken as part of detailed studies of other aspects of biology (see Food, Social Organization, Breeding, and references to detailed studies therein). Few obvious ritualized displays. **Maintenance behaviour** Bathe by repeatedly wetting plumage with brief immersion in standing water or by splashing water over body by flapping wings (Best & Bellingham 1991). A nesting female left nest to bathe in nearby creek, returned quite wet and shook feathers before sitting back on nest; returned to creek to bathe later in day (St Paul 1963). At Puketi in 1982–84, daytime resting and self-preening noted throughout year but more time spent in these activities in summer, when birds moulting; often preened for 20–30 min throughout year. Birds often rested after they had been feeding intensively for 10–20 min or more (Best & Bellingham 1991). For details of allopreening, see Courtship behaviour, though members of pair also allopreen during confrontations with other Kokako (see Agonistic behaviour).

   Agonistic behaviour Territories advertised and defended by Song, and agonistic interactions at boundaries (Williams 1976; Hay 1981; Hay *et al.* 1985a; Best & Bellingham 1991; Innes & Hay 1995; McLeod 1998; Hudson 2001). Both males and females advertise ownership of territories by singing from tall trees in visually conspicuous locations, usually with head erect and wings slowly flapping, touching behind back (Colbourne 1986; Innes & Hay 1995; see Voice: Non-vocal sounds). However, in close boundary interactions, when pairs can see each other, birds do not normally give Song but instead use softer Took vocalizations and occasionally other song-type vocalizations (L.E. Molles; see below; also see Voice). **Threat, Chases** Aggressive interactions at territorial boundaries consist of series of chases accompanied by Took vocalizations and vigorous wing-beats; chases may continue for several minutes, with birds seesawing back and forth across territorial boundary. Interactions usually involve two pairs or single birds, though sometimes three pairs or singles involved (Hay 1981). In response to playback of calls, one bird either ran or hopped quickly through understorey, or flew with laboured flapping to nearest perch, c. 10 m from tape-recorder. It then puffed itself up and broke into a chorus of chattering and Song accompanied by wing-beating, synchronizing calls with those on tape (Colbourne 1986). Members of pair allopreen often during confrontations with other Kokako (I. Flux & P. Bradfield). **Attack, Fighting** Territorial disputes occasionally end in fights, in which birds seen to grapple on ground and peck at each other's wattles (Hay *et al.* 1985a). Once, in response to playback, probably at territorial boundary, two pairs responded, all birds quietly mewing and chirring and moving about quickly for c. 30 s. Of the four, two (gender unknown) then began to fight; one called in distress and, with much flapping, both birds fell some 10 m to ground, locked together and seemingly using bills, wings and feet to fight, though one seemed to use wings to slow their descent to ground; though they landed c. 2 m from where observer stood, they continued fighting on the ground for 5 s before parting and leaping up through understorey (Saunders 1980). Three similar fights also induced by tape playback when neighbouring pairs or families gathered in one or another bird's territory (which occurs only in non-breeding periods); on playback of vocalizations of visiting bird, territory-owner attacked visitor in same manner as above (J.D. Hudson). On SI, males said to be very pugnacious, fighting wherever they meet (Travers 1871). **Alarm** Give soft Took vocalizations in response to mild disturbances such as by human observer and also may scream in alarm, such as when netted or handled (see Voice). (For interactions with predators and people at nests, see Relations within family group.) Generally ignore other forest birds, except for predators; often freeze in dense cover when Swamp Harriers pass, and always vacate nests without contest during Harrier predation (L.E. Molles, J. Innes, I Flux).

   Sexual behaviour Courtship ARCHANGEL DISPLAY: During pre-breeding period assumed male raises wings and moves rapidly about in tree close to mate, often with some vegetation in its bill (Flux & Innes 2001a); also described as male displaying to female by spreading wings and tail and stretching out neck, while moving like dancing, sometimes accompanied by Chirr (Turbott 1967; Williams 1976; Hay 1981; Innes & Hay 1995). Similar behaviour described for SI, with male making 'extraordinary evolutions (sic) before the female, similar to the European wood grouse' and 'bows his head, spreads his wings, and erects and spreads his tail, making at the same time a gurgling noise' (Reischek 1885a). In related Saddlebacks *Philesturnus carunculatus rufusater*, Archangel Display is ritualized pair-reinforcement ceremony that evolved from, and still functions as, a nest-invitation display; and is performed throughout year but mostly before and during breeding season, especially when new pair-bonds forming (Lovegrove 1980; see Saddleback account). **Maintenance of pair-bond** Pairs keep close to one another and, during nesting period, often seen to meet and touch bills, both at and away from nest (McLean 1912; HJNC 1975; Hay 1981; Overdyck 1999). Bonds continually reinforced by Songs, including Song Duets, Mew and Took calls, allopreening and courtship feeding (Hay 1981; Hay *et al.* 1985a; see Voice; see below). Members of pairs perform complex Song Duets in bouts that last for up to 30 min (Hay *et al.* 1985a; McLeod 1998; see Voice); members of pair regularly perch within a few metres of one another when singing in duets, sometimes in physical contact, but also duet while separated by tens of metres (Molles & Waas In press) and even while female on nest (Innes & Hay 1995). Members of pair maintain contact with low Mewing vocalization, which also used to call mate from a distance (hundreds of metres) and also with Took vocalization (McKenzie 1951; Maning 1960; see Voice). Male also seen to come to edge of nest and bend forward, and sitting female bent her head backward and vibrated feathers and body, with caress continuing for 10 s before male flew away; no food was passed to female (HJNC 1975). **Allopreening** Members of pair often preen round bases of each other's bills while perching side by side (Hay 1981); also allopreen often during confrontations with other Kokako (I. Flux & P. Bradfield). **Courtship feeding** Courtship feeding occurs throughout year but males appear to offer food to mates more often as breeding season approaches (Flux & Innes 2001b; I. Flux & P. Bradfield). Feeding may be ritualized, with items of food being passed back and forth between male and female. During breeding season, male feeds female on and away from nest (Williams 1976; Hay *et al.* 1985a; Innes & Hay 1995). When being fed by male, female flaps her wings slowly behind her back (Innes & Hay 1995); and pair members call softly, at least sometimes with Mewing calls (McKenzie 1953; CSN 26). Males usually feed females, though very occasionally females feed males (McKenzie 1953; Flux & Innes 2001b). **Copulation** Seen to take place in a tree; male mounted female with vigorous flapping of wings, uttering bubbling and clucking calls during copulation. Birds then flew round before returning to same perch and performing a courtship display, in which pair faced each other on branch and bowed to each other several times in quick succession. Birds then flew round again and perched in a tree where copulation occurred a second time, again with vigorous flapping of wings, this latter lasting c. 10–15 s. After copulation, they flew away (Lovegrove & Towle 1974).

   Relations within family group Only female broods; both parents feed nestlings and remove faecal sacs, with male also feeding female on nest; both parents also feed and attend fledgelings. For details of roles and attentiveness of parents in

brooding and feeding young, see Food (Young), and Breeding (Young, Fledging to independence). Female seen to 'spread her feathers and tail to protect the chicks from the rain and wind' (HJNC 1975). Male often gives soft Tooks or a single Mew nearby, and female would leave nest to join him (Innes & Hay 1995); male joins female when she leaves nest (St Paul 1963). At one Auckland nest, male approached nest secretively, pausing before moving directly to nest, particularly when watched by observer; and would often wait for female and approach nest with her (McKenzie 1951). At one Pureora nest, female approached hurriedly and less cautiously than male, often flying in without hesitation, but always very quiet when leaving nest (Innes & Hay 1995). There, and at a Te Kauri Park (Waikato) nest, both sexes gave Took vocalizations when feeding nestlings (HJNC 1975; Innes & Hay 1995; see Voice). Hughes (1981) noted that a female feeding chicks at a Coromandel nest often responded with 'soft song' before feeding. Nestlings usually quiet, adopting begging posture (legs spread, neck vertical, large gape [I. Flux]) and giving Begging Calls when adult approached with food; also called when disturbed (McKenzie 1951; Innes & Hay 1995). From *c.* 10 days after hatching, nestlings frequently stretch legs and wings. After fledging (ie. first nest-leaving), fledgelings hop actively about nest-tree but return to nest to be fed and to roost; gradually move increasing distances from nest into branches before flying back. Female seen to lead fledgeling away from nest, calling softly and keeping *c.* 1 m ahead of young, then returning to nest. Finally, one or both adults led all fledgelings away with frequently repeated Took vocalizations, feeding leading fledgeling and calling to others (McKenzie 1951; Innes & Hay 1995); one adult seen holding onto trunk, with fledgeling in tree, then adult moved upward in short springing hops and tapped bill on branch and called loudly; it appeared to be urging fledgeling to join it (Read 1966). At first, fledgelings clumsy and often misjudge movements, and so fall onto or near ground, usually scrambling back up into trees (Innes & Hay 1995). Young remain together after fledging (McKenzie 1949). Time to independence and length of time fledgelings remain in parental territory vary greatly, from being forced out immediately to staying till following breeding season, when *c.* 1 year old (see Social Organization: Dispersal of young). **Anti-predator response of young** Some observations, from 24-h video monitoring at *c.* 30 nests at Rotoehu and Mapara (Innes *et al.* 1996; I. Flux & P. Bradfield). In first half of nestling period (1–*c.* 17 days old), nestlings crouch at bottom of nest during attacks by Black Rats, Common Brushtail Possums or Swamp Harriers, and are usually eaten (see Threats). In second half of nestling period (*c.* 18 days old to fledging), nestlings increasingly likely to jump from nest during visit by predator or person, and will die on ground unless within a few days of natural fledging (Innes *et al.* 1996; Flux & Innes 2001a; I. Flux & P. Bradfield). At one nest at Rotoehu, a late-stage nestling leapt from nest when a Black Rat approached; chick was observed alive by parents and fed on ground next day, and survived (Innes *et al.* 1996). Young fledgelings shy and wary, and immediately hide in dense foliage on hearing Alarm Calls of parents (Turbott 1967). Nestlings utter various sounds when handled by observer (McKenzie 1951; see Voice: Young). **Parental anti-predator strategies** Responses of nesting Kokako to visiting people and predators well known from many nest-visits and from video-recording (McKenzie 1951, 1953; Innes *et al.* 1996; I. Flux & P. Bradfield). Responses vary greatly. Females usually leave as observer reaches nest, and return after they have departed. However, at Mapara, 1990–2000, a few females sat tight and had to be lifted from nest to allow observation of eggs or chicks; and on three occasions, females stayed on nest while chicks were removed, banded and returned beneath them. After leaving nest, some females remained 1–2 m from nest

and silent while observer present; others dived and flapped at observer and gave Alarm Calls (Innes *et al.* 1996; I. Flux & P. Bradfield; J.G. Innes). Response to predators similarly varying: some females leave nest when disturbed, with some attempting to defend nest (see below); other females sit tight when predator approaches; at Mapara, a Black Rat pushed under sitting female to obtain first egg, and a Possum sat on top of an incubating female for almost 1 min before she escaped through rim of nest (I. Flux & P. Bradfield). Some females attempt to defend nest, especially against Black Rats in later stages of incubation (thus predation by Black Rats most frequent in first half of incubation) but rarely against Possums and Stoats, and never against Swamp Harriers (Innes *et al.* 1996; I. Flux & P. Bradfield; J.G. Innes). During one filmed predation by a Stoat (at Mapara), at least one adult Kokako persistently dived at Stoat as it removed two of three nestlings; the remaining chick later died of its injuries but both parents survived (I. Flux & P. Bradfield). At two other nests at Mapara, females observed to leave nest to fly at and chase Long-tailed Cuckoos *Eudynamis taitensis* (I. Flux & P. Bradfield). Adults also seen to drive away Southern Boobook *Ninox novaeseelandiae* by flying at it (Innes & Hay 1995; I. Flux & P. Bradfield). Not seen to perform distraction displays (Innes & Hay 1995). On SI, parent bird allowed very close approach, gave no Alarm Call, and showed no inclination to defend nestling (Potts 1873).

VOICE Based on contribution by L.E. Molles and J.R. Waas. Several detailed studies: of duetting and response to playback, Rotoehu Forest, Bay of Plenty; 2001–04 (Molles & Waas In press; Molles *et al.* In press; L.E. Molles, J.D. Hudson, & J.R. Waas); of variation in Song repertoires on Kapiti I., 1999–2001 (Rowe 2001); of Song and territorial behaviour, Mapara Reserve, Rotoehu Forest, Te Urewera NP, and Hunua Ras, 1995–97 (McLeod 1998), and of vocal dynamics, Coromandel Forest Park, Pureora Forest Park and Mapara Forest, 1978–79 (Hughes 1981). Much recording and less formal study of dialects in Te Urewera NP (J.D. Hudson). Sonagrams in Hughes (1981), McLeod (1998), Rowe (2001), Molles *et al.* (In Press), Molles & Waas (In press); Song in musical notation in McLean (1911). A superior singer (Hartshorne 1973) with vocalizations often described as haunting or mournful (McLean 1912; J.D. Hudson; L.E. Molles); Song described as enchanting (McLean 1907, 1912) and seeming to express satisfaction and sheer joy (McKenzie 1949). Main Song a loud, long (30 s), slow-paced sequence of rich, organ-like notes (Molles *et al.* In press), often uttered from conspicuous perches (see Social Organization) and said to be audible up to *c.* 1.6 km (Maning 1960). Both males and females sing, individually and in duet. Some elements of Song described as ventriloquial; organ-like notes sounded as if overhead or very close at hand but birds were *c.* 30 m away (McLean 1912). Usually quiet, and often silent while feeding (McLean 1907, 1912; see Food); pairs maintain contact with quiet Took, Mew and other non-theme vocalizations (Molles *et al.* In Press; see below). ANNUAL AND DIURNAL PATTERN: Sing throughout year, but mainly in late spring and summer (Maning 1960; St Paul & McKenzie 1974; Colbourne 1986; Hudson 2001; CSN 1, 2, 4). Usually begin singing at or shortly after sunrise, rarely before, with most singing in first 60–90 min after sunrise; rarely vocalize during day, with only slight increase in rate in evening (McLean 1907; Maning 1960; St Paul & McKenzie 1974; Falla *et al.* 1981; Innes & Hay 1995; Rowe 2001; CSN 21, 22, 41; L.E. Molles). Anecdotally, said to sing more in warm, still conditions than in windy or cloudy weather; and to sing more or more loudly before or after rain (McLean 1907; Maning 1960; Turbott 1967; Rowe 2001). REGIONAL VARIATION: Nominate *cinerea* of SI said to have lower vocal output than *wilsoni* of NI (Buckingham 1987) but

little else known from SI populations. DIALECTS: Within NI, adults have distinctive Song dialects (L.E. Molles & J.D. Hudson). Adults pair only with birds that sing same dialect. However, young can change dialects and abandon all natal Song-phrases (Hudson 2001; see Fledgelings below). Recordings suggest structure of Song similar across populations, but with geographical variation in component phrases of Song. Several dialects can occur within contiguous habitat within a region (McLeod 1998; J.D. Hudson). Within a dialect region there is very little variation in full Song Duet; and phrases of Song and non-theme (including Took) widely shared by neighbouring pairs (Hughes 1981; L.E. Molles, J.D. Hudson & J.R. Waas). At Mapara, dialects stable over time, with little change in some dialects recorded 17 years apart (Hughes 1981; McLeod 1998). Calls and Songs of populations from Hunua Ras quite different from those farther S and, within Hunua Ras, Song has changed over time; for example, for a few years, full Song commonly comprised two long organ-like notes followed by three sharp pipes, but use of this Song gradually declined till it is now no longer used; this Song was also never heard farther S (St Paul & McKenzie 1974). Also in Hunua Ras, Cowbell Call recorded in early 1900s but not heard since mid-1940s (Maning 1960; St Paul & McKenzie 1974). In King Country, Cowbell Call formerly often heard but not noted more recently (St Paul & McKenzie 1974). RESPONSE TO PLAYBACK: Respond readily to playback, with full Song, calls and approach. Both members of pair normally approach together but when female incubating she may approach only briefly or not at all. When only one bird of a pair responds to playback, full Song not usually heard. However, unpaired territory-holders respond with full Song (L.E. Molles; see Social Behaviour). Also, counter-sing in response to playback (see Song, below). MIMICRY: Phrases resembling vocalizations of California Quail *Callipepla californica* and Tui have been noted (I. Flux). NON-VOCAL SOUNDS: Audibly slap wings together during some Took vocalizations; and Song often accompanied by audible wing-flaps or flutters that may produce soft sounds audible only at close range (Molles *et al.* In press). Once, described as fluttering noisily from tree (HJNC 1975).

Adult Song (= Theme of Molles *et al.*): Described as rich, musical and beautifully rendered, with many notes in chord (Falla *et al.* 1981); and usually including drawn-out flute-like and organ-like notes, intermixed with whistles, clicks and other call-notes, including short clucks and buzzes (McLean 1907, 1912; McKenzie 1949; Hamerton 1959; Maning 1960; Colbourne 1986; Heather & Robertson 1997), e.g. near Maungahaumi, Gisborne (in early 1900s), Song composed of sharp piping whistles *whe!*, drawn-out organ-like *twerr*, soft bell-like *tol*, long-drawn *twor*, fast *tor*, sharp whistled *twee*, soft low whistle or tapping *tu tu*, sharp, fast clicking *click*, and sucking note *kik*; one complete song rendition rendered as *whe! twerr tol-tol-tol-tol…twor tor-tor-tor-tor…twee tu tu tu tu…click-click-click…twee click-click-click…tu kik-kik-kik-kik…twerr click-click-click…whe! whe! whe! torr*; with each phrase separated by pause of 8–10 s, and c. 0.5 s separating some notes within phrases (McLean 1912). In detailed study of 17 pairs at Rotoehu, Song consisted of phrases of c. 2 s duration, each of 1–8 notes (Molles *et al.* In press); most notes are harmonically rich, usually with stable fundamental frequency (mean = 830 Hz) for duration of note, though harmonic structure can be altered mid-note (Hughes 1981; Molles *et al.* In press). Song also includes pure-tone whistles and clicks; and some specific phrases typically accompanied by audible wing-flaps. Repertoires of individual pairs comprise c. 18 different phrases (9–22 on Kapiti I.; Rowe 2001); Songs comprise 5–6 phrases which are combined in a loud, slowly paced theme of 30-s duration typical of population; phrases within the theme may be separated by silences of over 20 s (Molles *et al.* In press).

Sonagram **A** shows the first part of such a Song. Unpaired birds sing entire Song solo; paired birds seldom sing solo (Molles *et al.* In press). Paired birds usually sing in DUETS: Members of pair normally alternate phrases (e.g. if typical sequence of phrases in song is ABCDE, male sings A, C, and E, female sings B and D), though occasionally sing phrases in perfect unison (Molles *et al.* In press). Males usually contribute more phrases to duets (58% of phrases), and each may contribute particular phrases. However, phrases not strictly sex-specific (McLeod 1998; Molles *et al.* In press) and division of phrases may differ among pairs, singing bouts, or even successive renditions of the theme. Male–male pairs perform duets similar to those of male–female pairs but with somewhat more equal division of phrases and lower average pitch (McLeod 1998; J.G. McLeod & J.R. Waas). Birds often move to highest point in territory to utter Song (Best & Bellingham 1990; L.E. Molles). COUNTER-SINGING: When counter-singing with neighbouring pairs or playback of tape, often reply to phrases of Song with either matching, identical phrase or the next phrase that would normally occur in Song (McLeod 1998; L.E. Molles, J.R. Waas & J.D. Hudson); in response to playback, one bird noted to give chorus of chattering and Song, synchronized with calls on tape (Colbourne 1986). Pairs counter-sing across distances of tens to hundreds of metres (Best & Bellingham 1990). REGIONAL VARIATION: Song varies with location and probably over time (see Regional Variation above). FUNCTIONS OF SONG: Loud singing functions to maintain territories (Innes & Hay 1995; Hudson 2001; see Social Organization and Behaviour). Duets appear to function in forming and maintaining pair-bond (Rowe 2001; see Sexual behaviour). Song possibly also has role in mate-guarding (L.E. Molles). Female parent often gave Soft Song before regurgitating food for nestlings (Innes & Hay 1995).

Other song-type vocalizations Single, stereotyped vocalizations, structurally similar to elements in phrases of Song. Sonagram **B** shows one such vocalization, followed by four Took Calls (see below). May be given between Songs in bout of singing or used independently (Molles *et al.* In press; see Song above). When given independently of Song, used in
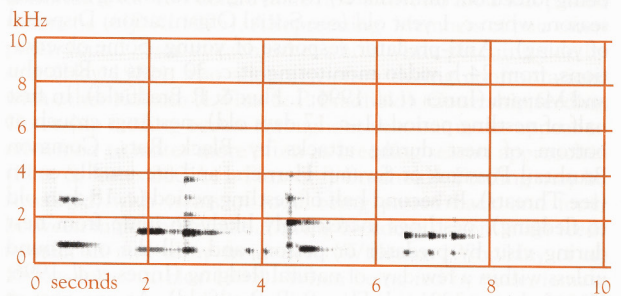
A L.E. Molles; Rotoehu Forest, Bay of Plenty, NI, May–June 2003; priv.
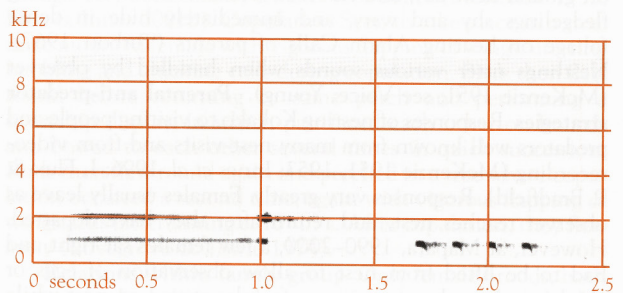
B L.E. Molles; Rotoehu Forest, Bay of Plenty, NI, May–June 2003; priv.

wide variety of circumstances; some appear to serve as contact calls, and also often used during boundary interactions and by paired birds who approach playback without their mates (L.E. Molles). Three vocalizations, Took, Mew and Chirr, and especially Took, used often and frequently mentioned as separate vocalizations; these discussed individually below. TOOK: A rather short and soft *took*, audible only at close range, and usually repeated: *took-took-took-took* or *pt-pt-pt-pt* (Morgan 1954; Maning 1960; Innes & Hay 1995). Four Took Calls, preceded by another song-type vocalization, are shown in sonagram **B**. In addition, Took can be uttered irregularly in variety of situations (Molles *et al*. In press). Circumstances of use include: by male when feeding female; when members of pair allopreening, foraging or travelling through territory; and by both sexes when feeding nestlings or fledgelings (for up to 5 min at one feed [HJNC 1975]), and when leading fledgelings from nest (Innes & Hay 1995; Molles *et al*. In press); also appears to be used when reacting to minor disturbance (McKenzie 1951; Innes & Hay 1995). Other calls that probably correspond to Took Call include: clucking noises by both sexes while feeding nestlings and by male feeding female (HJNC 1975) during copulation (Lovegrove & Towle 1974); soft clucking and cooing given during agonistic chases at territorial boundaries (Hay 1981); slowly repeated *putt, putt...* by parents when nestling handled (McKenzie 1951); and *tu tu tu* or *kik-kik* when settling at roost in evening (McLean 1912). MEW: Low musical vocalization, like mewing of cat, audible to *c*. 100 m and given by both sexes. Unusual among Kokako vocalizations in having a slow frequency sweep (Sonagram **C**); not recorded in all populations (L.E. Molles). Possibly functions as contact call (McKenzie 1951; Maning 1960; Turbott 1967; NZRD; L.E. Molles); once, in response to playback, probably at territorial boundary, all members of two pairs uttered quiet Mewing and Chirring (Saunders 1980; see Social Behaviour). CHIRR: *Chirring* sound given when feeding nestlings and sometimes during Archangel Display (Innes & Hay 1995; see Sexual behaviour, Relations within family group); once, in response to playback, probably at territorial boundary, all members of two pairs uttered quiet Mewing and Chirring (Saunders 1980; see Social Behaviour). Not recorded in all populations, e.g. recorded Mapara and Mangatutu, King Country, but not Te Urewera, Manawahe or Rotoehu (J.D. Hudson). On SI, gurgling noise given during apparent Archangel Display (Reischek 1885b; see Sexual behaviour) possibly Chirr. Chattering while feeding nestlings (HJNC 1975) possibly Chirr. OTHERS: Many other sounds described, probably equivalent to song-type vocalizations above, or phrases of Song: Bubbling call by male during copulation, like pebble dropped into still pool (Lovegrove & Towle 1974); *kio-kio*, which answered by others (McKenzie 1949); low musical twitter given by one pair while feeding (Turbott 1967); loud cackle (Turbott 1967); harsh *kaack* (McKenzie 1951); and clicking call (CSN 1). Two other vocalizations described by

Maning (1960): a short bell-like note immediately followed by short, abrupt note, like sharp *kik* or *ick* (Double Call), and which said to be not uncommon and seemed to be used to bring the mate from a distance; and a bell-like call similar to cowbell (Cowbell Call), which possibly same as *tol* note in Song (q.v.) and possibly confined to restricted area from where it has since disappeared (see Regional Variation above). SI: Only information is that one pair uttered low chuckling note (Turbott 1967); and one heard to call loudly, possibly to urge fledgeling to join it (Read 1966).

Calls ALARM CALL: Two types noted: (1) Very loud rapid *brr brr brr*, the final *r* rising in pitch; (2) when captured in mist nets or being handled, adults sometimes utter loud, harsh *craw* or screams similar to calls of crow or raven *Corvus* (J.D. Hudson). Undescribed distress call given when two birds fought (Saunders 1980; see Agonistic behaviour); and undescribed alarm calls given by some females when diving at observer at nest (Innes *et al*. 1996; I. Flux & P. Bradfield; J.G. Innes). Took often also used when mildly alarmed (see above).

Nestlings Very quiet until adults approach with food and when being fed (Innes & Hay 1995; see Relations within family group). BEGGING CALLS: At *c*. 10 days old, nestlings uttered small croaking noise when parents approached with food; at *c*. 17 days, hissed while begging (McKenzie 1951). At unknown age, nestlings gave whining noises while begging (Innes & Hay 1995). ALARM CALLS: Harsh calls (NZRD). At *c*. 10 days old, uttered croaking noise when disturbed; at *c*. 17 days, gave croaks and squawks while being handled, and one almost squealed (McKenzie 1951). OTHER CALLS: At *c*. 20 days, nestlings sometimes gave faint clicking sound (McKenzie 1951); heard to utter *wheezes* and *oos* (Innes & Hay 1995).

Fledgelings Give hoarse double croak, described as unmusical short *kwok-kwok*, repeated at long intervals; not like any known adult call (McKenzie 1951; St Paul & McKenzie 1974). DEVELOPMENT OF SONG: Early attempts at Song warbled, showing little stereotypy (J.D. Hudson; J.R. Waas); birds as young as 4–6 weeks after fledging have been heard attempting to sing, the timing and phrasing appearing correct but pitch varying, with long notes especially tending to slur or fall off (J.D. Hudson). Young males learn phrase repertoire from neighbours after establishment of territory; female Song-preference may develop during months after fledging, choosing males with Song components heard from neighbours during development (Rowe 2001; see Social Organization). However, nothing known about development of female Song. Adults can add or eliminate phrases to match repertoire of neighbours (may be open-ended learners), leading to local phrase-sharing (Rowe 2001).

BREEDING Based on contribution by I. Flux & J.G. Innes. NI subspecies fairly well known from detailed studies of nesting success at Rotoehu Forest, Bay of Plenty, 1990–94 (n=67 nests; Innes *et al*. 1996; J.G. Innes) and Mapara Wildlife Reserve, Waikato, 1990–2000 (n>200 nests; I. Flux & P. Bradfield); review of nesting accounts from 1880 to 1989 (Innes & Hay 1995); and observations of single nests in Hunua Ras (McKenzie 1951; St Paul 1963), including Moumoukai (McKenzie 1953), and at Te Kauri Park, near Te Rauamoa, Waikato (HJNC 1975). In good seasons can raise up to three broods (see below). Observation that some pairs do not attempt breeding each year (Hay 1981; Innes *et al*. 1996; I. Flux & P. Bradfield) previously attributed to shortage of food (Leathwick *et al*. 1983) but now known to be because both members of pair were male (Innes *et al*. 1999; Flux & Innes 2001a; McLeod 2001), an outcome of excessive predation on nesting females causing a gender imbalance in declining populations (Innes *et al*. 1999; Basse *et al*. 2003). However, some females do not breed in some years (see Season [Mapara], below). The percentage of pairs attempting breeding in
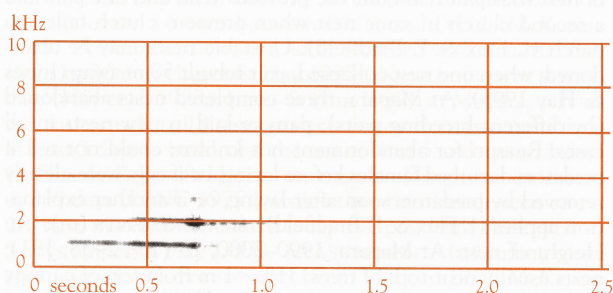
C L.E. Molles; Rotoehu Forest, Bay of Plenty, NI, May–June 2003; priv.

declining mainland populations routinely increases as management of predators increases number of females in a population, e.g. at Mapara, increased from 26% (4 of 15 pairs) in 1989 to 80–92% during 1994–97 (I. Flux & P. Bradfield). Information below for NI subspecies *wilsoni* unless stated; the little information available for SI nominate given separately at end of each section.

Season NI: Eggs laid Oct.–Mar. (Innes & Hay 1995; Heather & Robertson 1997; Oliver) with Mar. records when food abundant (Innes *et al.* 1999; Basse *et al.* 2003). Nestlings mid-Nov. to May (McKenzie 1951; MacDonald 1966; HJNC 1975; Innes & Hay 1995; I. Flux & P. Bradfield; J.G. Innes). Fledgelings recorded Dec.–May (McKenzie 1951; St Paul 1963; Turbott 1967; Meenken *et al.* 1994; Innes & Hay 1995; CSN 1, 33; I. Flux & P. Bradfield; J.G. Innes; see below). Otherwise, said to breed Sept.–Apr. (Hay *et al.* 1985a; Oliver), mostly Nov.–Mar. (Mathews 1930; Falla *et al.* 1981; Hay *et al.* 1985a; Innes & Hay 1995; Innes & Flux 1999; I. Flux & P. Bradfield; J.G. Innes). Breeding can continue for up to 6 months during favourable conditions, with individual pairs fledging up to three clutches in a single season (Innes & Flux 1999), *contra* earlier suggestions that only one brood raised per season (McKenzie 1951; Hay *et al.* 1985a; Innes & Hay 1995). Variation in number of breeding attempts attributed to climate and phenology; exclusion of predators had no effect on number of attempts (Innes *et al.* 1999). At MAPARA, 1990–2000 (>200 nests), mean date for start of incubation of first clutch was 25 Nov., with annual means ranging from 17 Nov. to 4 Dec.; earliest date 31 Oct. Pairs laid up to five clutches in a season when successive nests all failed (years when pest mammals not managed); in pest-managed years when pests managed, pairs fledged up to three broods and up to six fledgelings. Duration of breeding season varied with apparent biennial pattern of alternating 'good' and 'bad' years, good years correlating with heavy fruiting of important food plants. Duration of nesting season, from first egg laid to last, varied from 7 weeks in 1993–94 to 21 weeks in 1994–95. There were 1.8, 1.2 and 1.9 breeding attempts per breeding female during 1994–95 and 1996–97 seasons respectively. Latest recorded fledging in any year 19 May. Nearly all known females attempted breeding at least once each year. From 130 cases when known females were monitored through a breeding season, females did not attempt to breed in 11 cases; of these, six were newly paired and had never previously bred, and five had nested in at least one previous season. No known female missed more than one breeding in succession (I. Flux & P. Bradfield). At ROTOEHU, 1990–94 (67 nests), earliest date for start of incubation of first clutch ranged from 2 to 19 Nov. One pair laid four clutches in one season, all of which failed. As at Mapara, duration of breeding season varied with apparent biennial pattern of alternating 'good' and 'bad' years. Duration of nesting season, from first egg laid to last, varied from 4 weeks in 1991–92 to 12 weeks in 1992–93 (J.G. Innes). SI: Eggs, Dec.–Feb., with laying Dec.–Jan. (McKenzie 1951; Turbott 1967; Oliver). Nestlings, Jan.–Feb.; young fully grown by May (Oliver). While thought to breed only once per season (McKenzie 1951), could probably raise more than one as in NI (see above).

Site In forks, either horizontal or upright, in branches of trees and shrubs; sometimes close to main trunk (McLean 1912; McKenzie 1951, 1953; Turbott 1967; Falla *et al.* 1981; Innes & Hay 1995); also among masses of lianes or epiphytes (McKenzie 1953; St Paul 1963; HJNC 1975; Innes & Hay 1995; Heather & Robertson 1997; see below); also in top centre of tree-ferns where new frond stipes emerge (J.G. Innes; I. Flux & P. Bradfield). Mostly in understorey and subcanopy (Clout & Hay 1981; Innes & Hay 1995) but occur at all levels in vegetation (Turbott 1967; HJNC 1975; Innes & Hay 1995; Heather & Robertson 1997; CSN 1). Usually well supported

(Innes & Hay 1995). Of 191 nests at Mapara, 1990–2000, 89% were in trees and 11% in tree-ferns; either platforms of twigs built among branches, fronds or vine tangles (60%), or scooped into mass of humus at base of epiphytic lilies (*Collospermum* and *Astelia*) (40%). Platforms of twigs (n=129) built on main branches or against trunks of live trees or tree-ferns (38%), on small branches and twigs (31%), suspended in fine twigs and lianes (29%) or on branches of dead stumps (2%) (I. Flux & P. Bradfield). Normally well concealed, particularly from above, by dense foliage (Hay *et al.* 1985a; Heather & Robertson 1997; Innes & Flux 1999), mostly vines (I. Flux & P. Bradfield). At Mapara, nests were located for maximum concealment from above: 89% had dense overhead cover (<30% sky visible), 10% had moderate cover (30–69%) and only 1% had sparse cover (>70%) (I. Flux & P. Bradfield). General terrain varies, with nests recorded in gullies (McLean 1912; Innes & Hay 1995; Oliver), on flat terrain (Innes & Hay 1995), and on or round ridges (HJNC 1975; Innes & Hay 1995). At Mapara, sites evenly distributed between ridge-tops (61 nests), faces (sloping sides of ridges; 62 nests) and gullies (61 nests), which may represent bias towards ridges and gullies as faces make up greatest part of landscape; where nests on faces, there was no preference for a particular aspect (I. Flux & P. Bradfield). Reported to nest mainly on ridges in Hunua Ras (St Paul & McKenzie 1974). Vegetation can range from sparse (HJNC 1975) to dense (McLean 1912). NEST-PLANT: Commonly nest in Tawa *Beilschmiedia tawa* (McKenzie 1951, 1953; Innes & Hay 1995) or Toro *Myrsine salicina* (St Paul & McKenzie 1974; CSN 1, 6) but also recorded in wide variety of trees and shrubs including: Broadleaf *Griselinia littoralis*, *Coprosma* scrub, Gully Tree-fern *Cyathea cunninghamii*, Heketara *Olearia rani*, Hinau *Elaeocarpus dentatus*, Kiekie *Freycinetia baueriana*, Mahoe *Melicytus ramiflorus*, Miro *Prumnopitys ferruginea*, Pigeonwood *Hedycarya arborea*, Silver Fern *Cyathea dealbata*, Ramarama *Lophomyrtus bullata*, rata *Metrosideros*, Raukawa *Pseudopanax edgerleyi*, Rewarewa *Knightia excelsa*, Tawari *Ixerba brexioides*, Totara *Podocarpus totara* and Towai *Weinmannia silvicola* (McLean 1912; St Paul 1963; MacDonald 1966; Turbott 1967; St Paul & McKenzie 1974; HJNC 1975; Innes & Hay 1995; Oliver; CSN 32). In many instances nest-trees grow in close association with epiphytes and lianes (Innes & Hay 1995), including *Astelia* (Turbott 1967; Innes & Hay 1995), kahakaha *Collospermum* (Innes & Hay 1995), Kiekie (McKenzie 1953), Bush Lawyer *Rubus cissoides* (Innes & Hay 1995), Rata (St Paul 1963; HJNC 1975; Innes & Hay 1995) and Kareao Supplejack *Ripogonum scandens* (McKenzie 1953; Innes & Hay 1995), and nests are often placed among clumps of these plants as they grow on hosts (St Paul 1963; Turbott 1967; HJNC 1975; Innes & Hay 1995; Heather & Robertson 1997; I. Flux & P. Bradfield). RE-USE AND ABANDONMENT OF SITES: One nest reportedly built on remains of an old nest (Oliver). At Mapara, rarely used same site twice; only five of 191 nests were in previously used sites: two on different branches of same tree, one on top of nest that pair had built the previous year, and one pair laid a second clutch in same nest when previous clutch failed to hatch (I. Flux & P. Bradfield). Unstable nests may be abandoned; when one nest collapsed, pair rebuilt 50 m away (Innes & Hay 1995). At Mapara, three completed nests abandoned (by different breeding pairs); pairs re-laid in new nests in all cases. Reason for abandonment not known; could not tell if predators disturbed females before laying, or if eggs were cleanly removed by predators soon after laying, or if another explanation applies (I. Flux & P. Bradfield). MEASUREMENTS (m): NI: Height of nest: At Mapara, 1990–2000, 13 (7.9; 2–38; 191); nests usually near tops of trees: 31% <1 m from top of canopy and 68% <3 m (I. Flux & P. Bradfield); at Rotoehu, 1990–94, 15 (5; 6–30; 59) (J.G. Innes). From literature before detailed studies began in 1989, 8.4 (4.62; 2.5–23; 29)

(McLean 1912; McKenzie 1951, 1953; St Paul 1963; MacDonald 1966; Turbott 1967; St Paul & McKenzie 1974; HJNC 1975; Innes & Hay 1995; Oliver; CSN 1).

SI: Poorly known. One nest on outstretched limb above small creek; another on extended limb of Totara overhanging deep ferny valley; three others in damp situations in small patch of bush (Potts 1873). Nests recorded in Broadleaf and Totara (Potts 1873). Nest in thick scrub, close to ground (Reischek 1885b); five nests *c.* 3–5 m (Potts 1873).

Nest, Materials Build large, cup-shaped nest with base of twigs and leaves bound together with mosses, lichens and vines, and with complex multi-layered bowl and lining (McLean 1912; Mathews 1930; McKenzie 1951; Turbott 1967; Falla *et al.* 1981; Innes & Hay 1995; I. Flux & P. Bradfield). At Mapara, two types of nest-platforms used: (1) ready-made platforms provided by clumps of humus that form round the roots of epiphytic plants (40% of 191 nests); and (2) platforms of twigs built by Kokako (60%). Epiphyte nests involved little use of materials: likely to contain a few twigs that have no structural function, and nest-bowl formed by digging cavity in humus; bowl lined with dry fibre or tree-fern scales or both, as with twig-platform nests. With twig-platform nests, rigid twigs bound together with filamentous mosses, lichens, supple twigs of Tawa, Rata vines, orchid *Earina* stems and stipes of climbing ferns *Hymenophyllum* and *Pyrrosia eleagnifolius*; bowl was usually a multi-layered structure: moist inner layers included mosses, rotten wood-pulp and *Collospermum* leaf-bases; nest-lining then formed by addition of dry materials, including leaves of Bamboo Orchid *Earina mucronata*, fine grasses and shredded plant fibre (usually Kiekie or kahakaha), and scales from *Cyathea* tree-ferns; a long, leafy stipe of the climbing fern *Pyrrosia eleagnifolius* was added to the rim of most nests. Although materials varied little, quantities of each varied markedly, from a nest using >300 twigs and four litres of lining material, to a simple scoop with only a trace of lining material. All females in the study built both nest-types (I. Flux & P. Bradfield). Above description consistent with earlier accounts (McLean 1912; Mathews 1930; McKenzie 1951; Turbott 1967; HJNC 1975; Innes & Hay 1995; Innes & Flux 1999; Oliver). Nest becomes flattened if young survive to fledging (McKenzie 1951; Innes & Hay 1995). A nest examined for invertebrates contained fungus and detritus feeders but no parasites (Innes & Hay 1995). Nest usually built by female (McKenzie 1953; Innes & Hay 1995; Innes & Flux 1999; Flux & Innes 2001b), though male occasionally assists in gathering material (St Paul 1963; Innes & Hay 1995; Innes & Flux 1999; Flux & Innes 2001b). Female may be fed by male when constructing nest (McKenzie 1953). At Mapara, of 41 nests: in male–female pairings, female did all building, though males twice delivered twigs to a nest; male–male pairs may also build nests (I. Flux & P. Bradfield; see Bonds). Nesting material is obtained from near nest; at one nest, material was torn from a tree next to the nest (McKenzie 1951); at another, mud and sticks were collected 80 m from nest-site (Innes & Hay 1995). During observations of building at one nest, female visited on average every 5.5 min between 06:03 and 06:42 (McKenzie 1953). At another nest, one adult returned with material five times in 20 min (Innes & Hay 1995). Nests built over several days (Hay *et al.* 1985a; Innes & Flux 1999): at Mapara, at least two visits made to 19 nests under construction; two nests took at least 3 days to build, and the rest at least 5 and up to 11 days (I. Flux & P. Bradfield); at one nest, building time estimated at 8–9 days (HJNC 1975), while at another female seen carrying nest-material for 6 days; a captive pair built their nest in 5 days (Innes & Hay 1995). MEASUREMENTS (including some approximations): For six nests (from McLean 1912, McKenzie 1951, four unpublished): diameter of upper portion of nest (excluding twig platform) 25–30 cm; external depth (including twig platform) 16–20 cm; diameter of nest-cup 12–16 cm;

depth of nest-cup 6 cm (Innes & Hay 1995). External diameter (includes two of previous sample): 49.1 cm (7.79; 40.6–55.9; 3) (McLean 1912; McKenzie 1951; Turbott 1967). One nest had 'solid part' 27.9 cm wide, with external depth (including twig platform) of 16.5 cm; nest-cup 12.1 cm diameter and 6.4 cm deep (McLean 1912). In another, diameter of cup 16.5 cm (McKenzie 1951). Other records include one nest with external depth of 20.3 cm, and another in which main part of nest was *c.* 30.5 cm in diameter (Turbott 1967). At Mapara in 1990–2000 (n=115 nests), twig-platforms varied greatly in size depending on site and enthusiasm of the female, from 20–40 cm external diameter. Platforms included green, leafy and dead twigs, mostly 15–30 cm long but up to 60 cm. SI: One nest built on top of a previous structure: a strongly interlaced foundation of sticks and sprays supported a basin-shaped nest-bowl of twigs and *Sphagnum* moss, smoothly lined with soft grass (Potts 1873); Reischek (1885b) simply recorded nests 'of twigs and moss'. External diameter 40 cm, internal diameter 20 cm and depth 9 cm (Potts 1873).

Eggs Ovate or elliptical-ovate (Innes *et al.* 1996: photos of eggs damaged by predators; Innes & Flux 1999: photo, p. 7; Oliver). Variously described as grey, stone-grey, pale stone-grey, warm stone, dark purplish-grey, pale brownish-grey, pinkish grey, fawn and greyish white (Mathews 1930; HJNC 1975; Falla *et al.* 1981; Innes & Hay 1995; Innes & Flux 1999; Oliver), spotted and blotched light to dark brown, less often fawn, mauve, purplish, dull sepia, purplish or purplish grey (Mathews 1930; HJNC 1975; Innes & Hay 1995; Innes & Flux 1999; Oliver; I. Flux & P. Bradfield); markings can be concentrated at large end, sometimes markings as wavy lines in parts (Mathews 1930). At Mapara, one egg in a C/3 smaller and pale blue and found to be infertile (I. Flux & P. Bradfield); two similar eggs laid at Mt Bruce National Wildlife Centre were also infertile (P. Morton). MEASUREMENTS: At Mapara, 38.5 (2.65; 33.0–43.7; 42) × 26.0 (1.2; 22.6–28.3); 39.0 (4.87; 35.0–47.0; 5) × 26.8 (0.23; 26.5–27.0) (Oliver); 34.2–42.1 × 25.7–29.2 (Innes & Hay 1995). WEIGHT: At Mapara, 15.25 (0.5; 15–16; 4); *c.* 7% of mean adult female weight (I. Flux & P. Bradfield; see Weights). SI: Described as ovo-conical; warm stone with purplish and brown spots. Length 40.2 × 27.5) (Potts 1873).

Clutch-size NI: One to three, usually two or three (St Paul 1963; St Paul & McKenzie 1974; HJNC 1975; Hay *et al.* 1985a; Heather & Robertson 1997; Oliver). In summary of published and unpublished nest records to 1989, modal clutch-size three (n=9); four nests had two (Innes & Hay 1995). Little known despite many nests being found because climbing to nest affected predation research, so was uncommon (J.G. Innes). At Mapara in 1990–2000, mean 2.3 (0.74; 26): (I. Flux & P. Bradfield). While it had been suggested that broods of four might also occur, based on observations of family groups of six (two adults, four young) (Hatch 1979, 1980), observation of banded juveniles has since shown that family groups often contain more or fewer juveniles than are actually fledged, and on occasions a chick present in a family group may be unrelated to the adults (Innes *et al.* 1999). SI: Two to three eggs (Reischek 1885b; Potts 1873; Fulton 1907).

Laying Lay at interval of 1 day: at Mapara, at one nest checked daily in mid-afternoon, eggs of C/3 laid 1 day apart (I. Flux & P. Bradfield). At another nest three eggs laid between 07:50 on 6 Dec. and 18:25 on 11 Dec. (McKenzie 1953). Re-nest after success and after failure, and breeding can continue for up to 6 months during favourable conditions (Hay *et al.* 1985a; Innes & Hay 1995; Innes & Flux 1999; Innes *et al.* 1999); see Season for details. At Mapara, 1990–2000, most re-nesting attempts (81 nests), after failure or success, within 2 weeks of previous attempt: on three (3.7%) occasions, females re-nested up to 7 days before young had fledged from previous nest; five (6%) re-nested within

7 days of young fledging; 40 (49.4%) re-nested within 2 weeks; and rest >2 weeks. The longest period recorded between failure of nest and re-nesting 41 days, and between success and re-nesting 35 days (I. Flux & P. Bradfield).

Incubation By female only (St Paul 1963; Hay *et al.* 1985a; Innes & Hay 1995; Innes & Flux 1999; Flux & Innes 2001b; I. Flux & P. Bradfield; *contra* Heather & Robertson 1997 [erroneous]). Sitting bird seen to move eggs often, and appeared very restless, moving about and fluttering her wings quite often (HJNC 1975). At Mapara, female incubated irregularly during laying, spending long periods (>1 h) off nest; settled into regular incubation only after laying of final egg. In three nests with C/2 or C/3, chicks hatched *c.* 1 day apart (I. Flux & P. Bradfield). At two nests, incubation began at most 7–9 days after early nest-building (St Paul 1963; HJNC 1975; Innes & Hay 1995); a captive female began incubating 5 days after completion of nest, and 1 day after first egg laid (Innes & Hay 1995). At a nest in Hunua Ras, female incubated in stints ranging from 30–60 min, length of stints decreasing as eggs approached hatching; female left nest for periods of 5–15 min to feed, drink or wash (St Paul 1963). At another nest at Pureora, during last 7 days of incubation, female spent 80–92% of time incubating, in stints of 67 min (36–100; 13) with mean time away from nest (to feed and preen) 8 min (2–16; 20) (Innes & Hay 1995). Male usually feeds female during incubation (Innes & Flux 1999; Flux & Innes 2001b), though she will also feed herself (St Paul 1963); females fed on or off nest (St Paul 1963; Innes & Hay 1995) and males usually accompanied female when she left the nest (St Paul 1963). In central NI, males fed females every 10–85 min during incubation and early nestling period (Flux & Innes 2001b). At nest at Pureora, male visited nest on average every 36 min (11–76; 11), usually <10 s, and always <30 s; only 59% of 34 visits by male to female were at nest (Innes & Hay 1995). Eggshells appear to be removed by adults and dropped nearby (Innes & Hay 1995). INCUBATION PERIOD: Varies. Average *c.* 18 days based on data from seven nests, with periods of: 16–17 (HJNC 1975), 20 (unpubl.), 17 (captive pair) (Innes & Hay 1995), 13–19, 15–21, 17–19, and 18–20 days (I. Flux & P. Bradfield); at one of preceding (17–19 days) nests, checked daily during mid-afternoon, eggs hatched in order laid, first two at 17–18 days and third after 18–19 days (I. Flux & P. Bradfield). At one nest, time from building to hatching estimated at 26–29 days (HJNC 1975). At Mapara, two clutches that did not hatch were incubated for 18–25 and 15–21 days before abandonment (I. Flux & P. Bradfield). At Rotoehu, desertions at six nests (of 67) occurred after 11–28 days, 20 days, 23–29 days, 39–45 days, 20+ days and 21–33 days (J.G. Innes).

Young Altricial, nidicolous. At hatching, nestlings have partial covering of down above, and a bare underbody (McKenzie 1951; Gill 1993; Innes & Hay 1995; Oliver); for details of down and bare parts, see Plumages, Bare Parts. **Growth** For three nestlings in one brood, at 2–3 days old, eyes closed, egg-tooth prominent, and unable to lift heads; down along back, above each thigh and on top of head; feathers in pin on wings (and not separated from one another), and down centre of backs, with rest of body naked. At 7–8 days: eyes partly open and able to raise heads; feathers on head, mantle and back; primaries and secondaries and upperwing-coverts had burst from sheaths and *c.* 14 mm long. At 9–10 days, eyes fully open; and feathers on head, back, flanks, thighs and part of underbody; wing quills were open. The following day, measurements were taken: culmen 25 mm; length of middle rectrix from sheath 43 mm; length of p6 from sheath 54 mm. Remiges and rectrices still developing at 15–16 days, and some down still present at 20–21 days. At 22–23 days rectrices about half adult length, with many feathers still sheathed at base. Had fledged at 25–26 days (McKenzie 1951). At one nest at Mapara, primaries (in pin) emerged on Day 3; by Day 6, pin-feathers emerging on neck and tail, and sparse down opening on back; by Day 8, downy quills opening on back, neck and tail, and quills of primaries 14 mm long and quills of rectrices 8 mm long. Chicks fully feathered but with few downy plumes remaining by Day 18; black face last area to be feathered but completely so by *c.* Day 20 (I. Flux & P. Bradfield). At 15–25 days, large nestlings can be as big as adults (Flux & Innes 2001b). While some fledgelings said to be only two-thirds grown (CSN 1), growth of some body parts (e.g. legs, wattles) can be complete at 3 months (Flux & Innes 2001b). At fledging, typically have short tails (Flux & Innes 2001b), which are about half adult length (McKenzie 1951; CSN 1), for at least 10 days after fledging (I. Flux & P. Bradfield); tarsi tend to be close to adult length, with largest tarsi measured from male and female chicks in central NI 65.7 and 62.1 mm respectively (Flux & Innes 2001b). WEIGHT: At one nest at Mapara, three nestlings 15–16 g at 1 day old; gain of weight almost linear, at *c.* 10 g/day, over first 10 days. Useful field approximation for age (in days) in a healthy chick during first 2 weeks is thus 10% of its weight (g). At another nest at Mapara, for which all three nestlings weighed regularly, the last-hatched never gained weight and died after 3 days; other two developed in parallel but were distinguishable by weight and development of feathers till at least Day 21. At nests where more than one chick measured, weight differences of 20–40 g between nestlings were normal, and probably attributable to order of hatching. Differences of >40 g between nestlings often associated with signs of poor condition (lack of vigour, dry skin) in one brood member. At four nests where differences of >40 g recorded between siblings, the smaller runt nestlings did not survive (I. Flux & P. Bradfield).

Parental care BROODING: By female only, who is fed on nest by male (McKenzie 1951; St Paul 1963; HJNC 1975; Williams 1976; Hay *et al.* 1985a; Innes & Hay 1995; Innes & Flux 1999; Flux & Innes 2001b; I. Flux & P. Bradfield; see Food [Young]; Social Behaviour). Females brood less as nestlings get older (Innes & Hay 1995). At Mapara, 1990–2000, brooding erratic and varied individually. When chicks *c.* 7 days old, females returned to nest on average each 17 min (n=31) then brooded for mean 19 min (15; 24), though length of stints highly variable, and generally longer during wet or cold weather; females rarely brooded nestlings older than 10 days during day, though always brooded overnight throughout nesting period (I. Flux & P. Bradfield). For details of feeding visits by males through nesting period, see Food (Young). At one nest at Mapara (7.5 h obs. per day), proportion of time spent brooding by female 80% on day after hatching, 70% 8 days later, and 66% after 2 more days, with trend continuing till nestling taken by a predator. At a nest at Pureora, mean time spent on nest declined steadily from incubation; *c.* 1 day after hatching, female spent 76% of the day on nest; from *c.* 21–23 days after hatching, female did not sit at all, except to roost at night (Innes & Hay 1995: Fig. 1). Conversely, mean time between visits to nest by female increased from *c.* 10 min soon after hatching to about 25 min 1 week later, and remained between 20 and 25 min till fledging (Innes & Hay 1995: Fig. 2). Mean time away from nest tended to be greater after 15:00 (24.1 min) than before 11:00 (21.2 min) or between 11:00 and 15:00 (20.0 min); and mean times spent on nest 25.0 min before 11:00, 37.6 min between 11:00 and 15:00, and 59.2 min after 15:00 (Innes & Hay 1995). At one nest, female kept changing position and appeared to spread her feathers and tail to shelter chicks from wind and rain (HJNC 1975). On SI, nestlings were left for intervals throughout day (Potts 1873). FEEDING: Nestlings fed by both parents, though usually by male alone during first few days; once female begins feeding, visits to nests either by single parent or both together (McKenzie 1951; HJNC 1975; Hay *et al.* 1985a; Innes & Hay 1995; Innes & Flux 1999; Flux & Innes 2001b; I. Flux &

P. Bradfield; see below). Claim that female regurgitates food on nest (HJNC 1975) needs confirmation, as previously unreported for passerines. Food may be delivered to a single chick or divided among brood (McKenzie 1951; Innes & Hay 1995; Oliver). At Pureora, male alone fed nestlings for first few days after hatching; after this, young fed by both male and female, either by single parent or both together; from 9 days after hatching till fledging, 25% (7–54%) of feeding visits made by both adults together. At a nest at Coromandel, parents visited together on 54% of visits 9 days before fledging and 33% of visits 5 days before fledging (Innes & Hay 1995). At another nest, female received food from male, which she then took to chicks (McKenzie 1951). For further details of food and feeding of nestlings, including rates of feeding visits to nest, see Food (Young). *OTHER*: Both parents eat or remove faecal sacs, dropping them away from nest (McKenzie 1951; Innes & Hay 1995; I. Flux & P. Bradfield), though, at Mapara, diligence at this task varied greatly between individuals and decreased as nestling period progressed and at one nest, only female removed faeces (I. Flux & P. Bradfield); faecal sacs that stuck to outside of nest not removed (McKenzie 1951). After 2–3 weeks, nestlings defecate over edge of nest (Innes & Hay 1995), though some nests became heavily soiled and quite pungent by time young fledged (I. Flux & P. Bradfield). At single nest at Coromandel, female cleaned nest daily, often forcing chicks to edge of nest in doing so (Innes & Hay 1995). For anti-predator responses of young and adults, see Social Behaviour (Relations within family group).

Fledging to independence FLEDGING PERIOD: Estimates of period from hatching to fledging range from 27 to 42 days, but are usually between 32 and 37 days (McKenzie 1951; Hay *et al.* 1985a; Innes & Hay 1995; Heather & Robertson 1997; Innes & Flux 1999; Flux & Innes 2001b; I. Flux & P. Bradfield; J.G. Innes). At Mapara, 1990–2000, in only nest for which hatching and fledging dates known, single nestling remained in nest for 34 days before fledging (I. Flux & P. Bradfield). Fledgelings fed by both parents, with almost all food provided by parents at first; timing of foraging independence varies greatly, but can be as little as a few days if young ejected quickly from parents' territory, or young sometimes continue to receive at least some food from parents for 1 year (see Food [Young]; Social Organization). After fledging, young may remain in vegetation surrounding nest, moving about a lot and returning to nest to be fed or to roost (I. Flux & P. Bradfield). Newly fledged young ungainly, often misjudging movements and ending up on or near the ground before hopping back up into a tree; gradually roam farther from nest, though they may continue to be fed there (for 3 days at one 1950 Auckland nest) (McKenzie 1951; Innes & Hay 1995). Fledged young typically remain in parental territories for several months, but may be ejected from natal territory immediately after fledging or remain in natal territory for up to 1 year (see Social Organization: Parental care [Dispersal of young]). In central NI, when adults raised two broods, fledgelings from first brood always left natal territories before second brood fledged (Innes *et al.* 1999).

Success Breeding failure primarily results from predation, particularly by introduced mammalian predators (McKenzie 1951, 1953; St Paul 1963; HJNC 1975; Rasch 1992; Meenken *et al.* 1994; Innes & Hay 1995; Innes *et al.* 1999). Success studied in detail in central NI during 1989–97; few nests fledged young unless mammalian predators controlled (Innes & Flux 1999; Innes *et al.* 1999; Basse *et al.* 2003). In central NI, during 1989–97, 42% (24; 14) of pairs fledged young when browsing and predatory mammals were actively controlled, while only 13% (10; 8) were successful when pest mammals went unchecked (see Innes *et al.* 1999: Fig. 5) for annual breakdown at individual locations). At Rotoehu, the proportion of pairs successfully rearing young increased from 17%

(8; 8–30; data from four seasons) to 54±12% (data from three seasons) after pest control. During 1995–96 season at Rotoehu, 61% of 13 pairs fledged young at pest-managed site, while only 29% of 14 pairs were successful in adjacent, unmanaged forest. At Kaharoa, when pest control ceased, number of successful pairs fell from 48±32% (data from three seasons) to 10±13% (SD=13; data from four seasons). Predator control also increased the number of young that were fledged (see Innes *et al.* 1999: Fig. 8) for number of young fledged each year at individual locations) and the proportion of successful nesting attempts. At Rotoehu and Mapara, at least one chick was fledged in 13.7±2.9% (data from three block/seasons) of nesting attempts before management, while 48.8±17.3% (data from nine block/seasons) of attempts were successful once predators controlled. At Mapara, an estimated 75% of pairs (12 of 16) did not attempt breeding in 1989–90, before management; this dropped to 56% (5 of 9) in 1991–92 after pest control began, and continued to decrease steadily, reaching 8% (2 of 24) by 1996–97. Decline in pairs not attempting to breed was caused by young single females that fledged from successful nests pairing with older males, thus breaking male–male pairs. At Rotoehu, 23–39% (3 of 13 to 5 of 13) of pairs failed to breed during 1990–94, when pests were unmanaged; during 1994–97, when pests controlled, only 8–20% (1 of 13 to 4 of 20) of pairs failed to attempt breeding. The proportion of apparent pairs attempting to breed was reduced in some declining populations because some males formed male–male pairs, an outcome of male excess after predation of females at nests (Innes & Flux 1999). On Little Barrier I. (Hauturu), which lacks major mammalian predators, 75–85% of pairs fledge young annually (Rasch 1992; Innes *et al.* 1999). Results from detailed research consistent with earlier, mostly anecdotal, literature or of small numbers (McKenzie 1951, 1953; St Paul 1963; HJNC 1975; Hay 1981; Hay *et al.* 1985a; Meenken *et al.* 1994; Innes & Hay 1995; CSN 1, 31). During early 1950s, breeding losses to pest mammals were estimated at 90% or more (McKenzie 1953). PREDATORS: Much known from use of 24-h time-lapse video-recording at nests at Rotoehu and Mapara (Innes *et al.* 1994, 1999; I. Flux & P. Bradfield; J.G. Innes). At Rotoehu, 237 days and nights of footage obtained from 11 nests, enabling direct observation of predator behaviour and prey response, and characterization of distinctive predator sign (Innes *et al.* 1999; J.G. Innes). Black Rats and Common Brushtail Possums are the major predators. Rats feed mainly on eggs during first 10 days of incubation, and occasionally on young nestlings (to 10 days old); Possums eat eggs, nestlings and occasionally adults (Brown *et al.* 1993; Innes *et al.* 1996; Innes & Flux 1999; Innes *et al.* 1999; I. Flux & P. Bradfield). Both can also cause nestlings to fledge prematurely (Innes *et al.* 1999). The other main predator is native Swamp Harrier, which known to take eggs and nestlings (Innes *et al.* 1996, 1999; Innes & Flux 1999), and can be a serious threat to very small populations, such as during early stages of translocations (Innes & Flux 1999). Mustelids, especially Stoats *Mustela erminea*, are known nest-predators (I. Flux & P. Bradfield) and may have been the main cause of loss of breeding females at Mapara in 1997–2000 when control of pests stopped (Basse *et al.* 2003; I. Flux & P. Bradfield). However, Stoats are not usually targeted for recovery of Kokako populations (Innes & Flux 1999; Flux & Innes 2001b). While other mammals, such as feral Cats and House Mice *Mus musculus*, are potential predators, there is no evidence that they in fact are (Clout & Hay 1981; MacMillan & McClure 1990; Innes & Flux 1999; Innes *et al.* 1999). Nests vulnerable to predation by mammals regardless of location of nest- or tree-height because Common Brushtail Possums and Black Rats arboreal and agile climbers, and easier access usually provided by branches and vines (Clout & Hay 1981; Hay *et al.* 1985a; Innes *et al.* 1999). Further, the long nesting

period coincides with seasonal increases in populations of Rats and Stoats (Innes *et al.* 1995; see Innes *et al.* 1999: see Figs 5b,c, 7 for success in relation to abundance of Rats and Possums). Fledgelings can be exposed to predators if they end up on or close to the ground (Innes & Hay 1995). Predation by Black Rats on eggs is characterized by one large remaining shell piece with jagged margins and several smaller shell pieces in nest; there are often also Rat scats. Possums eat eggs roughly, leaving no large fragments, and all fragments have crushed (not jagged) margins. Both Black Rats and Possums leave partly eaten chick carcasses with exposed upper body surfaces roughly eaten or bitten. Possums also produce characteristic regurgitated shell or feather pellets roughly 15 × 5 mm, formed in upper palate and then spat out. Filming at nests of Kokako (and other species) has shown that Possums always eat eggs they encounter, but are serendipitous predators of chicks, which may be ignored, bitten but not eaten, or mostly eaten (Flux & Innes 2001a). Swamp Harriers leave large fragments of shell with clean break margins, and either cleanly remove chicks to eat elsewhere or pluck and eat chicks in nest (Brown *et al.* 1993; Flux & Innes 2001a; see photos in Innes *et al.* 1996). Video-recording showed that multiple visits by predators or scavengers to one nest are common; at one nest at Rotoehu, over 1 month, there were visits by Black Rats, all fought off by the female; a visit by a Possum, which did not eat young chicks; then two more visits by Black Rats, then a Harrier predation in which one chick was eaten in nest and the other jumped out and later died on ground; then two scavenging visits by Black Rats the night after the predation; and a second scavenging visit by the Harrier the next day (Innes *et al.* 1996). OTHER CAUSES OF FAILURE: Collection of eggs and fledgelings by people has resulted in failed nests (Turbott 1967; Hay *et al.* 1985a). One or more eggs of clutch can sometimes be infertile and fail to hatch (McKenzie 1951; Innes & Hay 1995; I. Flux & P. Bradfield; J.G. Innes). At Rotoehu, 1990–94, of six of 67 nests deserted; two were disrupted by a tree-fern frond growing through base of nest; and one chick was filmed falling from a nest (J.G. Innes). At Mapara, 1990–2000, of 189 nests, only two failed owing to instability of nest: one fell between the large branches on which it was built, and another was tipped over by tree-fern fronds. A third nest was built with no rim on one side, and one chick from a brood of two fell when *c.* 15 days old (I. Flux & P. Bradfield).

PLUMAGES Prepared by J.S. Matthew. Hatch with dense covering of grey-brown natal down (Gill 1993). Fledge in juvenile plumage. Partial post-juvenile (first pre-basic) moult to first immature (first basic) plumage starts when 1–2 months old. Acquire adult plumage in complete first immature post-breeding (second pre-basic) moult, when *c.* 1 year old. A complete post-breeding (pre-basic) moult each cycle produces successive adult (basic) plumages with no change in appearance. Sexes alike. Two subspecies: nominate *cinerea* of SI probably extinct on NI and described below based on examination of skins of nine adults, eight first immatures and one juvenile (AM, AIM, NMNZ), and photos of live birds (Moon 1979; Moon & Lockley 1982; Hay *et al.* 1985a; Moore & Innes 1996).

Adult (Definitive basic). HEAD AND NECK: Lower forehead, lores, eye-ring and feathers above and below front half of eye, black (89), combining to form distinct black (89) mask, which is broad and large in front of eye and extends only narrowly around rear of eye. Most of rest of head and neck, dark bluish-grey (c78) with: (1) narrow pale bluish-grey (pale 88) border behind black facial mask, narrowest on lower forehead and slightly broader and more prominent behind eye, particularly on upper rear quadrant of eye, and separating black facial mask from bluish grey of rest of head; (2) ear-coverts slightly paler than top of head; and (3) interramal area

and chin, greyish black (c82) with dark bluish-grey (c78) tips to feathers. UPPERPARTS: Entirely dark bluish-grey (c78). All feathers have concealed pale-grey (pale 87) bases and concealed dark-brown (22) or brown (219B) shafts. UNDERPARTS: Breast, most of belly and anterior flanks, dark bluish-grey (c78) with faint brown (119B) tinge formed by partly exposed brown centres to feathers. Rear-flanks, centre of lower belly, vent, undertail-coverts and thighs, brown (c28) or olive-brown (c29) with faint bluish-grey (c87) tinge formed by diffuse tips to feathers. All feathers have concealed pale-grey (pale 87) bases. UPPERTAIL: Rectrices, blackish brown (c19) with: broad and diffuse olive-brown (c29, c30) edges to t1; mostly olive-brown (c29, c30) outer webs to t2–t6, grading to dark brown towards shaft. Shafts, dark red-brown (221A). UNDERTAIL: Rectrices, blackish brown (c19); shafts, reddish brown (35). UPPERWING: All marginal and median coverts, dark bluish-grey (c78), grading to dark brown (c121) at bases. Greater secondary coverts, dark bluish-grey (c78) on outer webs, dark brown (c121) on inner webs. Greater primary coverts and alula, dark brown (c121) grading to dark bluish-grey (c78) on outer edges or on outer webs. Remiges, dark brown (121) with diffuse dark bluish-grey (c78) or, less often, olive-brown (c29) outer edges; edges terminate closer to bases on outer primaries. Shafts to remiges, red-brown (221A). UNDERWING: All coverts, dark brown (c119A) with indistinct bluish-grey (c87) tips or edges. Remiges, dark brown (121); outer edges as upperwing but concealed.

Museum skins possibly become duller and less bluish grey with time; adults collected from 1950s on have richer bluish tone to plumage compared with adults of same subspecies, collected from 1920s and earlier, which have duller, less bluish tone.

Nestling NI: Nestling 2–3 days old has a little dark-brown or slate-brown down along back, above each thigh and on top of head; at 7–8 days old has varying amount of wispy down; at 14–15 days old has a little brownish down, which persists till at least 19–20 days old (McKenzie 1951). Gill (1993) describes distribution of natal down on full-term embryo; there are 11 down-patches (all but one dorsal; some median, others paired) each comprising many long dark-coloured downs. SI: Young nestlings 'as yet unable to see' were partly covered with slate-coloured down, which, on head, stood up like a broad crest or crown; neck and underparts were bare (Potts 1873).

Juvenile Based on skin (NMNZ 25832) of 30-day-old fledgeling that had already started post-juvenile moult (see Moults below). Rather similar to adult, from which differs by: Feathers of head and body much softer and more loosely textured; and have down on thighs and head at fledging (Innes & Hay 1995). HEAD AND NECK: Lacks bluish tone of adults. Most of head and neck, grey (c84) with brown (119B) tinge, which more prominent on top of head. Lores and eye-ring, blackish (c89), not solid black as in adult. Pale bluish-grey (c88) or light greyish (pale 95) rear border to blackish facial mask more diffuse and less prominent than in adult. UPPERPARTS: Mantle, scapulars and back, grey (c84) with brown (119B) wash, grading to uniform brown (c28) on rump and uppertail-coverts. UNDERPARTS: Mostly grey (c84) with brown (119B) tinge, grading to more uniform brown (119B) on lower belly, rear-flanks, vent, thighs and undertail-coverts. TAIL: Rectrices narrower and more pointed at tips than those of adult; all rectrices, dark brown (c121) with narrow warm-brown (33, 121C) outer edges, which are less prominent on undertail. UPPERWING: Browner than adult. Marginal coverts not known as these already in moult in single skin examined. All median coverts and greater secondary coverts, dark brown (c121) with diffuse light-brown (c26) fringes. Greater primary coverts and alula, dark brown (c121) with faint bluish-grey (c87) outer edges, or tinge to outer webs. Remiges similar to

adult but outer edges warm brown (c121C), combining to form broad warm-brown (c121C) panel. UNDERWING: No information; cannot be examined without damaging skin.

First immature (First basic). Similar to juvenile, differing by: (1) feather-texture as adult (not soft and loosely textured as in juvenile); (2) head, neck and underparts as juvenile, but with warmer brown (c121C, c37) or olive-brown (c123) tinge or wash, more uniformly so on lower underbody (cf. plainer brown in juvenile); (3) upperparts, brownish grey (ne), grading to dark bluish-grey (c78) on upper mantle and uniform brown (c119B) or warm brown (c33) on rump and uppertail-coverts; (4) skins examined retained all juvenile rectrices; and (5) upperwing as juvenile but skins examined retained all juvenile greater coverts, alula and remiges. Marginal coverts as juvenile median coverts, dark brown (c121) with diffuse light-brown (c26) fringes.

Aberrant plumage Abnormal birds collected in Rimutaka Mts and Wairarapa region, NI: some birds pure white, others white with cream underparts, and others with pale grey and ashy-grey coloration (Oliver). Clout & Hay (1981) mention a 'partial albino' collected at Mt Franklin, SI, but give no further details.

BARE PARTS Based on photos (P. Bradfield [*Forest & Bird*, 1996, No. 282: p. 1]; Anon. [*Forest & Bird*, 1999, No. 293: p. 8]; D. Hansford [*Forest & Bird*, 2003, No. 308: p. 12]; Moon 1979; Moon & Lockley 1982; Moore & Innes 1996; Lee 1999; Hay *et al.* 1985a; unpubl.: I. Flux; also standard sources), museum labels (AM), and other information as cited. Subspecies *wilsoni* of NI unless stated. **Adult** Bill, black (89). Gape and distinctive fleshy wattle hanging below gape: in *wilsoni*, bright blue (69, c67); in captive *wilsoni*, can appear dull and shrunken when not breeding, but bright blue and tumid at start of breeding season (Flux & Innes 2001b). In nominate *cinerea*, wattles mostly orange becoming blue towards base of bill (Sharpe 1877; Oliver; NZRD). Rarely, birds with orange wattles recorded NI, both historically (Potts 1873; HJNC 1975) and currently (at Kaharoa near Rotorua, C. Richardson); these 'Orange-wattled Kokako' assumed to be colour-variants of subspecies *wilsoni* of NI, and not vagrant nominate. Orbital ring, black (89). Iris, black-brown (c119); also described as dark brown (Oliver; AM). Legs and feet, black (89). Soles, pinkish brown (219C). **Nestling** NI: During development, colour of wattles varies between bright pink and mottled pink and blue (I. Flux & P. Bradfield); evenly pink to pink-lilac at fledging (see below). For three nestlings in one brood, at 2–3 days old bare skin of body, smoky blue; egg-tooth prominent. Following changes in colour of wattles noted on three nestlings (McKenzie 1951): pinkish lavender when 2–3 days old; purple with bluish edge when 7–8 days; more blue when 9–10 days; cobalt with red near angle of gape when 10–11 days; pale pink-blue when 14–15 days; and pale blue with purplish underside when 19–20 days. Innes & Hay (1995) describe wattle of nestlings as pinkish lavender, edged pale blue, smaller and more rounded than in adults. Photo (Hay *et al.* 1985a) of two 20-day-old nestlings indicates: bill, black (89) with off-white (ne) gape and basal third to half of tomia; wattles, pale pink (c108D); orbital ring, light grey (85); iris, blackish. Another photo (Moon 1982) of well-developed nestlings (plumage similar to aforementioned 20-day-old nestlings) indicates: bill, blackish (c89) with off-white (ne) tomia; wattles, gape and palate, pink (c3); orbital ring, light grey (85). Photo (*Forest & Bird*, 1999, No. 293: p. 8) of well-feathered nestling shows wattle, mauve (c76), and legs and feet, pale pinkish-brown (c219D). SI: Wattles of young birds smaller and much lighter (Reischek 1885b). Bill, flesh-coloured, with greenish tinge at tip of upper mandible; rictal membranes, pale greenish, changing to blue; wattles, rosy pink, like an infant's hand; legs and feet, slate-grey in front,

dull flesh behind; claws, dull white (Potts 1873). **Juvenile** Photos of 15-day-old fledgeling *wilsoni* (Moore & Innes 1996; P. Bradfield) indicate following differences from adult: Bill, black (89) with whitish-grey (ne) basal third to tomia and dull pinkish (c3) at extreme base of lower mandible. Wattle, deep purple (2) with narrow violet (71) tinge around edge. At fledging, wattles also described as lavender (Innes & Hay 1995); pink or lilac (Flux & Innes 2001b); or evenly pink to pink-lilac and considerably smaller (*c.* 9 mm diameter) than those of adult (I. Flux & P. Bradfield). Orbital ring, dark grey (83) or grey-black (82). **First immature** As adult, though maturation of wattles can vary much; some birds have traces of pink coloration to wattle at 9 months after fledging. Most birds, however, have large blue wattles by 3 months after fledging (Flux & Innes 2001b).

MOULTS Based on examination of skins of seven adult, three first immatures and two juvenile subspecies *wilsoni*, and two adult nominate (AM, AIM, NMNZ). **Adult post-breeding** (Probably third and subsequent pre-basic). Little known. Complete. Primaries outward, starting at p1. In *wilsoni*, active moult of primaries recorded from: Apr. (2 of 4; PMS 48, 49) and May (1 of 1; PMS 36); in nominate, active moult of primaries recorded from Apr. (1 of 2; PMS 39). Others in Apr. with all primaries new; one in Jan., one in Aug. and one in Sept. with all primaries worn. Timing of moult of tail and body much as primaries. **Post-juvenile** (First pre-basic). Little known. Partial. Probably involves all feathers of body and marginal coverts. Skin (NMNZ) of 30-day-old fledgeling, collected in Jan., had already started post-juvenile moult and was replacing all marginal secondary upperwing-coverts and some scapulars and feathers of mantle. Another skin (NMNZ) from Feb. had not yet fully grown tail (juvenile rectrices about two-thirds grown) but had replaced most feathers of body and all marginal secondary coverts. This limited data suggests post-juvenile starts very soon after fledging (perhaps even before fledging) and occurs rapidly. **First immature post-breeding** (Second pre-basic). Timing and extent probably similar to adult post-breeding. One in Oct. with active moult of primaries (PMS 45), tail and body. One in Aug. and one in early Dec. not yet started moult.

MEASUREMENTS SUBSPECIES WILSONI: (1–2) NI, skins (AM, AIM, NMNZ): (1) Adults; (2) First immatures. (3) NI, live adults, sexed by role in incubation, with sex of subsample confirmed by DNA analysis (Flux & Innes 2001b; see Sexing).

		MALES	FEMALES	
WING	(1)	164.0 (3.16; 159–168; 7)	151, 160	
	(2)	156, 160, 160	156.4 (8.44; 145–167; 5)	
	(3)	158 (6.1; 48)	151 (6.3; 38)	**
TAIL	(1)	164.4 (7.98; 150–173; 6)	160, 166	
	(2)	156, 160, 160	165.3 (5.12; 160–171; 4)	
BILL S	(1)	34.0 (1.62; 31.2–35.6; 7)	28.9, 34.1	
	(2)	34.2, 35.0, 36.3	33.4 (1.24; 32.1–34.9; 5)	
THL	(3)	60.3 (1.3; 47)	58.1 (1.5; 37)	**
TARSUS	(1)	67.1 (2.89; 63.1–72.0; 7)	62.1, 72.1	
	(2)	66.1, 68.2, 72.2	67.0 (5.19; 62.3–72.8; 4)	
	(3)	68.6 (2.5; 74)	64.5 (2.3; 56)	**

NOMINATE CINEREA: (4) SI (including Stewart I.), adult skins (AM, NMNZ).

		MALES	FEMALES
WING	(4)	162.7 (1.95; 147–177; 6)	150, 154, 157
TAIL	(4)	171 (12.15; 150–181; 6)	147, 159, 162
BILL S	(4)	34.9 (2.62; 31.6–38.3; 6)	34.0, 35.0, 36.1
TARSUS	(4)	64.8 (4.11; 60.4–72.0; 6)	64.5, 64.7, 66.6

WEIGHTS SUBSPECIES *WILSONI*, NI: (1) Live, adults; sexed as sample 3 in Measurements, above. (2–3) From museum labels (NMNZ): (2) Adults; (3) First immatures.

	MALES	FEMALES	
(1)	233 (14.5; 75)	218 (16.8; 55)	**
(2)	–	224	
(3)	–	165, 193	

Hay *et al.* (1985a) give weight as 200–250 g (ages and sexes probably combined). At Mapara, NI, mean weight adult females 210 g (12.3; 32) and adult males 229 g (13.1; 46); at Rotoehu, NI, mean weight adult females 231 g (14; 14) and adult males 235 g (9.2; 17) (Flux & Innes 2001b). Flux & Innes (2001b) recorded gain in weight of 22% within 1 year (from 211 g to 257 g) in a female at Rotoehu.

STRUCTURE Wing rather short, broad and rounded at tip; tip of longest primary falls to about one-quarter length of tail when wing folded. Ten primaries; p4 and p5 longest; p10 58–71 mm shorter than p4 and p5, p9 31–36, p8 16–20, p7 5–14, p6 1–4, p3 1–6, p2 4–7, p1 8–12. Slight emargination to outer webs of p5–p8 and inner webs of p8–p10. Nine secondaries, including three tertials; tip of longest tertial falls short of tip of secondaries on folded wing. Tail long, graduated, slightly rounded or rather square at tip when closed; ten rectrices; t1 usually longest, sometimes t2, t5 18–26 mm shorter than t1; shaft of rectrices extends slightly beyond venation to form small projection. Juvenile rectrices narrower than those of adult. Bill rather short and stout, very robust; upper mandible strongly decurved and tip extends *c.* 3 mm past tip of lower mandible; culmen has ridge that narrows basally; nasal groove well feathered on basal half; large oval-shaped nasal aperture. Bill and palate uniquely modified for mastication of leaves: upper and lower mandibles have opposing horny sheaths, each with transversely rugose ridges that interlock when bill closed and form distinctive callus-like structure. Tongue structure distinctive (see introduction to Family). Tarsus long, compressed laterally; hind (plantar) surface sharply ridged; scaling laminiplantar. Tibia full feathered. Feet large and powerful. Middle toe with claw 43.2 (1.71; 41.5–45.1; 5); inner and outer front toes 65–75% length of middle toe, hindtoe 80–90%. Hindclaw 16–20 mm long.

SEXING No differences in plumage. Flux & Innes (2001b) use discriminant analysis of morphometrics to determine sex in adults. Using combined data from various sites on NI (Rotoehu, Mapara and elsewhere), 82.6% of birds were sexed correctly using the equation: $x = (0.397 \times \text{Tarsus}) + (0.038 \times \text{Wing}) - 32.424$, where $x \geqslant 0$ = male and $x \geqslant 1.19$ = female; the probability of correct sexing was >0.9 when $x \geqslant 1.19$ for males, and $x \leqslant -1.19$ for females. In the study of Flux & Innes (2001b) the sex of birds was generally determined by breeding behaviour (see Social Behaviour, Breeding). DNA analysis, using a sex-linked gene found on the W chromosome, corroborated sexing based on behavioural observations. See Innes & Flux (2001) for further details on site-specific discriminant functions.

GEOGRAPHICAL VARIATION Two subspecies; nominate *cinerea* from SI (including Stewart I.) and now probably extinct; and *wilsoni* from NI (described above in Plumages and Bare Parts). Nominate *cinerea* differs from adult *wilsoni* mainly in colour of wattle (see Bare Parts) but also by subtle differences in plumage (see below). Examination of skins of *wilsoni* suggests old specimens (n=4 collected before 1920s) have become foxed and are duller than more recently collected specimens (n=5 collected after 1950s). This may bias comparison of NI and SI birds as all SI specimens examined in this study were collected before the 1920s. Taking possible bias into account, examination of skins (AM, NMNZ) of 15 adult nominate indicates these differ from adult *wilsoni* by: (1) all except one SI skin lack pale bluish-grey border to rear edge of black facial mask (present on all NI birds); the one exception (NMNZ 1461; no details on locality) has just as distinct pale bluish-grey border as any NI birds, but there are no locality details on the label of this skin so the provenance of this bird is not certain; (2) plumage of body tends slightly darker (colour number the same as *wilsoni*) but some nominate look no different from *wilsoni* collected in late 1800s; (3) outer edges of t1, and outer webs of t2–t6, dull bluish-grey (c78) (cf. olive-brown in *wilsoni*); (4) facial wattle, bright orange grading to blue at base and on gape; on skins, wattle dull fleshy-yellow (cf. dull bluish-grey on skins of *wilsoni*). (For description of nestling, see Nestling, above.) No difference between subspecies in measurements of adult males but sample size small (see Measurements).

The absence of geographical clustering of genetic haplotypes in different extant NI populations suggests that contemporary populations are not genetically distinct despite currently being isolated (Double & Murphy 2000). The largest remaining population in Te Urewera NP has greater variability than the smaller Mapara and Rotoehu populations, but differentiation between the populations is low to moderate (Hudson *et al.* 2000). There is therefore no genetic barrier to translocations between populations, nor has the population bottleneck at Mapara significantly reduced the genetic variability there (Double & Murphy 2000; Hudson *et al.* 2000).

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Volume 7 (Part A), Plate 29

Kokako *Callaeas cinerea*   (page 965)
NOMINATE *CINEREA:* **1** Adult
SUBSPECIES *WILSONI:* **2** Adult; **3** Immature; **4** Adult

Saddleback *Philesturnus carunculatus*   (page 986)
NOMINATE *CARUNCULATUS:* **5** Adult; **6** Juvenile
SUBSPECIES *RUFUSATER:* **7** Adult; **8** Immature

Piopio *Turnagra capensis*   (page 958)
NOMINATE *CAPENSIS:* **9** Immature
SUBSPECIES *TANAGRA:* **10** Adult

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