

Order STRIGIFORMES

A rather homogeneous group of small to large, soft-plumaged birds with raptorial adaptations of feet and bill, and mainly nocturnal habits. Two families recognized: Strigidae (typical owls, including boobook or hawk-owls, scops-owls, eagle-owls, fish-owls, and pygmy-owls) and Tytonidae (barn or masked owls); between 133 and 178 species in 24–29 genera. On all continents except Antarctica, with centres of diversity in N. and S. America, Eurasia and Africa (Sibley & Ahlquist 1990; Schodde & Mason 1997). Most closely allied to Caprimulgiformes (nightjars and allies) (Burton 1973; Sibley & Ahlquist 1990; Christidis & Boles 1994; BWP). Based on DNA–DNA hybridization studies (Sibley *et al.* 1988; Sibley & Ahlquist 1990; Sibley & Monroe 1990) it has been suggested that the Caprimulgiformes should be placed within the Strigiformes (see Caprimulgiformes) but this view has been challenged (Christidis & Boles 1994) and not followed here. In the past, have also been placed with the Falconiformes (diurnal birds of prey), but this no longer accepted (Burton 1973; Christidis & Boles 1994).

Strigiformes characterized by (from Sibley & Ahlquist 1990; Schodde & Mason 1997; BWP): Palate schizognathous with desmognathous tendency, or desmognathous; vomer small and discrete. Basipterygoid processes functional. Nares holorrhinal and impervious. Syrinx bronchial with one pair of muscles. Fourteen cervical vertebrae. *Musculus expansor secundariorum* and biceps slip absent; *M. tensor patagium brevis* with wristward slip. Pelvic muscle formula A or AD. No *M. ambiens*. Two carotids. Coracoids connected. Flexor tendons Type 1. Hypotarsus simple. Tongue fleshy. Caeca large, long, with expanded ends. No crop. Oil gland (uropygial gland) well developed. Nostrils hidden by stiff bristles. Wings large, broad in proportion to length of body; 11 primaries, p11 much reduced; 12–18 secondaries; diastataxic. Tail short to moderate; 10–13 rectrices, usually 12. Hypotarsus with single deep furrow. Strong powerful feet with sharp curved claws (shared only with Falconiformes, which resemble Strigiformes only by convergence). Three toes forward and one hindtoe (anisodactylous); outer toe reversible; have strong talons for catching prey.

Appearance distinctive and familiar, with eyes facing forward and encircled by a facial disk or mask of modified feathers. See well by day but better by night, though said not to see in absolute darkness; hearing excellent, apparently most highly developed in Tytonidae (Thomson 1964; Fry *et al.* 1988; Schodde & Mason). Structure of facial disk aids in directing sound toward ears, at least in some species (see below). Ear-openings often placed asymmetrically on skull to aid in pinpointing origin of sounds. Eyeballs shaped like tapering cylinders; cannot rotate up, down or sideways; to focus on an object, must rotate whole head to bring it into view; neck can be moved through c. 270°. Bill hooked, with cere at base. Body plumage generally rather dense and soft, and edges of remiges frayed; these characters aid in silent flight. See introductions to Strigidae and Tytonidae for other general features, development of plumage, and moult strategies.

Occur in most habitats, from arid and semi-arid zones to tropical rainforest, alpine regions, and arctic moorland and tundra. Some species regularly in cultivated country, at least when foraging. Arboreal, terrestrial or both. Many require hollows, and therefore old trees, in which to nest, and are adversely affected by the removal of hollow-bearing trees (see below). Others nest in caves, in disused buildings, or on ground among rank vegetation (see below).

Worldwide, range from sedentary, to irruptive and dispersive, to migratory (mostly forms breeding in temperate zones); most Tytonidae considered sedentary or resident. In HANZAB region, *Ninox* mostly sedentary, with post-fledging dispersal poorly known; some of Tas. population of Southern Boobook *Ninox novaeseelandiae leucopsis* migrate N across Bass Str. in winter; Brown Hawk-Owl *Ninox scutulata* vagrant to HANZAB region and has resident tropical populations and migratory temperate populations. Three of five *Tyto* in HANZAB region sedentary or resident; Barn Owl *T. alba* and Grass Owl *T. capensis* irruptive and dispersive, with movements and breeding depending on abundance of their main prey, so that numbers in a region may follow a boom-and-bust cycle; coastal populations of Grass Owl, however, appear more stable perhaps because supply of food more consistent.

Raptorial predators. Some species occasionally take carrion (e.g. Powerful Owl *Ninox strenua*). Mainly nocturnal or crepuscular, though some diurnal or partly so (BWP). Use highly developed night vision, acute hearing, and silent flight to locate and catch prey, sometimes in complete darkness. Carnivorous; feed exclusively on animals: from earthworms, snails and insects, to frogs and reptiles and small and medium-sized birds and mammals; many species feed on small mammals, especially irruptive species; many Aust. forest-dwelling species feed on arboreal marsupials. Methods of hunting vary, both methods of searching and methods of attack; individual species will use variety of methods depending on type of prey being hunted. SEARCH METHODS include: (1) LOW SLOW QUARTERING, in silent flights (e.g. Masked Owl *Tyto novaehollandiae*, Grass Owl in HANZAB region); and (2) CONCEALED and UNCONCEALED PERCH-HUNTING, birds perching on fence posts, low branches and the like, scanning for prey using sight and hearing; long-stay, short-stay or both (e.g. Barking Owl *Ninox connivens*, Southern Boobook, Sooty Owl *Tyto tenebricosa*, Masked Owl); and (3) SUSTAINED HOVERING (e.g. Barn Owl). KLEPTOPARASITISM, or attempted kleptoparasitism, also observed

(see Southern Boobook). ATTACK METHODS include: *SALLY-STRIKING*, taking prey directly from foliage, branches or trunks of trees (e.g. Sooty Owl), or from air (e.g. Powerful Owl); *SALLY-POUNCING* from perches to catch prey on ground (e.g. Barn Owl); and *HOVER-DROP* from aerial searches (e.g. Barn Owl). Occasionally attack in direct *TAIL-CHASES* (e.g. Powerful Owl); *FLUSH-PURSUIT*, crashing into foliage to disturb prey (e.g. Rufous Owl *Ninox rufa*); or *GROUND-HUNTING AND STALKING*, running after prey on ground (e.g. Little Owl *Athene noctua*). Use any method singly or in combination depending on type of prey being hunted. In Barn Owl in ne. Vic., use of different search and attack methods varied seasonally; success also varied between methods (McLaughlin 1994). DETECTION OF PREY: By both sight and sound; Tytonidae highly adapted for detection by sound, probably more so than Strigidae. Adaptations well known in Barn Owl, which relies largely on hearing for detection of prey (e.g. Glue 1974; Knudsen 1981; Bunn *et al.* 1988). The facial disk of the Barn Owl is composed of modified feathers (see Tytonidae) and acts as a reflector of high-frequency sounds; two troughs running through the facial disk, from the forehead to below the bill, funnel sounds to the ears, which are long slits positioned asymmetrically near the eyes; the left ear is oriented downward and more sensitive to sounds from below, and the right is oriented upward and more sensitive to sounds from above; the asymmetry of the ears and differences in loudness between the ears used to determine elevation of sounds; horizontal location determined by using minute differences in loudness and timing of sound waves reaching each of the ears. Direction of movement of prey can also be determined by using sound. To increase the likelihood of a successful attack, the Barn Owl spreads its talons and aligns them with long axis of the body of prey; experimental studies showed that even in complete darkness alignment of strike changed with changes in the axis of the body of the prey. Claimed that can locate prey to within 1–2° in both horizontal and vertical planes (Knudsen 1981).

Capture prey with hawk-like talons; tear and eat prey using short hooked bill, often holding food with feet. Usually eat food soon after capture, though sometimes cache prey (e.g. Little Owl); *Ninox* often roost during day with remains of prey held in talons (e.g. see Powerful Owl). If flying with prey, often carry small prey in bill, large prey in talons. Small prey usually swallowed whole; large to medium-sized prey eaten piecemeal, often from head down (e.g. Glue 1967, 1974; Morton 1975; Schodde & Mason). Indigestible matter, such as arthropod exoskeleton and vertebrate bones, hair and feathers, regurgitated as pellets, which are roughly cylindrical, with rounded ends, and varyingly compressed. Fresh pellets of Aust. *Tyto* have dark glazed appearance, a result of the drying of the mucous coating secreted on the pellet before egestion; those of more insectivorous species, for example Southern Boobook, generally smaller, rounder and of looser composition (Morton 1975; Smith 1983). Suggested that pellets formed by muscular action in the gizzard during digestion; it is then passed to the proventriculus where it is stored till the stimulus for egestion received (Smith & Richmond 1972). Regurgitated pellets usually contain a good skeletal record of all vertebrate prey consumed, plus the hair of mammals; it is possible to recover evidence of each prey item consumed that forms a pellet (e.g. Ticehurst 1935; Wallace 1948; Glue 1967; Raczynski & Ruprecht 1974); such pellets often used in studies of diet of owls (see species accounts). Owls have acidic stomachs, with pH of 2.35, which digest 20–50% of skeletal material swallowed (see Schodde & Mason).

Owls characteristically nocturnal or crepuscular; roost during daylight, often in dark holes, such as tree-hollows or among dense foliage; some diurnal or partly diurnal (Thomson 1964; Fry *et al.* 1988; BWP); some normally crepuscular or nocturnal species known to hunt during daylight, probably when food in short supply (e.g. Grass Owl). In HANZAB region, all basically nocturnal or crepuscular or both, though Barking Owl sometimes vocal and active by day (Schodde & Mason). Cryptically patterned and coloured plumage camouflages birds when roosting during day (Thomson 1964; Campbell & Lack 1985; Schodde & Mason). Sleep with head erect and eyes closed by twin eyelids (Schodde & Mason). Roosting owls often harassed by smaller species of birds (e.g. McNabb 1994; Fleay; Schodde & Mason). Food often taken to habitual roosts to be eaten, and such sites often marked by pellets, remains of prey and excreta (e.g. Fleay; Schodde & Mason). Some species seem to sunbathe, e.g. Little Owl (Thomson 1964).

Social organization, behaviour and breeding best known for the cosmopolitan Barn Owl (Tytonidae) (e.g. Bunn & Warburton 1977; Bunn *et al.* 1982; Fry *et al.* 1988; Taylor 1994; BWP). Strigiformes usually monogamous, nesting in individual pairs which are apparently permanent. Outside HANZAB region, some males of some species known to be polygynous (e.g. Tawny *Strix aluco*, Snowy *Nyctea scandiaca*, Short-eared *Asio flammeus* and Boreal *Aegolius funereus* Owls). Some species of Tytonidae show some flexibility in social organization, usually breeding as solitary pairs but sometimes forming loose colonies (e.g. Grass Owl, Barn Owl), and such species may not form permanent pairs (includes Barn and Grass Owls in Aust.); others both permanently paired and territorial, with some such species also having ritualized evening duets by males and females during courtship (includes Lesser Sooty *Tyto multipunctata*, Sooty and Masked Owls in Aust.; see Schodde & Mason). Said that young owls can breed when c. 1 year old (Campbell & Lack 1985); in HANZAB region, some may breed at 10–11 months (e.g. Barking Owl, Barn Owl), and others may pair when 1 year old but not breed till 2 years old (e.g. Boobook Owl, Powerful Owl) (Fleay). During breeding, parents partition labour: usually only female incubates while male hunts and brings food to female; both sexes care for young (Thomson 1964; Campbell & Lack 1985; Fry *et al.* 1988; BWP) but usually only female broods and feeds young nestlings (Schodde & Mason). Most appear to be territorial (Campbell & Lack 1985), though some within HANZAB region can form loose colonies (see above). Few quantitative studies of territories or of home-ranges within HANZAB

region, and most claims of use and defence of territories and, especially, size of territories or home-ranges speculative and unsubstantiated, with few claims supported by studies of individually marked birds. Territorial owls can be very aggressive towards other birds of prey, especially during the breeding season; birds of prey and smaller owls form as much as 3–5% of the total food of the Eurasian Eagle-Owl *Bubo bubo* (Campbell & Lack 1985). In circumstances of aggression or threat, often respond with loud bill-snapping or clicking sounds (Thomson 1964; Fleay). Many species perform threat displays with head lowered, eyes wide open, feathers of back raised and wings held out; some also lower wings when feigning injury (Fry *et al.* 1988; Fleay). In defence, masked-owls often hiss, churr and snap bills, while crouching and swaying from side to side with wings outstretched and head thrust forward (Fleay; Schodde & Mason; Hollands). Calls probably important in social behaviour of all nightbirds; in owls, they are diagnostic of species and announce existence of occupied areas or territories and presence of individuals (Campbell & Lack 1985). Strigidae often call monotonously in territories and, during incubation, males seem to call brooding females away from the nest to feed them (Schodde & Mason). Compared with Strigidae, Tytonidae show some very different behaviour: do not call monotonously and, in Aust., only the Sooty Owl seems to call territorially from perches; have more ritualistic defence displays; males feed incubating females at and in nests, apparently never calling females off nest to be fed outside (Schodde & Mason). All *Ninox* breeding in HANZAB region utter double-noted call for advertisement or contact; in Aust. Tytonidae, advertising or contact calls are screeches, except in Sooty and Lesser Sooty Owls, which utter long siren-like descending whistles. Use of playback of calls commonly used to locate owls and is a standard procedure in survey work (e.g. Debus 1995). However, unnecessary use of playback, particularly during breeding season, can disturb and stress owls (McNabb 1994; Debus 1994, 1995).

Some species breed seasonally, others when conditions favourable, especially when food abundant (Thomson 1964; Campbell & Lack 1985); in HANZAB region, *Ninox* strictly seasonal (Fleay; Schodde & Mason); some species of *Tyto* breed opportunistically at any time of year (Debus 1994; Hollands). Most nest in holes in trees, rocks, cliffs or buildings, or sometimes in old nests of other species of birds, such as corvids and hollows of woodpeckers; the most well-known tytonid, the Barn Owl, often nests in hay-lofts, as well as other structures. Usually do not construct nests (Thomson 1964; Campbell & Lack 1985; Fry *et al.* 1988; Schodde & Mason); eagle-owls *Bubo* sometimes dig nest cavities into uninhabited anthills; some, such as Snowy Owl and Grass Owl, nest on ground or in low vegetation, and they may make a shallow scrape and even add some nest-material (Campbell & Lack 1985). Eggs white (Campbell & Lack 1985; Fry *et al.* 1988; Schodde & Mason); rounded in *Ninox*, oval in Tytonidae (Fleay; Schodde & Mason). Clutch-size varies, from one to 14; size of clutch sometimes related to availability of food (Thomson 1964; Campbell & Lack 1985). Olsen & Marples (1993) summarize breeding season, clutch-size and dimensions, shape and volume of eggs for all Aust. breeding species except Lesser Sooty Owl and Christmas Island Hawk-Owl *Ninox natalis*. Lay at intervals of 48 h (Schodde & Mason) or several days (Campbell & Lack 1985). Incubation begins with laying of first egg, resulting in asynchronous hatching, which enables stronger young to survive if food becomes short (Thomson 1964; Campbell & Lack 1985; Fry *et al.* 1988; Schodde & Mason). Usually female incubates (always in *Tyto*). Incubation period often >30 days (Thomson 1964); it is for all Aust. species. Little nest-hygiene in Tytonidae; said to be somewhat better in *Ninox* (Fleay; Hollands). Adult strigids seem to enter nesting hollows feet first; most tytonids head first, at least in Aust. species (Hollands). Young semi-altricial and nidicolous; hatch with eyes and ears closed, and a sparse covering of white natal down; unable to regulate temperature independently (Thomson 1964; Campbell & Lack 1985; Fry *et al.* 1988; Schodde & Mason). Nestlings either then begin pre-juvenile moult to juvenile plumage (Strigidae) or develop a second (mesoptile) down (Tytonidae), usually within c. 2 weeks of hatching (see Family accounts). In Aust., *Tyto* have longer fledging period and, size for size, are slower to develop than species of *Ninox* (Hollands).

Worldwide, 26 species of owls considered threatened. Overall, the major threatening process is extensive clearance and fragmentation of habitat, particularly in tropical zones (Collar *et al.* 1994). In HANZAB region, the only extinct taxa are Laughing Owl *Sceloglaux albifacies* of NZ and the Lord Howe I. and Norfolk I. subspecies of the Southern Boobook (*Ninox novaeseelandiae albaria* and *N.n. undulata* respectively); several other taxa threatened, either vulnerable (Christmas Island Hawk-Owl), rare (Powerful Owl, Rufous Owl *N. rufa queenslandica*, Masked Owl *Tyto novaehollandiae novaehollandiae*, Sooty Owl *T. tenebricosa tenebricosa*) or insufficiently known (Rufous Owl *N. rufa meesi*, Masked Owl *T. novaehollandiae kimberli*, *T.n. melvillensis*) (Garnett 1993). The impact of forestry on populations of forest-dwelling owls in Aust. contentious and not fully understood in HANZAB region. Several species of forest owls in Aust. thought to be threatened both by clearance of forests for agriculture and intensive forestry, which result in a shortage of large hollows suitable for nesting (see Milledge *et al.* 1991; Kavanagh & Peake 1993; Debus 1994; Kavanagh & Bamkin 1995; Kavanagh *et al.* 1995; Kavanagh 1997; also see accounts for Sooty, Masked, and Powerful Owls [Habitat, Distribution]). Fragmentation and degradation of forests by altered fire regimes, urbanization and clearance of habitat also threats; in n. Aust., changed fire regimes, in particular increased frequency of fires late in dry season, destroy nesting trees at edges of forests (Roberts 1977; Lundie-Jenkins 1993; Garnett 1993; Chafer & Anderson 1994). Use of rodenticides in canefields in n. Qld implicated in local declines of several species (Young & De Lai 1997).

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Family STRIGIDAE typical or hawk owls

Small to very large owls with forward-facing eyes within weakly developed facial disks. Vary considerably in size, from the Eurasian Eagle-Owl *Bubo bubo bubo* (66–75 cm total length and weighing 1.2–2.9 kg) to the tiny Least Pygmy-Owl *Glaucidium minutissimum* (12–14 cm total length). About 123–161 species in 22–27 genera; found on all continents except Antarctica, and on many islands. Ten species in five genera recorded HANZAB region: most in *Ninox* (five breeding species and one vagrant); monotypic Laughing Owl *Sceloglaux albifacies* of NZ extinct; one species of *Ketupu* recorded as early vagrant to Cocos-Keeling Is; one introduced species of *Athene* extant in NZ; and a species of *Strix* introduced to NZ but not established. Strigidae sometimes split into two subfamilies, Buboninae and Striginae, based on rather poorly defined differences in the structure of the ear (e.g. BWP).

The following characters differentiate Strigidae and Tytonidae (based on Sibley & Ahlquist 1990; Schodde & Mason 1997; BWP). Facial disk weakly developed (= mask) and more or less circular. Skull rather broad. Ears large, often positioned asymmetrically, with little covering or flap. Manubrium present in sternum. Metasternum deeply two-notched each side. Furcula free from carina. Oil gland (uropygial gland) naked. Emarginations on inner webs of 1–6 primaries; edges of remiges frayed. No aftershafts. Tail rounded. Feathers of tarsi point forward. Tarsometatarsus has bony ring on ventral surface of proximal end. Inner toe shorter than middle toe; claw of middle toe not pectinate.

Adults of most species have generally brown or reddish-brown plumage, often with paler barring, spotting or streaking. Face has modified feathers radiating out around eye forming small indistinct mask or facial disk. Many species (but not in HANZAB region) have flexible tufts of feathers above the eyes that are under muscular control; these possibly aid individual identification and communication (Burton 1973). All contour feathers rather soft. Iris usually rather bright, often yellow, red, or orange; other bare parts usually rather dull brown, yellow, grey or black. Sexes usually similar in plumage. Often sexually dimorphic in size, but which sex is larger varies between species. Post-breeding moult of adults complete. Primaries moult outward.

Nestlings hatch in sparse covering of natal (protoptile) down. Natal down replaced in pre-juvenile moult to juvenile plumage, which on body appears very downy. This plumage often referred to as a second, mesoptile, down or a mesoptile plumage (e.g. BWP) but treated as a juvenile plumage in this work because (1) most body-feathers in this plumage are semi-pennaceous with distinct shafts and loosely knot projecting barbs and are not truly downy; and (2) the semi-pennaceous body-plumage grows at the same time as clearly pennaceous and undeniably juvenile remiges and rectrices. See Tytonidae for further discussion of pre-juvenile and juvenile plumages. Adult plumage attained at 2–15 months old (BWP). For discussion of general biology, see introduction to Strigiformes.

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Sceloglaux albifacies Laughing Owl

Athene albifacies G.R. Gray, 1844, *Zool. Voy. 'Erebus' and 'Terror'*, *Birds* p.2, pl. 1 — Waikouaiti, South Island.

The generic name refers to the long, feathered legs (Greek σκέλος, leg, γλαύξ, owl); the specific name refers to the white facial disks (Latin *albus*, white, and *facies*, face).

OTHER ENGLISH NAMES Rock Owl, Rufous Laughing Owl, South Island or North Island Laughing Owl.

POLYTYPIC Nominate *albifacies*, SI and Stewart I., NZ; subspecies *rufifacies*, Buller, 1904, NI, NZ.

EXTINCT

HABITAT Based on contribution by R.N. Holdaway and T.H. Worthy. Early records indicated a preference for open areas or edges of forests or scrub (Williams & Harrison 1972). Recent studies have shown that Owls inhabited interior of dry (<1500 mm annual rainfall) temperate forests and tall shrublands; often round cliffs and rocky outcrops. Forests often complex, multi-storeyed assemblages of broadleaf, podocarp, beech or hardwood, with canopy dominated by tawa *Beilschmedia*, kamahi *Weinmannia*, beech *Nothofagus*, totara *Podocarpus*, rimu *Dacrydium*, matai *Prumnopitys* or kahikatea *Dacrycarpus*; sometimes with tall rata *Metrosideros* or rimu as emergents; and may contain stands of open kowhai *Sophora*, ribbonwood *Plagianthus* or kanuka *Kunzea* woodland. Also inhabited tall manuka *Leptospermum*, kanuka and *Coprosma* shrubland, sometimes with patches of grassland, or as mosaic with forest. Sometimes in forest confined to patches on floor of valleys or in moist gullies, which are surrounded by shrubland on slopes (McGlone 1989; McGlone & Neall 1994; McGlone *et al.* 1995; Worthy & Holdaway 1994a,b, 1995). Absent from moist forests where annual rainfall >2000 mm (R.N. Holdaway; T.H. Worthy).

Bred within forest: in caves, crevices in cliffs, and sometimes beneath boulders (R.N. Holdaway; T.H. Worthy). One pair said to have persisted in cleared farmland near Takaka for a short time (Worthy & Holdaway 1994a; Worthy 1997a).

Probably mostly foraged in lower levels of interior of

forests; taking prey from or near ground, and also from lower parts of trees (Holdaway & Worthy 1996; Worthy & Holdaway 1996a,b). Said also to have hunted in open or at edge of forests or scrub (NZRD).

Roosted in dry crevices in cliffs. Once found roosting in Maori hut (Buller 1905).

Clearing and burning of temperate forests and tall shrublands for conversion to farmland probably caused extinction, at least in part (Holdaway & Worthy 1996).

DISTRIBUTION AND POPULATION Based on contribution by R.N. Holdaway and T.H. Worthy. Extinct. Formerly endemic to NZ, on both main islands and Stewart I. Worthy (1997a,b) provides details of all historical specimens.

NI Formerly scattered but widespread. Holocene fossils recovered in Far North, at C. Reinga, Tom Bowling Bay and Tokerau Beach; said to have been heard on Little Barrier I.; remains also found at Waitomo and in Wairarapa. Most widespread in s. areas, S of line from Waikohu, near Te Karaka to Mt Egmont; occurred S to near Porirua (Hutton 1868; Williams & Harrison 1972; Millener 1981, 1983; Gill 1996; *contra* Scarlett 1967). Two records in 20th century: L. Waikaremoana, 1927 (Blackburn 1982); and near Purangi, c. 1930 (Williams & Harrison 1972). **SI** Formerly widespread E of main divide. Scattered records in Nelson, from Goulard Downs SE to Mt Maude; also at Mokihinui R. In Marlborough, fossil bones recovered at L. Grassmere; also scattered records at Rakautara,

Kaikoura and Conway R. Widespread in Canterbury, from Pyramid Valley and Waipara, S to Kurow and inland to Ls Wanaka and Ohau. Scattered records in Otago, mostly in E, from Ototara S to Dunedin; inland to Earnsclough, Waikaka and Popotunoa. In Southland, recorded from Castle Rock S to Riverton and Invercargill; also at L. Thomson and in Manapouri–Te Anau area. Also on Stewart I. (Moncrieff 1929; Williams & Harrison 1972; Gill 1996). Sight, or auditory, records since 1914 include: Mt Horrible, till 1915 (Williams & Harrison 1972); Goulard Downs, 1916–19 (Williams 1960); Raincliff, 1920s (Worthy 1997a); L. Thomson, 1930 (Bull & Falla 1951); Mokihinui R., Mar. 1935 (Moncrieff 1935); Mt Maude, c. 1939 (CSN 7); Waitati, 1930s (Williams & Harrison 1972); Manapouri–Te Anau area, c. 1950 (Williams & Harrison 1972). Reports at Waitohi R. persisted till 1970s. Fragments of eggs were found at Waianakarua in 1960 (Williams & Harrison 1972).

Chatham Is No acceptable records. Bones, said to be of this species, recovered in 19th century, identified by Forbes (1893) and confirmed by Dawson (1960); now discounted (R.N. Holdaway; T.H. Worthy).

Breeding Probably bred throughout range.

Status Extinct. Last specimen collected in 1914. Probably caused by introduction of predators, especially mustelids and cats, coinciding with clearance and burning of habitat (Williams & Harrison 1972; Holdaway & Worthy 1996; Oliver). On NI, formerly common in some areas, e.g. around Urewera (St Paul 1977; Oliver). Declines in populations coincided with European settlement, though range may have already been contracting at time of first contact. Decline said to have first become apparent in 1840s (Buller 1905; Williams & Harrison 1972; Millener 1981). On SI, populations said to have declined rapidly after c. 1860 (Millener 1981). Reduction of range said to have been obvious by end of 19th century (Williams 1962).

MOVEMENTS Sedentary. Thought to have occupied restricted territories or home-ranges (Holdaway & Worthy 1996).

FOOD Account prepared by R.N. Holdaway & T.H. Worthy. Carnivorous and insectivorous; mainly beetles, lizards, birds, bats, mice and rats. **Behaviour** Mainly nocturnal, but probably also crepuscular (Holdaway & Worthy 1996). Probably hunted by sound. Facial feathering arranged in disk, which would allow directional sight and hearing (R.N. Holdaway & T.H. Worthy). Most information on diet from sites with large deposits of prey remains. In any area, prey taken reflects availability of nocturnal or crepuscular animals of appropriate size. Remains of insects usually preserved only in very dry environments, hence apparent absence from diet in wetter w. and n. SI. At present, no information from NI. Introduced taxa in much lower numbers than native taxa at most sites, because they have been available and taken as prey for much shorter period. However, Pacific Rat (Kiore) *Rattus exulans* very common in some sites. Kiore have been in NZ for much longer than other introduced predators (Holdaway 1996) and replaced natural prey species as they became extinct (Holdaway & Worthy 1996). Adults ate mainly small vertebrates and large invertebrates; birds (<600 g, and mainly <200 g) largest proportion of prey biomass in all areas, at least before introduction of rodents (Kiore and mice); mystacinid bats, rats, geckos and Tuatara *Sphenodon punctatus* provided most of rest; skinks, amphibians (leiopelmatid frogs) and fish contributed little; rarely, took carrion (Worthy & Holdaway 1994a,b, 1995, 1996a,b; Holdaway & Worthy 1996; Worthy 1997a).

Detailed studies In N. CANTERBURY (all Holocene; Rich et al. 1979; Worthy & Holdaway 1996a,b): INSECTS: Carabidae: *Holcaspis subaenea*; *Mecodema costellum lewisi*; *M. sulcatum*; *Megadromus antarcticus*; *M. rectangulus*; *Metaglymma monilifer*; *Oregus*; Cerambycidae: *Somatidia*; Curculionidae: *Anagotus rugosus*; *A. stephenensis*; *Clypeolus cineraceus*; *Crisius longulus*; *C. ornatus*; *Didymus impexus*; *Ectopsis*; *E. ferrugalis*; *Epitimetes cuprealis*; *E. grisealis*; *E. lutosus*; *Irenimus aequalis*; *Phrynixus terreus*; *Psepholax sulcatus*; *Sargon suturalis*; *Strongylopterus hylobioides*; *Tychanopais fougieri*; *Tychanus verrucosus*; Elateridae: *Amychus* cf. *granulatus*; Histeridae; Lucanidae: *Lissotes reticulatus*; Scarabeidae: *Odontria* cf. *striata*; Tenebrionidae: *Mimopeus*; *M. costellus*; *M. lateralis*; *M. opaculus*. FISH: Anguillidae: *Anguilla*. REPTILES: Gekkonidae: *Hoplodactylus* cf. *duvaucellii*; *H. cf. maculatus*; Scincidae: *Oligosoma*; Sphenodontidae: *Sphenodon*. BIRDS: Kiwi *Apteryx*; Common Diving-Petrel *Pelecanoides urinatrix*; Mottled Petrel *Pterodroma inexpectata*; Cook's Petrel *P. cookii*; Fluttering or Hutton's Shearwater *Puffinus gavia* or *huttoni*; Grey-backed Storm-Petrel *Garrodia nereis*; *Euryanas finschi*; New Zealand Quail *Coturnix novaeseelandiae*; Weka *Gallirallus australis*; Hodgen's Rail *Gallinula hodgeni*; Double-banded Plover *Charadrius bicinctus*; Shore Plover *C. novaeseelandiae*; New Zealand Snipe *Coenocorypha aucklandica*; Black-fronted Tern *Sterna albobriata*; New Zealand Pigeon *Hemiphaga novaeseelandiae*; parakeet *Cyanoramphus*; New Zealand Owllet-nightjar *Megaegotheles novaeseelandiae*; Rifleman *Acanthisitta chloris*; wren *Xenicus*; South Island Stout-legged Wren *Pachyplectras yaldwyni*; Stephens Island Wren *Traversia lyalli*; Richard's Pipit *Anthus novaeseelandiae*; Yellowhead *Mohoua ochrocephala*; Grey Warbler *Gerygone igata*; Grey Fantail *Rhipidura fuliginosa*; New Zealand Robin *Petroica australis*; New Zealand Tomtit *P. macrocephala*; Tui *Prosthemadera novaeseelandiae*; Bellbird *Anthornis melanura*; European Goldfinch *Carduelis carduelis*; Common Starling *Sturnus vulgaris*; Piopio *Turnagra capensis*; Saddleback *Philesturnus carunculatus*; New Zealand Crow *Palaeorax moriorum*. MAMMALS: Chiroptera: Mystacinidae: Lesser Short-tailed Bat *Mystacina tuberculata*; Greater Short-tailed Bat *M. robusta*; Leporidae: European Rabbit *Oryctolagus cuniculus*; Muridae: Kiore; Brown Rat *Rattus norvegicus*; House Mouse *Mus domesticus*.

S. CANTERBURY (all Holocene; Worthy 1997a): FISH: Unident. REPTILES: Gekkonidae: *Hoplodactylus* cf. *duvaucellii*; *H. cf. granulatus*; *H. maculatus*; *Naultinus*; Scincidae: *Oligosoma* cf. *lineocellatum*; *O. cf. nigriplantare*; Sphenodontidae: *Sphenodon*. BIRDS: Kiwi; Grey-backed Storm-Petrel; Common Diving-Petrel; Mottled Petrel; Cook's Petrel; Fluttering Shearwater; Hutton's Shearwater; *Euryanas finschi*; New Zealand Quail; Weka; *Gallinula hodgenorum*; Double-banded Plover; New Zealand Snipe; New Zealand Pigeon; parakeet; Southern Boobook *Ninox novaeseelandiae*; New Zealand Owllet-nightjar; Rifleman; wren; South Island Stout-legged Wren; Stephens Island Wren; Skylark *Alauda arvensis*; Richard's Pipit; Common Blackbird *Turdus merula*; Song Thrush *T. philomelos*; Fernbird *Bowdleria punctata*; Yellowhead; Brown Creeper *Mohoua novaeseelandiae*; Grey Fantail; New Zealand Robin; New Zealand Tomtit; Tui; Bellbird; Yellowhammer *Emberiza citrinella*; European Goldfinch; House Sparrow *Passer domesticus*; Common Starling; Piopio; Kokako *Callaeva cinerea*; Saddleback. MAMMALS: Mystacinidae: Greater Short-tailed Bat; Muridae: Kiore; Brown Rat; House Mouse.

WEST COAST (last glacial; Worthy & Holdaway 1994a,b): FISH. AMPHIBIANS: Leiopelmatidae: *Leiopelma hamiltoni*. REPTILES: Scincidae: *Ligosoma*; Gekkonidae: *Hoplodactylus*. BIRDS: Kiwi; Fairy Prion *Pachyptila turtur*; *Puffinus speleus*, Common

Diving-Petrel; storm-petrel; *Eurynas finschi*; Weka; New Zealand Snipe; parakeet; New Zealand Owllet-nightjar; Rifleman; wren; South Island Stout-legged Wren; Richard's Pipit; Yellowhead; New Zealand Robin; New Zealand Tomtit; Piopio; Kokako. **MAMMALS:** Chiroptera: Greater Short-tailed Bat.

NELSON (Takaka Hill, Worthy & Holdaway 1994a,b, 1996a,b; Holdaway & Worthy 1996): **AMPHIBIANS:** Leiopelmatidae: *Leiopelma markhami*; *L. hamiltoni*. **REPTILES:** Scincidae: *Oligosoma*; Gekkonidae: *Hoplodactylus cf. duvaucellii*; *H. granulatus*; *H. maculatus*. **BIRDS:** New Zealand Snipe; parakeet; Southern Boobook; New Zealand Owllet-nightjar; Rifleman; wren; Stephens Island Wren; South Island Stout-legged Wren; Skylark; Richard's Pipit; Yellowhead: Brown Creeper; Grey Warbler; Grey Fantail; New Zealand Robin; New Zealand Tomtit; Tui; Bellbird; Piopio; Saddleback. **MAMMALS:** Chiroptera: Vespertilionidae: New Zealand Long-tailed Bat *Chalinolobus tuberculatus*; Mystacinidae: Lesser Short-tailed Bat; Greater Short-tailed Bat; Muridae: Kiore; House Mouse.

Young Fed large earthworms (Smith 1884). In captivity, readily accepted beetles, lizards, mice, rats, rabbits, and pieces of meat; young rats preferred (Turbott 1967).

SOCIAL ORGANIZATION AND BEHAVIOUR Account prepared by R.N. Holdaway and T.H. Worthy. Very little information; mainly from captivity (Smith 1884; Buller 1888). Apparently bred as solitary monogamous pairs; anecdotal evidence suggests that members of pair remained together. Most incubation by female (Buller 1888). Breeding sites probably 0.5–1 km apart along cliffs. Thought to have occupied restricted territories or ranges in forest as many other nocturnal forest owls. Roosted mainly during daylight and hunted at night, but probably some crepuscular hunting (Holdaway & Worthy 1996). Roosted in dry crevices in rocky cliffs; once in a Maori hut (Buller 1905). At rest, feathers of crown raised, increasing apparent size of head, and long tarsi concealed by plumage of underbody. Both members of one pair called when waking in evening. Male fed female at nest during incubation, male giving low call and female twittering in reply. Otherwise silent during breeding season (Smith 1884).

VOICE Account prepared by R.N. Holdaway and T.H. Worthy. Not well known. Call said to have varied considerably during year; very vocal in fortnight before nesting (Buller 1888). Voice of male much stronger and harsher than that of female (Buller 1888). Flight noiseless (Potts 1871, 1882).

Adult **LAUGHING CALL:** Prolonged *cack-cack-cack...* Also described as doleful shrieks, unearthly clamour, and dismal cries (Potts 1871, 1882). Described as similar to, but slower and more guttural than, call of Mottled Petrel (Williams & Harrison 1972); also described as similar to call of Cook's Petrel (Potts 1871, 1882); these species bred in areas supporting Laughing Owls (T.H. Worthy). Uttered when flushed (Potts 1882), and in flight every few minutes, particularly on dark and drizzly nights (Buller 1888). Heard incessantly on rainy nights (Williams & Harrison 1972), though this could, in part at least, be result of confusion with calls of Mottled and Cook's Petrels (T.H. Worthy). **TWO-NOTE CALL:** Loud hailing *cooey* by members of captive pair on waking in evening (Smith 1884; Buller 1888). Loud piercing prolonged *kee-wee*, each syllable of same length and intensity, and heard just after dark in 1927, may have been from this species (Blackburn 1982). **TWITTER:** Low peevish twitter by incubating female when offered food by mate (Buller 1888).

Young No information.

BREEDING Account prepared by R.N. Holdaway & T.H. Worthy. Little information; records in 1800s mostly of captive birds (Smith 1884; Buller 1888). Bred solitarily.

Season Eggs, Sept.–Nov. (Smith 1884; CM, NMNZ). Laying began Sept. (Smith 1884; Buller 1888). One bird incubating an egg on 25 Sept.; egg would have been laid about start of Sept. (contained well-grown embryo). A captive bird laid 23, 27 and 29 Sept. and 20 and 22 Oct. (Buller 1888).

Site Usually on floor of rock crevices, or caves, in cliffs or boulder ruckles; favoured sunny, often nw. aspect; sheltered and not drafty, or at least sheltered from drafts; most caves or fissures 1–5 m deep, which allowed birds to retreat into darkness. Buller (1888) found birds 5–6 m from entrance in dry crevices with narrow entrances; in some, 'birds must have forced their way in, but the crevice then widened'. Where crevices and caves not available, sometimes nested under large boulders and probably in hollows in trees. Many sites near bases of cliffs. Possibly some sites traditional or favoured. At least one site abandoned at, or shortly after, surrounding forest destroyed (Worthy & Holdaway 1994a); another site in farmland used till adults vanished (Worthy 1997a).

Nest, Materials One at Albury composed of small quantity of dried grass (C. Richardson); another at Ardenest, N. Canterbury, of *Scirpus* plants and other perennial herbs torn out with roots; remains of prey in matrix of nest (Worthy & Holdaway 1996b).

Eggs Broadly elliptical, blunt at both ends; surface chalky; white or creamy white (Oliver; R.N. Holdaway & T.H. Worthy). **MEASUREMENTS:** SI: 47.3 (2.08; 44.0–51.5; 14) × 39.2 (1.51; 37.3–43.0) (Oliver; CM [measured by R.N. Holdaway]); two eggs, locality unknown, 48.1 × 38.8, 45.5 × 38.9 (NHM [measured by R.N. Holdaway]). **Clutch-size** Two (Oliver); also two in various museum collections (BMNH; CM). **Incubation** Mainly by female (Buller 1888). **INCUBATION PERIOD:** c. 25 days (Buller 1888).

Young Altricial, nidicolous (R.N. Holdaway & T.H. Worthy). **Fledging to maturity, Success** No information.

PLUMAGES Prepared by A.M. Dunn. Hatched with sparse covering of down. Very little known on plumages other than adult. Probably underwent a complete post-breeding (pre-basic) moult each cycle, without change in appearance. Sexes similar. Two doubtfully distinct subspecies; nominate *albifacies* described below. Some skins slightly paler than description below; all but two of skins examined here were formerly mounts, some of which may have faded with exposure to light. There is no mention of paler birds in literature.

Adult (Definitive basic). Large dark heavily streaked owl with pale facial disk. Description based on examination of two male, three female and three unsexed adult skins (CM, NMNZ). **HEAD AND NECK:** Feathers of forehead, crown, nape, hindneck, and sides of neck, dark brown (21) with yellow-brown (c123C) edges, giving boldly streaked appearance. Feathers of lores, cheeks, ear-coverts and chin, cream (c92) with black (89) bristle-like shafts that extend past tip of vanes; feathers radiate outward from eyes and form pale facial disk. Feathers closest to bill have long black (89) bristle-like shafts and very little vane. Feathers on lower edge of facial disk, brown (119B) with broad off-white edges. Throat and foreneck, black-brown (c19) to dark brown (c21) with broad yellow-brown (c123C) to buff (c123D) edges to feathers giving streaked appearance. **UPPERPARTS:** Mantle, dark brown (21) with well-defined yellow-brown (c123C) edges to feathers giving boldly streaked

appearance (as hindneck). Feathers of back, rump and uppertail-coverts, brown (28) to dark brown (121) with a pair of large off-white (ne) to cream (c92) oval spots near sides of each feather. Scapulars, dark brown (121) with large cream (54) paired oval spots near sides of each feather. Whole of upperparts appear boldly streaked, but streaking appears more regular on mantle than on rest of upperparts. **UNDERPARTS:** Wholly black-brown (c19) to dark brown (c21) with broad yellow-brown (c123C) to buff (c123D) edges to feathers giving boldly streaked appearance. Ground-colour and colour of streaks grades from darkest on upper breast to lightest on undertail-coverts. Thighs and whole tarsus feathered, buff (123D to 124). **TAIL:** Rectrices, dark brown (c121) to black-brown (119) with widely spaced cream (54) bars and narrow cream (54) tip; bars c. 6 mm wide, spaced c. 22 mm apart. Underside slightly paler (colour matches do not differ). **UPPERWING:** Marginal and smaller lesser secondary coverts near leading edge of wing, dark brown (c21) with buff (c123D) fringes. Rest of secondary coverts, dark brown (c21) with large paired off-white to cream (92) spots at sides of tips and an off-white to cream (92) bar or partial bar in middle of feather. Lesser primary coverts near leading edge of wing, off-white with dark-brown (c21) mottling. Alula and median and greater primary coverts mostly dark brown (c21) with small off-white spots or partial bars. Remiges, dark brown (c121) with cream (c92) barring; on outer primaries, bars broken near shafts, giving a more spotted appearance. Bars 5–10 mm wide and spaced c. 20 mm apart. **UNDERWING:** Lesser and median coverts, mostly buff (c123D); many with dark-brown (21) shaft-streaks. Ground colour of greater coverts slightly lighter but dark-brown (21) streaking heavier. Remiges as upperwing but appear slightly paler.

Downy young At hatching, sparsely covered with coarse yellowish-white down (Buller 1888).

Juvenile Based on single specimen (MV) that had not quite reached fledging age and not yet in full juvenile plumage. All feathers of head, neck and body (except of small facial disk) soft and down-like, giving somewhat fluffy appearance. **HEAD AND NECK:** Mostly covered with soft down-like dark-brown (21) feathers with very narrow off-white (ne) tips. Feathers of lores, cheeks and ear-coverts like those of adult, forming small facial disk. **UPPERPARTS:** Mantle and rump, dark brown (21). Back and scapulars similar to adult but feathers softer and down-like. Uppertail-coverts, dark brown (c21) with diffuse cream (54) bars and cream (54) tips. **UNDERPARTS:** Wholly brown (c28) with light grey-brown (119D) edges to feathers; underparts appear diffusely streaked; feathers very soft and down-like, giving a fluffy appearance. **TAIL:** Not fully grown on specimen examined. Probably similar to adult but with more pointed tips to rectrices. **UPPERWING:** Similar to adult but primaries more pointed at tips. **UNDERWING:** No information.

BARE PARTS Based on published descriptions (Buller 1888; Gurney 1896). **Adult** Bill and cere, greyish horn. Iris, very dark brown or bright hazel. Orbital ring, grey. Feet and soles, reddish brown. Claws, greyish horn with dark tips. **Downy young, Juvenile** No information.

MOULTS Almost no information. No specimens examined in moult or had dates. Smith observed heavy moult in captivity between Dec. and Feb.; birds said to have become almost naked (Buller 1883). Loss of feathers noted in this observation possibly resulted from poor health of birds.

MEASUREMENTS (1) SI, adult, skins (CM, NMNZ).

	MALES	FEMALES
WING	(1) 247, 249	257, 264, 268
TAIL	(1) 141, 141	148, 152, 158
BILL C	(1) 17.9, 18.5	16.8, 19.2, 20.8
BILL S	(1) 28.7, 30.1	27.5, 29.6, 29.9

Females probably much larger than males, but few data.

(2) SI, adult, skins (CM, NMNZ). (3) NZ (location not specified), two fresh specimens and one skin (Potts 1871).

	UNSEXED
WING	(2) 262, 262, 268 (3) 257, 277, 325
TAIL	(3) 146, 150, 152
BILL C	(2) 16.8, 17.9
BILL S	(2) 27.9, 29.0, 30.4 (3) 36, 36
TARSUS	(2) 70.7, 70.7 (3) 64, 72, 85
TOE C	(2) 35.8

WEIGHTS Fresh adult specimen, c. 600 g (Rowley 1876–78).

STRUCTURE Wing long and broad. Eleven primaries: p6 or p7 longest or equal longest; p10 c. 58 mm shorter, p9 c. 18, p8 c. 3, p5 c. 7, p4 c. 18, p3 c. 35, p2 c. 48, p1 c. 60; p11 minute. P6–p9 emarginated on outer web, p7–p10 on inner web. Thirteen or 14 secondaries, including three or four tertials; tips of longest tertials fall between p3 and p4 on folded wing. Tail long and square; 12 rectrices. Bill short and broad: Upper mandible broad and straight at base, strongly downcurved near tip, which sharp and extends slightly beyond tip of lower mandible; cutting edges of upper and lower mandibles slightly downcurved. Lower mandible straight with rather blunt tip. Cere covers basal third of bill, with oval-shaped nostrils in front edge. Tarsus very long and fully feathered. Tibia fully feathered. Toes sparsely covered with hair-like feathers or bristles. Middle toe longest and hindtoe shortest; inner toe longer than outer toe. Claws robust and slightly curved.

GEOGRAPHICAL VARIATION Two subspecies currently recognized (NZCL), though validity of subspecies doubtful (see Williams & Harrison 1972; Fuller 1987; Gill 1996); *albifacies* occurred SI and Stewart I.; and *rufifacies* occurred NI. Only two specimens of *rufifacies* ever taken and both now lost. Some controversy over type-specimen of *rufifacies*; parts of specimen appeared to have been replaced with those of another species and specimen also showed signs of immaturity (see Williams & Harrison 1972; Fuller 1987; Gill 1996).

Little or no reliable information regarding consistent differences between subspecies and, in absence of specimens, not possible to confirm them. *Rufifacies* purportedly smaller than nominate, with more rufous face and with rufous suffusion through upperparts (Buller 1904; see also Williams & Harrison 1972). However, many individuals from SI rufous or rufous-faced (R.N. Holdaway). It has been suggested that rufous plumage possibly a morph (see Fuller 1987; Worthy 1997b). The little available osteological data indicate that NI birds possibly smaller (Gill 1996), but clinal variation cannot be ruled out.

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Sponsor: Mr HA Phillipps