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A fossil vertebrate fauna accumulated by laughing owls (*Sceloglaux albifacies*) on the Gouland Downs, northwest Nelson, South Island

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Abstract A rich fossil fauna accumulated by laughing owls (*Sceloglaux albifacies*) during the Holocene, is described from GD101 Cave, on the Gouland Downs, northwest Nelson, South Island, New Zealand. Twenty-eight species of bird, a tuatara, 3 frogs, at least 4 geckos, 1 skink, 2 bats, and 2 fish contribute to the species diversity. The fauna includes the first inland fossil record of New Zealand dotterel (*Charadrius obscurus*). The taphonomy of the deposit and the diet of the owl are discussed.

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INTRODUCTION

Fossil faunas reveal something of the past life in a region and provide valuable insights on past distributions and ecology of animals. In addition, where a fossil deposit results from the feeding activities of a predator, it can be invaluable in understanding that predator's biology. This paper describes a unique fossil fauna from the Gouland Downs in Northwest Nelson, South Island, New Zealand.

Although fossil faunas have not been described from the Gouland Downs area before, others have been from Honeycomb Hill Cave in the Oparara Basin (Worthy & Mildenhall 1989; Worthy 1993) and Megamania Cave in the Gunner River Valley to the south (Worthy 1998). To the west, small faunal assemblages are known from caves on the coast near Paturau (author's unpubl. data). East of Gouland Downs, faunas are known from Mt Arthur and Mt Owen (Worthy 1989) and the Takaka region (Worthy & Holdaway 1994b). However, except for 3 on Takaka Hill, these sites are not comparable. The many sites in Honeycomb Hill Cave are all at a lower elevation, and those at Megamania lower still. All are primarily pitfall deposits with the occasional vagrant death represented as well. On the high altitude sites on Mt Arthur and Mt Owen, all faunas have a pitfall origin, as do most in the Takaka area. The exceptions are the 3 faunas from Takaka Hill, which have been attributed to laughing owls (*Sceloglaux albifacies*). Two of these, Predator Cave and Hawke's Cave owl deposits, have been described (Worthy & Holdaway 1994a, 1996), but a 3rd in Kairuru Cave, has been only recently excavated by the author and R. N. Holdaway (MNZ collection, unpubl. data).

The fauna described here from the Gouland Downs is attributed to the activities of laughing owls and comes from a site at relatively high altitude in an area with both open and forested habitats. Laughing owls preyed on a wide variety of species (Worthy & Holdaway 1994a,b; Holdaway & Worthy 1996), and so deposits accumulating their prey remains differ greatly from the pitfall trapped faunas more commonly found in caves. The latter are dominated by flightless species and there is a heavy bias towards larger species being both preserved and found. The rich and diverse fauna reported here adds significantly to knowledge of the prehuman fauna of the area, particularly of the small vertebrates, and to knowledge of the diet of the laughing owl.

SITE LOCATION

The fossil site is in GD101 Cave at an elevation of *c*.620 m on the Gouland Downs, Northwest Nelson, South Island (Fig. 1). The cave lies within an outcrop of limestone about 250 m wide and 1 km long in the floor of the Gouland Downs and it carries a stream westward through a beech forest remnant.

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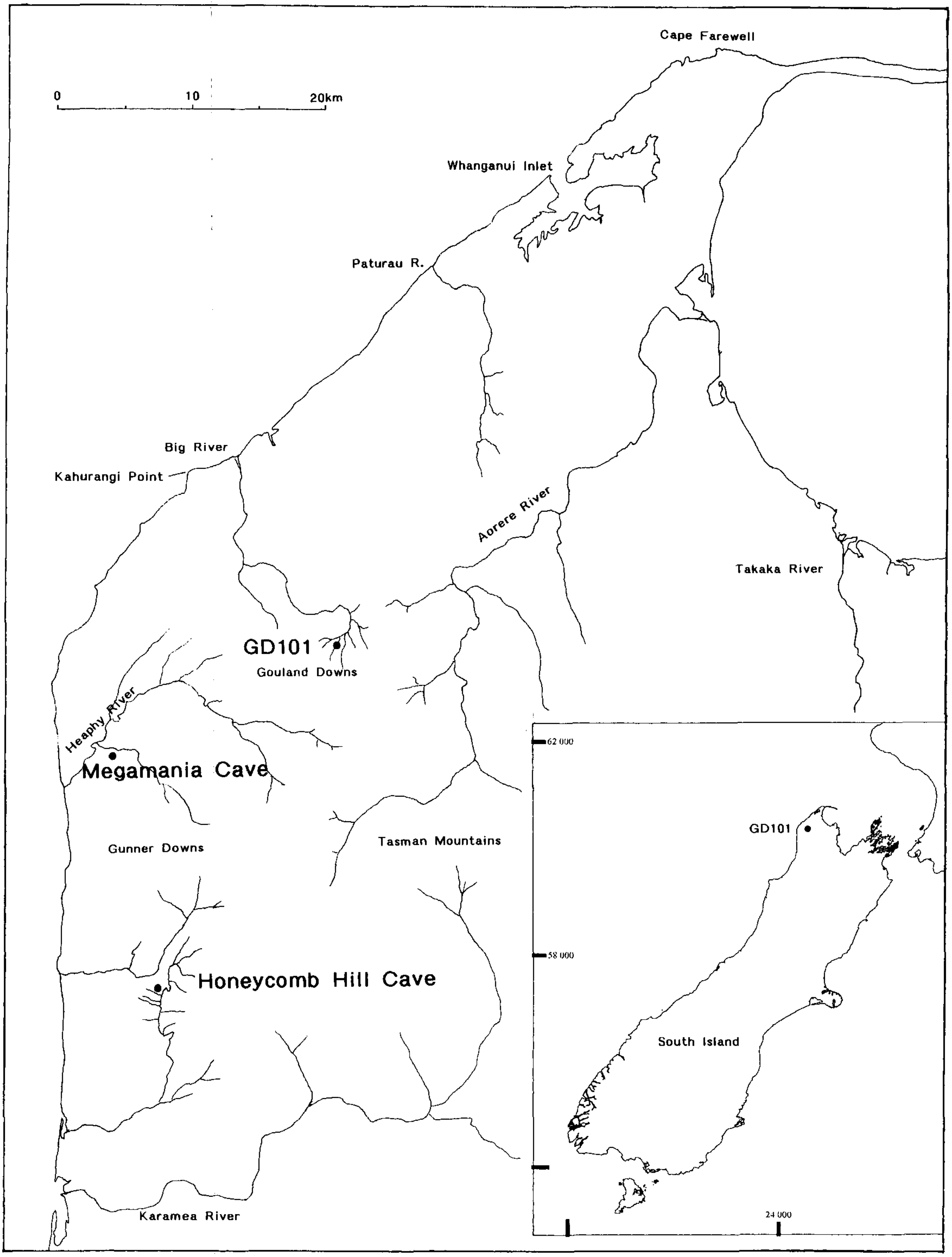

Fig. 1 The location of GD101 Cave, South Island, New Zealand, showing major rivers and the nearby major fossil sites of Megamania Cave and Honeycomb Hill Cave. Other major fossil localities include Mount Arthur, about 40 km east of Honeycomb Hill Cave, and Takaka Hill on the range east of and parallel to Takaka River. New Zealand metric grid.

The fossils were found in the resurgence entrance of this cave, NZMS 260, 1:50,000, M26 554350. The entrance is *c.*10 m wide and is *c.*6 m high in the middle and opens to the west, so receiving afternoon sun. The floor of the entrance is, at its lowest point, *c.*3 m above the ground below, but the fossil-bearing ledges are *c.*5 m above the ground and face towards the centre of the entrance. The edge of the ledge is U-shaped, so is furthest back from the entrance drip-line in the centre and converges on the drip-line at either side. Walking or climbing access is not possible from this western opening, but rather is effected through a tomo entrance *c.*20 m back from the cliff edge, and then negotiating a series of rockfall slopes.

The fossil deposit is on the ledge on the true right (northern) side of the entrance where the sediment slopes down from the wall for *c.*3 m to the vertical drop. The sediment is composed of the weathering products of the Oligocene limestone roof and walls. It is a yellowish-brown sandy loam with many fragments of barnacles, and includes many pieces of limestone spalled from the roof. Material that has slid downslope off the ledge has been washed away by the stream flowing from the waterfall in the centre of the entrance. Fossils were found along *c.*5 m of this ledge from a point where the sediment extends closest to the drip-line of the entrance on the northern wall. Sieving of test samples showed that bones were concentrated in the middle of the zone around a hollow *c.*500 mm across and 200 mm deep against the cave wall. The top 150 mm of the deposit in this region had a greater organic component appearing as a reddish loam, but below this the sediments were yellowish and had no bone. The hollow was probably a nest.

Extant vegetation and fauna of the study area

Druce & Simpson (1974) described the vegetation of the Gouland Downs. The limestone areas are vegetated in a mixed silver beech (*Nothofagus menziesii*) and mountain beech (*N. solandri*) forest, in which the forest floor and tree trunks are covered in moss. There is a very sparse lower understorey of shrubs in which young *Nothofagus* spp., *Pseudowintera traversii, Dracophyllum traversii,* and *D. townsonii* are prominent. Around the forest remnant, and especially in front of the western entrance to GD101 is a red tussock (*Chionochloa rubra*) grassland many square kilometres in extent, associated with the wire rush (*Empodisma minus*). Several species of *Celmisia* are common in the grassland. The better-drained slopes next to the forest have a cover of small shrubs, mainly the grass trees (*Dracophyllum* spp.), tree daisy (*Olearia virgata laxiflora*), and *Hebe albicans.* In other areas, the heath-like *Epacris alpina* and manuka (*Leptospermum scoparium*) scrub are common. Occasional granitic rocky outcrops support a low, sparse forest of *Nothofagus* spp. and *Dacrydium* spp. The Downs are crossed at regular intervals by swift-flowing streams with gravel or stony beds.

The native avifauna of the Gouland Downs area is limited at present. On 6 September 1999, I saw or heard the following birds within 1 km of the cave: great spotted kiwi (*Apteryx haastii*), blue duck (*Hymenolaimus malacorhynchos*), morepork (*Ninox novaeseelandiae*), weka (*Gallirallus australis*), kea (*Nestor notabilis*), rifleman (*Acanthisitta chloris*) [very common], tomtit (*Petroica macrocephala*), welcome swallow (*Hirundo tahitica*), pipit (*Anthus novaeseelandiae*), fernbird (*Bowdleria punctata*), grey warbler (*Gerygone igata*), bellbird (*Anthornis melanura*), silvereye (*Zosterops lateralis*), blackbird (*Turdus merula*), and goldfinch (*Carduelis carduelis*). Of other species, yellow-crowned parakeets (*Cyanoramphus auriceps*) are uncommon in the area, and kaka (*Nestor meridionalis*) and falcon (*Falco novaeseelandiae*) could be expected to visit the area. Brown creeper (*Mohoua novaeseelandiae*) are present in nearby forests.

The extant herpetofauna in the area is unknown.

METHODS

I first identified fossil bones at the site on 6 September 1999 and found that the deposit contained a diverse fauna of birds and reptiles. On 9 May 2000, Don Fraser and I excavated about 2.5 m^2 of the site, leaving fossiliferous sediment extending at least 2 m on either side. Within the 2.5 m^2, working upslope from the cliff-edge, all sediment trapped behind larger limestone blocks was sieved first, followed by an area *c.*1 m wide about the 'nest-hollow'. The sediment was excavated to a depth of *c.*250 mm because bones were concentrated in the top 150 mm; the sediment below 250 mm was barren. The sediment was passed through a sieve (6 mm-mesh) onto a 2 mm-mesh sieve. Bones were sorted on site from the material retained in the 6 mm sieve, but the material retained on the 2 mm sieve was bagged for later sorting in the laboratory. The sediment was dry and dusty, and contained many limestone fragments, so about 95% of it was separated from the fossil bearing concentrate on site. I sorted *c.*14 kg of the dry concentrate by spreading a teaspoonful at a time on a white tray so that all particles were separated from one another, then picked identifiable bones, teeth, and bone fragments from it. All fragments of eggshell were also collected.

I identified the fossils using reference specimens previously identified by comparison with museum specimens or prepared from modern animals. Additional material was borrowed from the Museum of New Zealand (MNZ). Geckos other than *Hoplodactylus duvaucelii,* were identified by features of the frontal bone outlined by Worthy & Holdaway (1995: 350) and Worthy (1997). Gecko bones very much larger than those of *H. granulatus* were referred to *Hoplodactylus* sp. cf. *H. duvaucelii*. All fossils are catalogued in the MNZ fossil bird collection (MNZ S38776-38826).

RESULTS

The 650 bird bones identified represented 27 species and at least 87 individuals (Table 1). In addition, the vertebrate species diversity was enhanced by 2 bats (41 elements, 7 individuals); 1 species of tuatara (76 bones, 3 individuals), 3 frogs (60 bones, 7 individuals); 4 geckos (1000s of bones from 225 individuals as determined by the number of frontals); 1 or more skinks (100s from 17 individuals); and at least 2 fish (17 bones). A total of at least 346 individuals was represented.

Eggshell fragments found in the sediment were readily separated into moa and non-moa by shell thickness: a thinner shell with a mean thickness of 0.255 mm (SD = 0.018, range 0.22-0.28 mm, n=10) and white moa shell with a mean thickness (apparently normally distributed) of 0.98 mm (SD = 0.172, range 0.63-1.35 mm, n=25).

Two taxa can be singled out of this fauna as perhaps not originally deposited with the rest. The New Zealand falcon (*Falco novaeseelandiae*) was represented by a single, fresh-looking sternum found on the surface. It showed no sign of predation so may have had a separate and more recent origin. Secondly, the single Pacific rat (*Rattus exulans*) bone was found on the first visit to the site on the surface and not in the area of the main deposit. It is severely digested, so was undoubtedly deposited by an avian predator. As no other bones of this species were found in the main deposit, the rat bone probably had a separate and later origin.

The taphonomy of the material in the deposit points clearly to its having been accumulated by an avian predator. The bones commonly have greenstick fractures, especially on larger pieces, and most bones show signs of erosion resulting from digestion as described and figured by Worthy & Holdaway (1994a) and Bochenski (1997). Bones of larger species (*Ninox, Nestor, Strigops*) were very fragmented, whereas smaller taxa were successively less broken, and most bones of the smallest (e.g., *Acanthisitta chloris* and *Hoplodactylus* spp. were whole). Only fragments of crania of *Strigops* and *Nestor* were present. *Strigops*, the largest prey species, was represented mainly by fragments of crania, basihyoids, and paraglossals (tongue bones), and phalanges, suggesting that only the feet and heads of this species were brought back to the site.

The prey species composition was dominated by nocturnal animals. Of the birds, nocturnal taxa included *Apteryx, Pelecanoides, Coenocorypha, Ninox, Aegotheles,* and *Strigops*. Of the other vertebrates, all the frogs (*Leiopelma* spp.), all the *Hoplodactylus* geckoes, the *Sphenodon*, and all bats (*Mystacina* spp.) are or were nocturnal as well. In total, 251 (72.5%) of the individual vertebrates represented were nocturnal.

DISCUSSION

Identification of the predator

The rich and localised nature of the fossil deposit in sediment of autochthonous origin, i.e. from within the area of the site, suggests the fossils derived from predator activity, and were not washed into the site. That many of the bones have greenstick fractures, which imply breakage pre- or perimortem, also suggest that the deposit was accumulated by a predator (Andrews 1990; Worthy & Holdaway 1994a). Avian predators eject partially digested material in pellets in which bones characteristically have rounded edges to breaks, shaft thinning, and erosion holes (e.g., Andrews 1990; Worthy & Holdaway 1994a; Bochenski 1997). Bochenski & Tomek (1997) showed that soil-weathering processes can create rounded off fracture edges on bones similar to those caused by digestion. However, they also showed that weathering created pitting and flaking on whole bones and holes with sharp edges and rough bases, whereas digestion resulted in holes with rounded edges concentrated at the articular ends. Moreover, weathering does not cause extensive shaft thinning.

The bones from GD101 exhibit a variety of features including rounding of greenstick fractures, severe shaft thinning, holes with rounded edges at articular ends and, significantly, varying degrees of each of the above. Weathering should act uniformly on all specimens in a deposit, its effect depending on time of exposure but varying with bone robustness and density. Therefore, each element of a given species would be affected in a similar way if soil weathering was the primary modifier. However, predatory birds retain bones for varying intervals before ejecting them in a pellet, so some bones are heavily digested and others little affected. Moreover, bone digestion is delayed by surrounding tissues (at the time of ingestion) so that it occurs preferentially at greenstick fractures (the torn edges of bites). Phalanges can often be little digested as often they are protected by scaly skin. The sum of these effects is that the same bone from a single species may be digested to varying degrees in a single deposit.

The principal predators in prehuman New Zealand were birds. Avian predators such as falcons and owls cough up the partially digested remains of bones and feathers as pellets, which are often discarded at nest or roost sites. However, the taphonomic signature these birds leave in and on

Table 1 List of taxa recovered from sediments in the fossil site at GD101 Cave, Gouland Downs, Heaphy Track, northwest Nelson. NISP, number of specimens, MNI, minimum number of individuals; %Group is percentage the MNI of a taxon is for the group (birds, bats, herpetofauna) totals. %Total is the percentage the MNI that a taxon is of the total MNI of vertebrates from the site. All specimens are identified as prey items because of the presence of greenstick fractures and digestion features on the bones, unless otherwise stated in Notes.

Taxon	Vernacular name	NISP	MNI	% Group	% Total	Notes
Dinornithiformes	moa chick	8	1	1.15	0.29	
Apteryx owenii	Little spotted kiwi	2	1	1.15	0.29	
Pelecanoides sp.	Diving petrel, sp. indet.	2	1	1.15	0.29	
Charadrius obscurus	New Zealand dotterel	3	1	1.15	0.29	
Coenocorypha sp.	South Island snipe	9	2	2.30	0.58	
Falco novaeseelandiae	Falcon	1	1	1.15	0.29	Not prey item
Gallirallus australis	Weka	6	1	1.15	0.29	
Ninox novaeseelandiae	Morepork	27	3	3.45	0.87	
Cyanoramphus sp. cf. *C. auriceps*	cf. Yellow-crowned parakeet	74	6	6.90	1.73	
Nestor meridionalis	Kaka	15	3	3.45	0.87	
Strigops habroptilus	Kakapo	116	8	9.20	2.31	
Aegotheles novaezealandiae	Owlet-nightjar	64	4	4.60	1.16	
Pachyplichas yaldwyni	Stout-legged wren	2	2	2.30	0.58	
Acanthisitta chloris	Rifleman	189	26	29.89	7.51	
Xenicus sp.	Bush / Rock wren	25	4	4.60	1.16	
Traversia lyalli	Stephen's Island wren	2	1	1.15	0.29	
Anthus novaeseelandiae	New Zealand pipit	1	1	1.15	0.29	
Bowdleria punctata	Fernbird	4	1	1.15	0.29	
Mohoua ochrocephala	Yellowhead	7	1	1.15	0.29	
Mohoua novaeseelandiae	Brown creeper	4	2	2.30	0.58	
Petroica macrocephala	Tomtit	6	2	2.30	0.58	
Petroica australis	South Island robin	42	7	8.05	2.02	
Philesturnus carunculatus	South Island saddleback	9	1	1.15	0.29	
Prosthemadera novaeseelandiae	Tui	8	1	1.15	0.29	
Anthornis melanura	Bellbird	12	4	4.60	1.16	
Callaeas cinerea	South Island kokako	2	1	1.15	0.29	
Turnagra capensis	South Island piopio	10	1	1.15	0.29	
Rattus exulans	Pacific rat	1	1		0.29	suspect not part of main fauna, found on surface
Mystacina tuberculata	Lesser short-tailed bat	7	3	42.86	0.87	
Mystacina robusta	Greater short-tailed bat	34	4	57.14	1.16	
Fish		17				includes 2 dentaries
Sphenodon sp.	Tuatara	76	3	1.20	0.87	
Leiopelma hamiltoni	Hamilton's frog	3	2	0.80	0.58	
Leiopelma hochstetteri	Hochstetter's frog	3	2	0.80	0.58	
Leiopelma hamiltoni/ hochstetteri		18				
Leiopelma markhami	Markham's frog	36	3	1.20	0.87	
Hoplodactylus sp. cf. *H. granulatus*	cf. Forest gecko	204	204	81.27	58.96	frontals
Hoplodactylus sp. not *H. granulatus*	cf. Common gecko	9	9	3.59	2.60	frontals
Hoplodactylus sp. cf. *H. duvaucelii*	cf. Duvaucel's gecko	15	2	0.80	0.58	
Naultinus sp.	Green gecko	9	9	3.59	2.60	frontals
Gecko sp.		1000s				bones other than frontals
Skink sp.		100s	17	6.77	4.91	MNI by frontals
Total birds		650	87	25.14		
Total bats		41	7	2.02		
Total herpetofauna		373	251	72.54		
Total all		1082	346			

the ejected material varies. Falcons break up their prey to a greater degree than owls and digest the material much more severely so deposits formed by falcons consist of numerous small, heavily-digested pieces (Andrews 1990; Worthy & Holdaway 1995). Owls, especially tytonids, tend to swallow their prey whole, and their digestive acids are not as strong as those of falcons. Their deposits are characterised by numerous lightly- to moderately-digested whole bones and a good representation of all elements (Andrews 1990). However, strigid owls typically tear their prey into bite-sized fragments before swallowing them, so many more bones are broken (Andrews 1990; Bochenski *et al.* 1993; Bochenski & Tomek 1994; Bochenski 1997). Bones of small prey are less affected by breakage than those of large prey (Bochenski *et al.* 1993).

Some characteristics of avian predator deposits in New Zealand have been described by Worthy & Holdaway (1994a, 1996) and Holdaway & Worthy (1996) for laughing owls, and Worthy & Holdaway (1995) and Worthy (1997) for New Zealand falcons. Falcon prey deposits had extremely fragmented bones that were heavily digested and most bones were of diurnal species. The deposits from Hermit's Cave and the Predator Cave attributed to the strigid laughing owl (tytonids do not occur in New Zealand) had a high frequency of nocturnal species, and different skeletal elements were usually well represented, with some complete bones of most. Damage on specific elements varied according to the robustness of prey species. For example, a coracoid of a parakeet (*Cyanoramphus* sp.) was more likely to survive than that of a robin (*Petroica australis*). In falcon deposits, the nocturnal geckos are rare and diurnal skinks common.

The fauna from GD 101 is represented by numerous bones often with greenstick fractures and exhibiting a variety of digestion features, all of which indicate that an avian predator was responsible for their deposition. The bones from GD101 include most elements of the skeleton, many being whole, with only bones of large species being very fragmented. Digestion features are generally not severe. Because, as noted above, falcons characteristically leave highly-fragmented, heavily-digested remains of mainly diurnal species, they can be discounted as the accumulating agent. In New Zealand this leaves just the 2 owls - the laughing owl and morepork. Again, the domination of the prey fauna by nocturnal taxa (72.5% of MNI) is consistent with the predator being an owl. Moreporks rarely roost in caves, and eat mainly insects and microvertebrates. They could not overpower the larger species represented in the fauna. Moreover, the prey remains in GD101 include morepork bones, so it is reasonable to assume that the predator responsible the laughing owl.

Why was the eggshell there?

The eggshell in the site could have come from eggs laid in the site or represent fragments carried to the site. The thin shell is probably from laughing owl eggs because the bone remains indicate this species used the site. The thickness compares well with the 0.23-0.29 mm reported for modern laughing owl eggshell by Worthy & Holdaway (1994). Alternatively, it could be from similar-sized eggs of another species. Both blue duck (*Hymenolaimus malacorhynchos*) and kakapo (*Strigops habroptilus*) use caves for nesting but because the eggshell was intimately associated with the bone accumulation the eggshell is probably from laughing owl eggs.

The thicker shell can only be from moa eggs. It is relatively thin for moa eggshell so is assumed to be from one of the smaller species, which in the area include only *Anomalopteryx didiformis* and *Megalapteryx didinus*. The latter has green eggshell so can be excluded (McCulloch 1992; Worthy 1997: 95). How the eggshell came to be in the site is of interest, because moa could not get to the site now. Two scenarios seem possible. First, the moa could have gained access along a ledge since collapsed from the adjacent hillside. This would mean that the laughing owl and moa nested in the same place, as the moa shell was not found elsewhere in the entrance chamber. Alternatively, the laughing owl may have brought fragments of the moa shell to its nest. A series of dates on the eggshell and bones might resolve the alternatives, because if the eggshell and bones are of different ages then they would have had separate origins in the deposit. However, moa eggshell has been found in other owl sites and in places where no moa could presently get, such as J38/f73 on Glenlea Station and J39/f239 in Limestone Valley Road (Worthy 1997), so it seems likely that laughing owls either ate moa eggs or used parts of them to adorn their nest.

The age of the deposit

The age of this fauna has not been measured directly. The primary deposit lacks any introduced taxa, including the Pacific rat (*Rattus exulans*), so is older than 800 years assuming the rat arrived with Polynesian settlers (Anderson 1991), or possibly older than about 2000 years assuming it arrived with earlier visitors (Holdaway 1996, 1999). The fossil assemblage contains many of the species living in the area at present which suggests that it was derived from a living fauna occupying a mixed forest and open country habitat such as now exists around the site. The environment in the area during the Pleistocene would have been severely affected by an average drop in temperature of 5º C and the associated lowered treeline from the present 1200 m to about 400 m (McGlone 1988). As the site is at *c.*640 m altitude the area around it can now support forest, but then would have been well above the treeline and so could only have supported a grassland at best, and probably had extensive fellfields. Forest and tall shrubland species such as riflemen, tomtit, and morepork could not have lived in such open areas, so it seems likely that the deposit was laid down in the Holocene (<10,000 years B.P.).

Faunal composition

Birds

At least 27 species of bird are represented in the GD101 owl site to which can be also added the laughing owl even though there were no bones of it preserved there. The laughing owl weighed *c.*600 g and probably rarely preyed on animals very much larger than itself. The extensive Predator Cave deposit indicates that the owl preferred birds the size of parakeets and bellbirds – 100-250 g (Holdaway & Worthy 1996). At Hermit's Cave the commonest prey was fairy prion (*Pachyptila turtur*) (Worthy & Holdaway 1994a). In the GD101 owl site, larger animals were restricted to a single moa chick and kaka and kakapo though most of the individuals of these were also juvenile and so probably more easily killed. The largest taxa are represented mainly by fragments of the skull and phalanges, suggesting that the owls preferentially ate the head region of the carcasses. Any ingestion of muscle alone would not be recorded in the deposit, but significantly, the data suggest that the whole carcasses were not brought back to the nest, as no long bones were found.

The fauna from GD101 differs significantly from that at Hermit's Cave, which is near Charleston, further south on the West Coast. The Otiran age deposit of Hermit's Cave is closer to the coast than GD101 and had numerous fairy prions (*Pachyptila turtur*), diving petrels (*Pelecanoides* sp.) and Scarlett's shearwaters (*Puffinus spelaeus*) (Worthy & Holdaway 1994). Hermit's Cave and the Mimiomoko Pocket fauna in the Waipara River of North Canterbury (Worthy & Holdaway 1996) suggest that if a petrel colony was within the normal foraging range of an owl site petrel bones were likely to be numerous in the fauna. Only 2 bones of diving petrel were present in the GD101 fauna. Diving petrels have been found as pitfall trapped specimens in Honeycomb Hill Cave and Megamania Cave indicating that there were colonies close to those sites, only a few kilometres to the south of GD101. Possibly, the bird caught by an owl on Gouland Downs was en route to a nearby colony.

A significant record in the GD101 fauna is that of a New Zealand dotterel (*Charadrius obscurus*). This is the first inland fossil record of this species and suggests that it bred in the open areas near the site. Southern populations of this species breed, or bred historically, mainly inland and often in the subalpine zone in isolated pairs (Dowding & Murphy 1993; Dowding 1994). The southern subspecies breeds now only on Stewart Island on the tops of various ranges and possibly in the inland dunes at Mason Bay where I saw territorial defence behaviour in December 1997 (author's unpubl. data).

As in the Predator Cave fauna, parakeets were important in the diet of owls on the Gouland Downs. However, in GD101, all were very small individuals, probably yellow-crowned parakeet (*C. auriceps*) or orange-crowned parakeets (*C. malherbi*) rather than red-crowned parakeet (*C. novaezelandiae*) (Worthy & Holdaway 1994b: fig. 12). In contrast, in the large sample from Predator Cave on Takaka Hill, most fossils were in the size range of red-crowned parakeets (Worthy & Holdaway 1994b). Only the yellow-crowned parakeet survives in northwest Nelson. The orange-fronted parakeet formerly lived in northwest Nelson. It has been recorded only from forest and subalpine scrub (Oliver 1955) and now survives only in beech forest in North Canterbury (Boon *et al.* 2000).

Passerines account for more than half the avian diversity in the deposit, but most species are represented by few individuals. The most common, the rifleman (*Acanthisitta chloris*), comprised 30% of the avian prey. Rifleman were also very common in the Predator Cave fauna. At least 4 wren species were present but I did not distinguish *Xenicus gilviventris* and *X. longipes*. The only wren not represented is the extinct *Dendroscansor decurvirostris*, which is exceedingly rare as a fossil. Other than wrens, only robin and bellbird were common, as they were also in the Predator Cave fauna.

Herpetofauna

The herpetofauna, particularly the geckos, were the most important prey for owls at GD101, accounting for 72% of the minimum number of individual vertebrates in the site. The most common species was a *Hoplodactylus* sp. similar to the forest gecko (*H. granulatus*). As forest geckos are bigger than rifleman, the commonest bird prey, they must have contributed a large proportion of the owl's diet. A smaller *Hoplodactylus* sp. with flat frontals may be one of the *H. maculatus* superspecies complex that is yet to be described (Daugherty *et al.* 1994). Of significance is the recovery of bones that probably belong to *H. duvaucelii*, or a closely related and similar-sized species. Bones of similar, large, *Hoplodactylus* have been found elsewhere in the South Island (e.g., Worthy & Holdaway 1994b, 1995) but are generally rare. At least 9 individuals of a green gecko *Naultinus* sp. were also present.

Both adult and juvenile tuatara were present. This is consistent with their former widespread mainland distribution that included the montane zone (Worthy & Holdaway 1995; Worthy 1998).

Fish were represented by 17 unidentified bones. Several are large and probably *Anguilla* sp., but 2 small dentaries with teeth could well be an eleotrid from their size. Fish have been recorded in laughing owl sites previously, albeit rarely, in North and South Canterbury (Worthy & Holdaway 1996; Worthy 1997). Their presence underscores the wide range of prey taken by the owls in an undisturbed environment.

Summary

The fossil assemblage from GD101 on the Gouland Downs indicates that laughing owls in that area preyed on a wide variety of birds, bats, lizards, frogs, and fish, as they did at all other sites. The assemblage reinforces previous conclusions that laughing owls were not specialised predators and took whatever they chanced upon and could subdue. This doubtless results from an absence of competition, as there were no other similar-sized owls in the New Zealand fauna, unlike the situation in all continents. Therefore, sites containing faunas accumulated by laughing owls provide a relatively unbiased sample of the fauna within the laughing owl's prey size range. Because the more common typical pitfall or swamp deposits are biased towards terrestrial and large taxa, the relatively unbiased samples, especially of the smaller taxa, provided by laughing owl deposits are of great importance in palaeoenvironmental and palaeoecological reconstructions.

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