Diet and biology of the laughing owl *Sceloglaux albifacies* (Aves: Strigidae) on Takaka Hill, Nelson, New Zealand

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(With 6 figures in the text)

The faunal composition of two Holocene fossil deposits of small vertebrates provided new information on the diet and biology of *Sceloglaux albifacies*, a strigid owl endemic to New Zealand. The taxonomic composition and several measures of diversity of the prey accumulation are given. Most taxa in the deposit had a mass of 50–150 g, but species up to 400 g were also present. The owl was a generalist feeder, but the prey biomass distribution showed that a few taxa provided most of its energy requirements. Changes in the diet appeared to coincide with the appearance of *Rattus exulans*, the Polynesian rat, and the consequent decline or extinction of several prey. The ecologies of extant taxa represented in the deposit suggest that the owl was primarily a nocturnal forest species. Many prey taxa were terrestrial. Species richness was higher for both diurnal (by 50%) and nocturnal (by 63%) vertebrates in the deposit than in the present fauna around the site. Analysis of possible guilds in the pre-human and present faunas of Takaka Hill suggests that ground-frequenting taxa were most severely affected by extinctions; three guilds vanished entirely.

Introduction

The Quaternary avifauna of New Zealand contained many taxa of smaller birds in addition to 11 species of very large flightless moa (Dinornithiformes). Little was known of the distribution of relative abundance of the smaller taxa because of taphonomic and collection biases towards the robust bones of the larger birds. Until recently, few sites rich in small vertebrates were known (Worthy & Mildenhall, 1989). There was sufficient material for taxonomic studies (e.g. Scarlett, 1968; Millener, 1988; Millener & Worthy, 1991) but not enough for faunal analyses. The discovery of predators' sites has changed the situation (Worthy & Holdaway, 1993, 1994*a, b*).

There was also little information on the biology of the endemic strigid owl *Sceloglaux albifacies*, only a few anecdotal reports of the diet and behaviour dating from the late 19th Century (Williams & Harrison, 1972). As the largest nocturnal predator in New Zealand, the owl was potentially a major selective force in the evolution of the behaviour and ecology of small vertebrates.

The first fossil deposit recognized to be an accumulation of degraded pellets of *Sceloglaux albifacies* was from Hermit's Cave (Worthy & Holdaway, 1993, 1994*a*). Although the sample was small, a wide variety of small vertebrates was represented. The variety of prey showed that the owl was an opportunistic predator (Worthy & Holdaway, 1994*a*), but the staple item in the diet

was a relatively large bird, the fairy prion *Pachyptila turtur*, a seabird that visits land only at night.

Material from two further deposits, at Hawkes and Predator Caves (Worthy & Holdaway, 1994*b*, In press) has allowed a fuller investigation of the owl's biology and of the community of which it was part. The identification of the predator as *Sceloglaux albifacies*, the laughing owl, and a characterization of its taphonomic signature are covered elsewhere (Worthy & Holdaway, In press). The present paper covers aspects of laughing owl biology, probable foraging and feeding behaviour, and territorial habits. The community composition near the deposit during the Holocene, and changes following the introduction of the Polynesian rat (*Rattus exulans*) are also discussed.

Sites

The sites at Hawkes Cave (41°00′46.8″S, 172°54′04.8″E; NZMS 260, N26 017217; Site 10 (Worthy & Holdaway, 1994*b*), Geological Society of New Zealand fossil record no. N26/f64) and Predator Cave (41°01′06.3″S, 172°54′04.7″E; NZMS 260, N26 017211; fossil record no. N26/f70) were described in Worthy & Holdaway (1994*b*, In press). Briefly, both sites were in old phreatic caves cut in Ordovician marble on Takaka Hill, Nelson, New Zealand. Both were within sight of entrances that formed long after the processes of cave formation had ceased and the passages had been abandoned by streams.

The Hawkes Cave deposit was in calcareous mud on the floor of a passage under a slight overhang on the wall opposite the entrance. The Predator Cave deposit was in three sections that differed primarily in organic content which we assume is related to the relative period of weathering. The upper 'black' section accumulated in a depression (500 mm wide, 200 mm deep) at the top of a rock pile. Spillage from the 'black' had percolated between the rocks beneath the depression into a 1–2 m high chamber within the rock pile forming a sloping 'brown' talus layer down one wall of the chamber and across part of the floor. The 'brown' layer was assumed to be on average older, its organic content was considerably less, but it would also have received material that spilled from the domed top of the 'black' deposit.

The lower deposit consisted of three layers of white calcareous sediments, mainly secondary deposits of micro-crystalline calcite. The upper two were fossiliferous, but the lowest was 100 mm thick, barren, and contained marble clasts. The middle layer—the 'lower white'—was compacted and 50 mm thick. The 'upper white' was a looser consistency and thinned from 100 mm thick at the toe of the 'brown' to 50 mm at its furthest extent.

Both caves were surrounded by southern beech (*Nothofagus*) and Hall's Totara (*Podocarpus hallii*) forest until the late 1890s. The complex histories of the cave deposits were described in Worthy & Holdaway (1994*b*).

Methods

Collection and initial processing methods are described in Worthy & Holdaway (1994*b*). Common names of taxa are given in **Appendix 1**. Minimum number of individuals (MNI) for each were calculated as the number of ipsilateral examples of the best-represented element of that taxon.

The material summarized here was obtained from bulk sediment samples from each of the 4 parts of the deposit. A radiocarbon date of 10,870 ± 83 yrs BP (NZA 3065) was obtained from a *Petroica australis* bone from the base of the lower white layer (Worthy & Holdaway, 1994*b*). The bones are therefore samples of the

diet of different individuals over more than 10,870 years. During that time, the owls almost certainly cast most of their pellets elsewhere. The composite deposit contained residues from the unknown proportion of the pellets cast fortuitously over the sediment trap that were preserved. So, rather than containing a record of the diet of a particular individual, the deposit is a sample of the general composition and broad trends in the diet of a temporal population of owls.

Biomass was calculated for each taxon for each site from the MNI and standard masses for each taxon. Masses are as in Worthy & Holdaway (1994a). Taxa not listed there are: *Traversia*, taken to be as for *Xenicus* sp.; *Mohoua novaeseelandiae*, 10–20 g (Gill, 1980); *Anthornis melanura*, 20–40 g (Bartle & Sagar, 1987); *Rattus exulans*, 80–100 g, Kapiti Island population, from nearly the same latitude (King, 1990); *Mus musculus*, 10–20 g (King, 1990); and *Hoplodactylus duvaucelii*, 140 g (Daugherty, Gibbs & Hitchmough, 1993).

Shannon diversity indices and Hill numbers (Hill, 1973) were calculated for each sample, including that from Hermit's Cave for comparison. Shannon diversity was calculated for ease of comparison with data in Holdaway (1990). Rarefraction curves were calculated using the BASIC program RAREFRAC.BAS (Ludwig & Reynolds, 1988).

Material repositories

The *Rattus exulans* material from Hawkes Cave is held by the second author (THW), all other material is deposited in the Museum of New Zealand Te Papa Tongarewa. Catalogue numbers are: Hawkes Cave, S32309–S32325 inclusive; Predator Cave, S32326–S32424 inclusive.

Results

General

The samples included remains of a wide variety of small vertebrates, but few invertebrates. Snail shells were present, but had been secondarily incorporated in the matrix. They were not considered to be part of the prey assemblage (Worthy & Holdaway, In press). The sediment was damp and exposed to the atmosphere. Cuticular remains of invertebrates that may have been present in the original castings were probably destroyed by weathering and bacterial action in the damp substratum. Hence, references to diet composition and biomass must be taken to include the vertebrate component only.

Vertebrate remains

The taphonomy of the site has been described and discussed by Worthy & Holdaway (In press). The Hawkes Cave sample was relatively small. Most of the analysis was performed on the Predator Cave sample.

The bone samples included birds, lizards, frogs, bats, and the introduced rat *Rattus exulans* (Table I). Comparable data from Hermit's Cave, a site of Otiran (last glacial) age (Worthy & Holdaway, 1994a) are given for comparison (Table II).

The proportions of birds, bats, rats, geckos, skinks, and frogs were similar in the two white and the brown sections of the deposit, but rats were much more abundant in the black sediment (Fig. 1). Parakeets, probably *Cyanoramphus novaezelandiae* (Worthy & Holdaway, 1994b), were the most abundant group in the Predator Cave sample (Fig. 2). Acanthisittid wrens, *Petroica* flycatchers (mainly *P. australis*), honeyeaters (almost exclusively *Anthornis melanura*), and owlet-nightjars

TABLE 1

Summary of representation of vertebrate taxa in main entrance (Site 10: N26/f64) in Hawkes Cave and the pseudo-stratified deposit in Predator Cave, Takaka Hill, New Zealand. X, number of bones; Y, minimum number of individuals (MNI); %MNI, percentage of total vertebrate individuals; B(g), biomass in grams; %B, percentage of total vertebrate biomass. S, status on Takaka Hill; P, present, common; p, present but rare; e, extinct on Takaka Hill; E, extinct; ?, status uncertain. For common names of taxa, see *Appendix 1. NOTE: Identification of the two smaller species of Hoplodactylus, H. cf. granulatus and H. cf. maculatus, was based on the frontals (the largest bone, and diagnostic). Separation of the other bones of these taxa was not attempted, as in most sites MNI has been determined from the frontals (THW unpubl. data)*

Species	Hawkes Cave				Predator Cave—by layer																		
					Lower White				Upper White				Brown				Black					
	X/Y	%MNI	B(g)	%B	X/Y	%MNI	B(g)	%B	X/Y	%MNI	B(g)	%B	X/Y	%MNI	B(g)	%B	X/Y	%MNI	B(g)	%B	S
Birds																					
Ninox novaeseelandiae	—	—	0	0	—	—	0	0	1/1	0.3	174	1.8	3/1	0.4	174	2.1	—	—	0	0	P
Aegotheles novaezealandiae	19/2	2.8	184	10.8	15/5	4.8	460	13.4	59/8	2.7	736	7.7	62/5	2.1	460	5.5	9/2	3.8	184	3.3	E
Cyanoramphus sp.	25/3	4.2	210	12.3	200/17	16.4	1190	34.8	472/54	18.5	3780	39.3	506/44	18.8	3080	36.5	147/11	8.3	770	13.7	P
Coenocorypha cf. aucklandica	11/1	1.4	120	7.0	5/2	1.9	240	7.0	5/1	0.3	120	1.2	10/2	0.9	240	2.8	3/1	0.8	120	2.1	E
Acanthisitta chloris	15/2	2.8	16	0.9	41/6	5.8	48	1.4	117/15	5.1	120	1.2	115/14	6.0	112	1.3	40/4	3.0	32	0.6	P
Xenicus sp.	17/3	4.2	45	2.6	38/4	3.9	60	1.8	115/11	3.8	65	0.7	99/9	3.9	135	1.6	53/5	3.8	75	1.3	E
Traversia lyalli	—	—	0	0	3/1	1.0	15	0.4	5/2	0.7	30	0.3	5/1	0.4	15	0.2	1/1	0.8	15	0.3	E
Pachyplichas yaldwyni	8/2	2.8	60	3.5	21/2	1.9	60	1.8	79/10	3.4	300	3.1	81/8	3.4	240	2.8	34/5	3.8	150	2.7	E
Petroica australis	23/4	5.6	120	7.0	59/4	3.9	120	3.5	148/13	4.5	390	4.1	142/13	5.6	390	4.6	73/7	5.3	210	3.7	P
P. macrocephala	4/1	1.4	10	0.6	3/1	1.0	10	0.3	18/3	1.0	30	0.3	19/4	1.7	40	0.5	3/1	0.8	10	0.2	P
Mohoua ochrocephala	3/1	1.4	30	1.8	4/1	1.0	30	0.9	21/3	1.0	90	0.9	24/3	1.3	90	1.1	5/2	1.5	60	1.1	e
M. novaeseelandiae	—	—	0	0	6/3	2.9	39	1.1	3/1	0.3	13	0.1	6/2	0.9	26	0.3	4/1	0.8	13	0.2	P
Rhipidura fuliginosa	—	—	0	0	1/1	1.0	8	0.2	1/1	0.3	8	0.1	—	—	0	0	1/1	0.8	8	0.1	P
Gerygone igata	—	—	0	0	1/1	1.0	6.5	0.2	—	—	0	0	3/1	0.4	6.5	0.1	—	—	0	0	P
Prosthemadera novaeseelandiae	—	—	0	0	—	—	0	0	2/1	0.3	100	1.0	—	—	0	0	1/1	0.8	100	1.8	P
Anthornis melanura	4/1	1.4	28	1.6	43/6	5.8	168	4.9	110/10	3.4	280	2.9	88/11	4.7	308	3.6	37/5	3.8	140	2.5	P
Anthus novaeseelandiae	—	—	0	0	—	—	0	0	—	—	0	0	2/1	0.4	25	0.3	—	—	0	0	P
Alauda arvensis	—	—	0	0	—	—	0	0	—	—	0	0	1/1	0.4	30	0.4	—	—	0	0	P
Philesturnus carunculatus	5/3	4.2	270	15.8	5/1	1.0	90	2.6	21/3	1.0	270	2.8	27/3	1.3	270	3.2	3/1	0.8	90	1.6	e
Turnagra capensis	4/1	1.4	70	4.1	—	—	0	0	4/1	0.3	70	0.7	4/2	0.9	140	1.7	—	—	0	0	E
SUBTOTAL	138/24	33.6	1163	68.2	445/55	53.3	2544.5	74.3	1181/138	47.3	6576	68.6	1197/125	53.5	5781.5	68.6	414/48	36.4	1977	35.2	

Mammals—bats																					
Chalinolobus tuberculatus	—	—	0	0	2/1	1.0	18	0.5	—	—	0	0	—	—	0	0	—	—	0	0	e?
Mystacina tuberculata	24/6	8.5	108	6.3	66/13	12.5	234	6.8	224/42	14.4	756	7.9	158/31	13.3	558	6.6	69/14	10.6	252	4.5	e?
M. cf. robusta	26/5	7.0	150	8.8	27/4	3.9	72	2.1	87/20	6.9	600	6.2	61/14	6.0	420	5.0	15/4	3.0	72	1.3	E
SUBTOTAL	50/11	15.5	258	15.1	95/18	17.4	324	9.8	311/62	21.3	1356	14.1	219/45	19.3	978	11.6	84/18	13.6	324	5.8	
Mammals—rats																					
Rattus exulans	5/1	1.4	90	5.3	19/3	2.9	270	7.9	103/11	3.8	990	10.3	166/14	6.0	1260	14.9	368/35	26.5	3150	56.0	e
Mus musculus	—	—	0	0	—	—	0	0	—	—	0	0	3/1	0.4	15	0.2	4/2	1.5	30	0.5	P
SUBTOTAL	5/1	1.4	90	5.3	19/3	2.9	270	7.9	103/11	3.8	990	10.3	169/15	6.4	1275	15.1	372/37	28.0	3180	56.5	
Lizards—geckos																					
Hoplodactylus cf. granulatus	x/26	36.6	150	8.8	12/12	11.5	60	1.8	49/49	16.8	245	2.6	18/18	7.7	90	1.1	20/20	15.2	100	1.8	P
H. cf. maculatus	x/6	8.5	30	1.8	9/9	8.7	45	1.3	22/22	7.5	110	1.1	23/23	9.8	115	1.4	7/7	5.3	35	0.6	P
Hoplodactylus sp.	—	—			137/?	1.0			292/?	0.7			400/?	0.4			215/?	—			
H. duvaucelii	—	—	0	0	7/1	1.0	140	4.1	9/2		280	2.9	2/1		140	1.7	—		0	0	e
SUBTOTAL	x/32	45.1	180	10.6	165/22	21.2	245	7.2	372/73	25.0	635	6.6	443/42	17.9	345	4.2	242/27	20.5	135	2.4	
Lizards—skinks																					
Leiolopisma sp.	2/1	1.4	5	0.3	26/4	3.9	20	0.6	37/4	1.4	20	0.2	25/4	1.7	20	0.2	3/1	0.8	5	0.1	P?
SUBTOTAL	2/1	1.4	5	0.3	26/4	3.9	20	0.6	37/4	1.4	20	0.2	25/4	1.7	20	0.2	3/1	0.8	5	0.1	
Frogs																					
Leiopelma markhami	—	—	0	0	3/1	1.0	15	0.4	3/1	0.3	15	0.2	4/1	0.4	15	0.2	—	—	0	0	E
L. hamiltoni	13/2	2.8	10	0.6	8/1	1.0	5	0.1	16/3	1.0	15	0.2	8/2	0.9	10	0.1	3/1	0.8	5	0.1	e
SUBTOTAL	13/2	2.8	10	0.6	11/2	2.0	20	0.5	19/4	1.3	30	0.4	12/3	1.3	25	0.3	3/1	0.8	5	0.1	
TOTAL	x/71	99.8	1706	100.1	761/104	100.7	3423.3	100.0	2023/292	100.1	9607	100.2	2065/234	100.4	8429.5	100.0	1118/132	100.1	5626	100.1	100.1

TABLE II

Number of individuals and biomass of taxa in the Hermit's Cave laughing owl deposit (recalculated from Worthy & Holdaway, In press). Abbreviations as in Table I

Taxon	Hermit's Cave			
	X/MNI	%MNI	B(g)	%B
Birds				
Apteryx sp.	14/1	1.2	310	3.9
Pachyptila turtur	1057 + /28	34.2	3696	46.0
Pelecanoides urinatrix	28/3	3.7	360	4.5
Puffinus **sp. nov.**	180/6	7.3	1740	21.6
Storm petrel	4/1	1.2	54	0.7
Aegotheles novaezealandiae	19/3	3.7	276	3.4
Cyanoramphus sp.	7/3	3.7	210	2.6
Gallirallus australis	1/1	1.2	310	3.9
Euryanus finschi	1/1	1.2	310	3.9
Coenocorypha cf. *aucklandica*	3/1	1.2	120	1.5
Acanthisitta chloris	1/1	1.2	8	0.1
Xenicus sp.	11/2	2.4	30	0.4
Pachyplichas yaldwyni	2/1	1.2	30	0.4
Petroica australis	23/3	3.7	90	1.1
P. macrocephala	2/1	1.2	10	0.1
Mohoua ochrocephala	2/1	1.2	30	0.4
Anthus novaeseelandiae	13/1	1.2	25	0.3
Callaeas cinerea	3/1	1.2	140	1.7
Turnagra capensis	4/2	2.4	140	1.7
SUBTOTAL	61	74.3	7889	98.2
Mammals—bats				
Mystacina cf. *robusta*	32/2	2.4	60	0.8
SUBTOTAL	2	2.4	60	0.8
Lizards—geckos				
Hoplodactylus sp.	109/5	6.1	25	0.3
SUBTOTAL	5	6.1	25	0.3
Lizards—skinks				
Leiolopisma sp.	39/3	3.7	15	0.2
SUBTOTAL	3	3.7	15	0.2
Frogs				
Leiopelma hamiltoni	124/8	9.8	40	0.5
Leiopelma sp.	3	3.7	15	0.2
SUBTOTAL	11	13.5	55	0.7
TOTAL	82	100.0	8044	100.2

(the large endemic *Aegotheles novaezealandiae*) was also present in some numbers, but other birds were only minor components of the fossil fauna (Fig. 2).

Most taxa were represented more or less equally in the upper white and brown layers (Table I). The sample from the lower white layer was smaller, but the relative frequencies of taxa were similar to those in the upper white and brown layers.
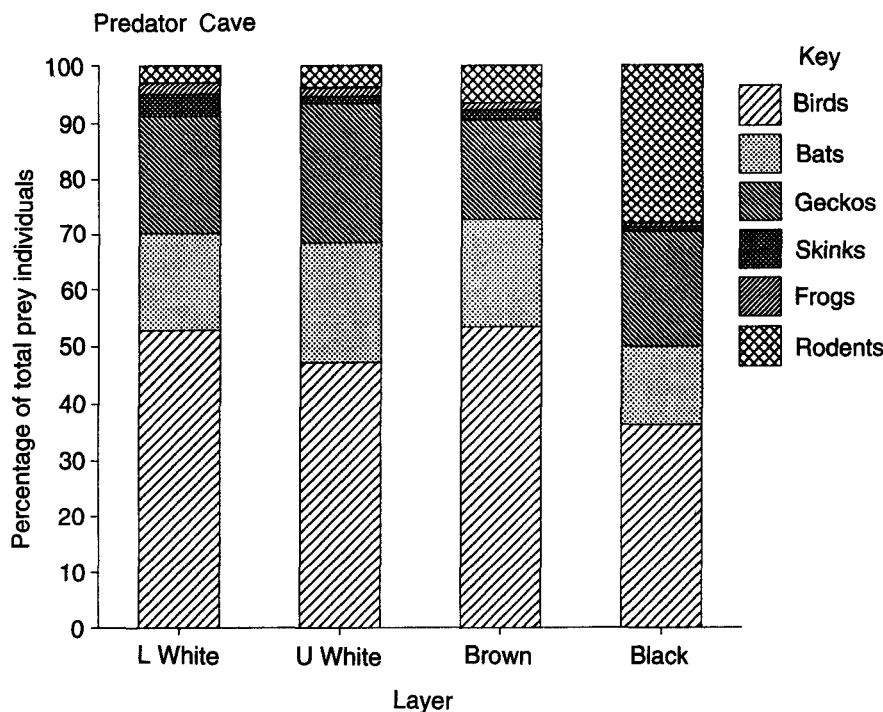
FIG. 1. Percentage of minimum number of prey individuals for major vertebrate groups recovered from the fossil deposit in Predator Cave, Takaka Hill, New Zealand. L White, lower white (oldest) layer; U White, upper white layer; Brown, brown deposit; Black, black (youngest) deposit.

The proportion of several taxa, especially the commoner ones, were lower in the black sediment than in the brown. Parakeets contributed 35.2% of MNI in the brown but only 22.9% in the black. The wrens and owlet-nightjar were also sharply less abundant in the black sediment (Table I).

In contrast, the relative abundances of two species were higher in the black: *P. australis*, 14.6% as against 10% in the brown, and *Anthornis melanura*, 10.4% against 8.8% of bird MNI. Both species survive in the forest near Predator Cave.

The vespertilionid bat *Chalinolobus tuberculatus* was very rare. Both mystacinids were, however, common, although they were much less abundant in the black sediment than in the brown. Bones of *R. exulans* were much more abundant in the black sediment (30% of the total fauna) than in any of the others, where they probably occurred as spillage from the black (Worthy & Holdaway, In press). Spillage was confirmed by the presence of *Mus* and *Anthus* bones in the brown layer which otherwise contained a characteristically pre-human fauna. Neither could have been present near the cave before the late 19th Century, *Mus* because it was not introduced until the 19th Century, and *Anthus* because suitable habitat was not available until a road was cut through the forest in the 1880s.

Geckos were common. *Hoplodactylus* cf. *granulatus* was most abundant in the upper white layer, but was relatively common throughout. *Hoplodactylus* cf. *maculatus* was, however, less abundant in the black sediment than in other parts of the site. The large arboreal gecko
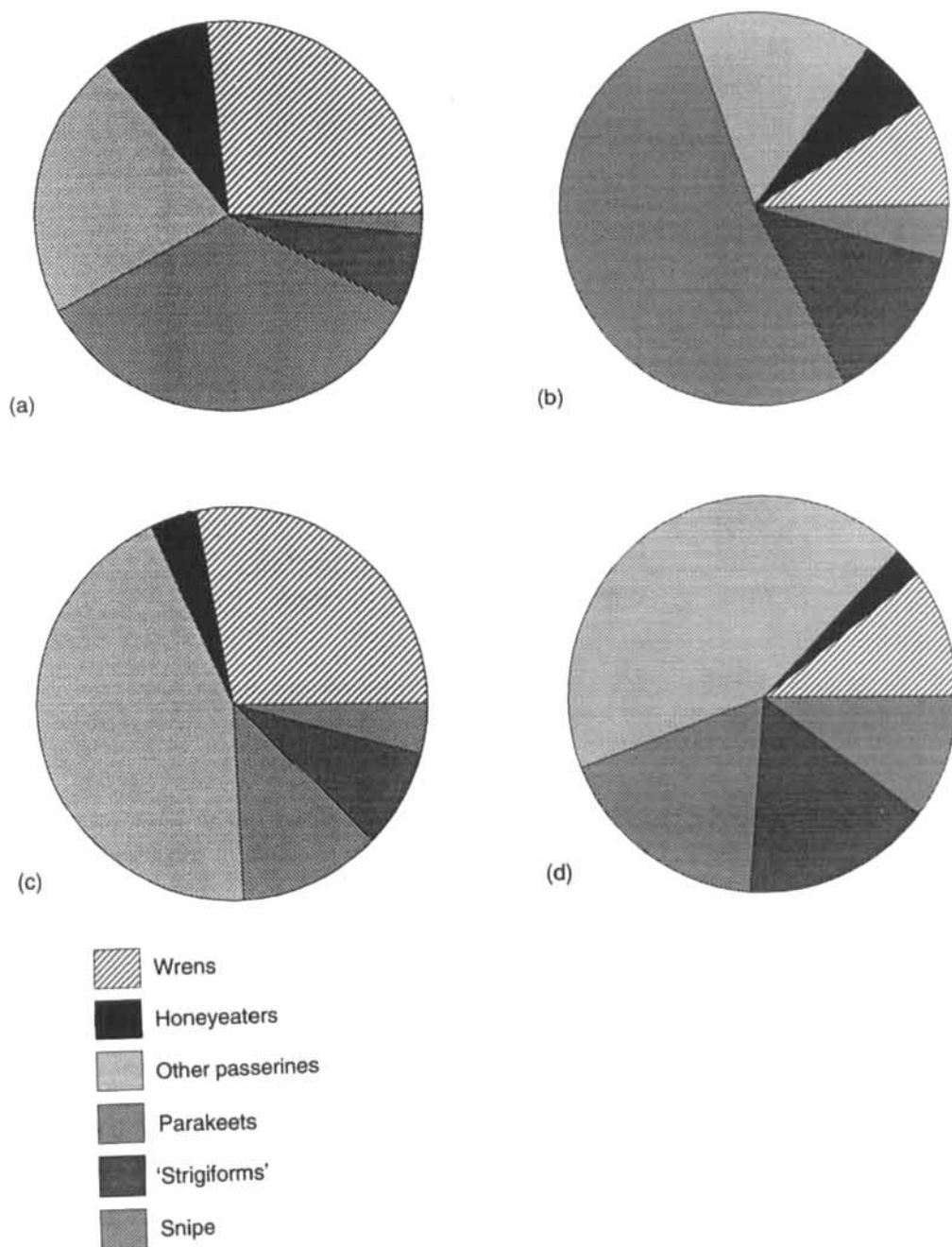
FIG. 2. Proportions of total minimum numbers of individuals (MNI) and biomass of selected bird taxa in Hawkes and Predator Caves: (a) Predator Cave MNI; (b) Predator Cave biomass; (c) Hawkes Cave MNI; (d) Hawkes Cave biomass.

Hoplodactylus cf. *duvaucelii*, rare in the lower layers, was absent from the black deposit. It is extinct on the mainland of New Zealand (Gill, 1986; Worthy, 1987a). So far as is known, all New Zealand *Hoplodactylus* geckos are mainly nocturnal. New Zealand skinks, found in low numbers in all parts of the site, are primarily diurnal.

There were a few frog bones in the sample. *Leiopelma markhami* was rare in the lower three layers, but absent from the black sediment. *Leiopelma hamiltoni* was, although present, much less abundant in the black sediment than in the other layers.

If laughing owls were opportunistic predators, taking a broad range of prey (Worthy & Holdaway 1994a, In press), then the changes in relative abundance for different species should reflect changes in their abundance in the living community around the site. However, as most owls will take advantage of short-term abundances of prey, it is possible that the observed proportions of numbers were biased by the effects of periodic irruptions of some species. Parakeets and rats are known to have undergone large fluctuations in local populations in historical times (Oliver, 1955).

Biomass

Most taxa in the Predator Cave deposit were under 100 g in body mass (Figs 3, 4). In contrast, the Hermit's Cave deposit was dominated by species with body mass greater than 100 g (Fig. 4). In Predator Cave, the owls took larger prey when it was available. However, procellariids were not available on Takaka Hill (Worthy & Holdaway, 1994b), as they were near Hermit's Cave. The major difference between the pooled sample for the three lowest layers and the black deposit was the greatest importance of prey in the 80–100 g range (rats) in the black.

Birds were by far the most important components of biomass in the older layers (i.e. before rats arrived), despite accounting for only about one-third of prey MNI (Table I, Fig. 3). Without compensating for the obvious slippage of material from the upper parts of the deposit, birds represented about 70% of the available biomass in the samples. For Predator Cave, parakeets contributed 35–40% of the total biomass. At Hermit's Cave, petrels constituted nearly three-quarters of the total biomass (Fig. 3a). For other species, the owls expended energy for less return. For example, the four acanthisittid wrens contributed little to the biomass (4.9%), despite their higher MNI.

Bats, rats, and geckos provided the bulk of the remainder of the biomass; skinks and frogs contributed negligible amounts. Although the larger of the mystacinid bats was only half as abundant as the other, the two contributed equally to the biomass. Together they were second in importance after birds, of the native fauna. The contribution made by the geckos may have been underestimated because their small bones were more likely to have been missed in the sediment. Even so, despite their numerical dominance, their biomass represented in the sample is unlikely to have exceeded that of the bats. Only five taxa at Predator Cave, and the prion and shearwater at Hermit's Cave, contributed more than 5% of the biomass represented in each deposit.

In view of the downslope creep or slippage of material from the upper parts of the deposit, the biomass represented in each part was adjusted by assuming that all rodent bones had entered the deposit during the time represented by the black sediment. If likelihood of spillage from the black to the brown and beyond was independent of taxon, then the proportional representation in any layer would not be greatly affected. When so adjusted, the percentages of biomass contributed by birds, bats, and geckos were uniform in the three lower layers. Rodents contributed more biomass than either birds or bats during the period in which the black deposit formed (Fig. 3b).
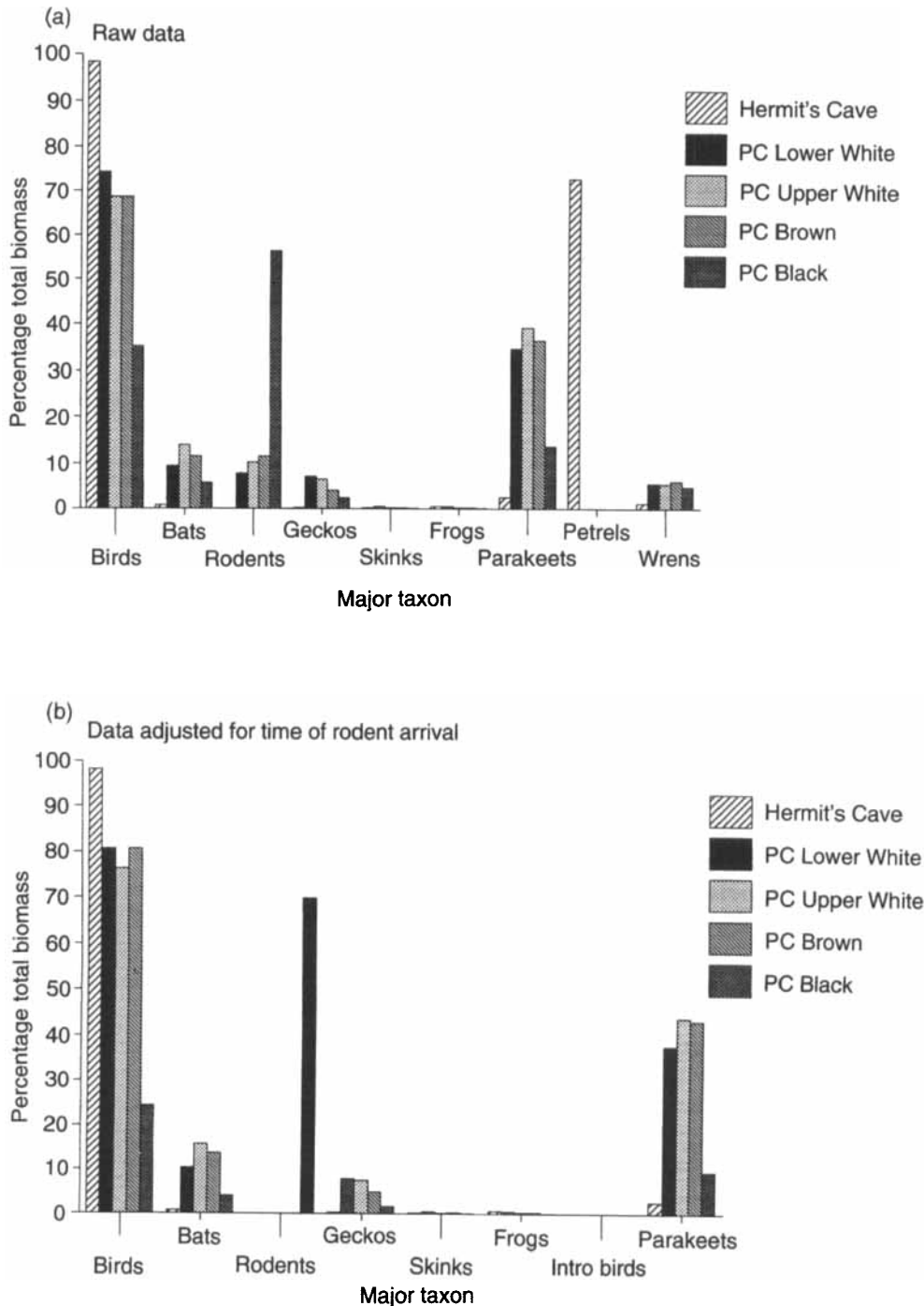
FIG. 3. (a) Percentage of total prey biomass represented by major vertebrate taxa in Predator Cave, with comparable data for Hermit's Cave: (b) percentage of total prey biomass adjusted for time of arrival of kiore rats. PC, Predator Cave; other abbreviations as for Fig. 1. Bars within groups are for deposits in order of decreasing age from left to right.
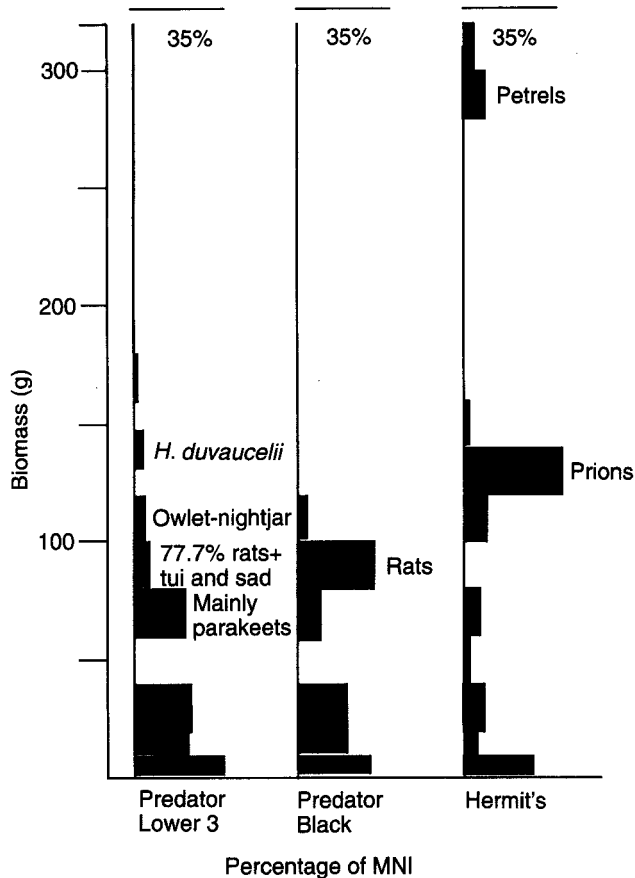
FIG. 4. Vertical histogram of distribution of individuals by taxon mass for lower three sections of the Predator Cave deposit and for Hermit's Cave. Major taxa represented in some bins shown: sad, *Philesturnus carunculatus*; for other names, see **Appendix 1.**

Diversity—measures and changes

Measures of diversity and evenness for all three sites are given in Table III. Although Hill's numbers (Hill, 1973) are preferred as being relatively unbiased indicators of diversity (Ludwig & Reynolds, 1988), the more traditional Shannon indices are given here for ease of comparison with published work on forest bird diversity in New Zealand (e.g. McLay, 1974; Holdaway, 1990).

Rarefraction curves (Ludwig & Reynolds, 1988) for Hermit's Cave and the separate parts of the Predator Cave deposit gave similar values for diversity at all sample sizes (Fig. 5a). The homogeneity suggests that the owls sampled from prey populations in similar ways over considerable periods of time, and that the source communities, of birds at least, were similar in species richness. The relatively low potential species richness of even the undisturbed New Zealand fauna also constrained the rise in taxa expected to be present in larger samples. The

TABLE III

Diversity of small vertebrates in bone samples from 'layers' in the Predator Cave deposit, Takaka Hill. Layers are in order of decreasing age, from Lower White to Black. Total fossil, values for all layers in Predator Cave combined; Total present, value for present fauna known from Takaka Hill; +4, values including four taxa not recorded from fossil assemblages but almost certainly present on Takaka Hill in the Holocene and rare everywhere in fossil deposits

| | | | | | | Takaka Hill | | | | |
| | | | | | Predator Cave | | | | | |
	Hawkes Cave	Lower White	Upper White	Brown	Black	Total	Total fossil	Total present	Hermit's Cave
Indigenous birds									
Species richness S	12	15	17	18	15	19	35($+4$)	($16+4$)	19
Shannon diversity H'	2.362	2.282	2.103	2.237	2.362	2.245			2.144
Evenness J	0.950	0.843	0.742	0.774	0.872	0.762			0.728
H_{max}	2.485	2.708	2.833	2.890	2.708	2.944	3.555	2.773	2.944
							3.638	2.996	
Hill N0	12	15	17	18	15	19			19
Hill N1	10.612	9.796	8.191	9.365	10.612	9.44			8.534
Hill N2	15.33	7.694	5.26	6.156	9.895				4.496
Modified Hill ratio	1.491	0.761	0.592	0.616	0.925				0.464
All vertebrates									
Species richness	19	25	26	28	23				24
Shannon diversity H'	2.358	2.796	2.588	2.740	2.502				2.545
Evenness J	0.801	0.869	0.794	0.822	0.798				0.801
H_{max}	2.944	3.219	3.258	3.332	3.315				3.178
Hill N0	19	25	26	28	23				24
Hill N1	10.57	16.379	13.303	15.487	12.207				12.743
Hill N2	6.471	13.804	9.835	11.756	8.493				7.347
Modified Hill ratio	0.572	0.833	0.718	0.742	0.669				0.540

smallest sample, from Hawkes Cave, gave rather higher expected species numbers, as a result of the relatively high number of taxa represented among the few bones recovered.

Diversity, as expressed in terms of logarithms of ranked abundance (James & Rathbun, 1981), was equal for equal sample sizes in the subsite pairs from Predator Cave—lower white vs. black, and upper white vs. brown (Fig. 5b). All four curves from the Predator Cave deposit showed the same pattern of relative abundance, with minor variations for the rarest taxa. The curves for Hawkes Cave lacked, however, the single dominant taxon characteristic of the three lower samples from Predator Cave (Fig. 5b).

The composite invertebrate fauna represented in the Holocene deposits on Takaka Hill was divided into broad guilds (Table IV). No closer differentiation was attempted, both because many of the taxa are extinct and hence their ecology can only be inferred from structure and habitat, and because New Zealand vertebrates tend to have broader niches than comparable continental taxa. Eleven guilds of diurnal vertebrates and five of nocturnal vertebrates were recognized. Species richness in these putative guilds in the pre-human and present faunas are compared in Table V.

Three guilds (terrestrial herbivores, nocturnal terrestrial insectivores, and the nocturnal generalists—the mystacinid bats) are absent from the present fauna. Diurnal guilds now have 50% fewer species, and nocturnal guilds 63% fewer, than before humans reached New Zealand. The least affected guilds are the diurnal arboreal insectivores and nectarivores, and the diurnal
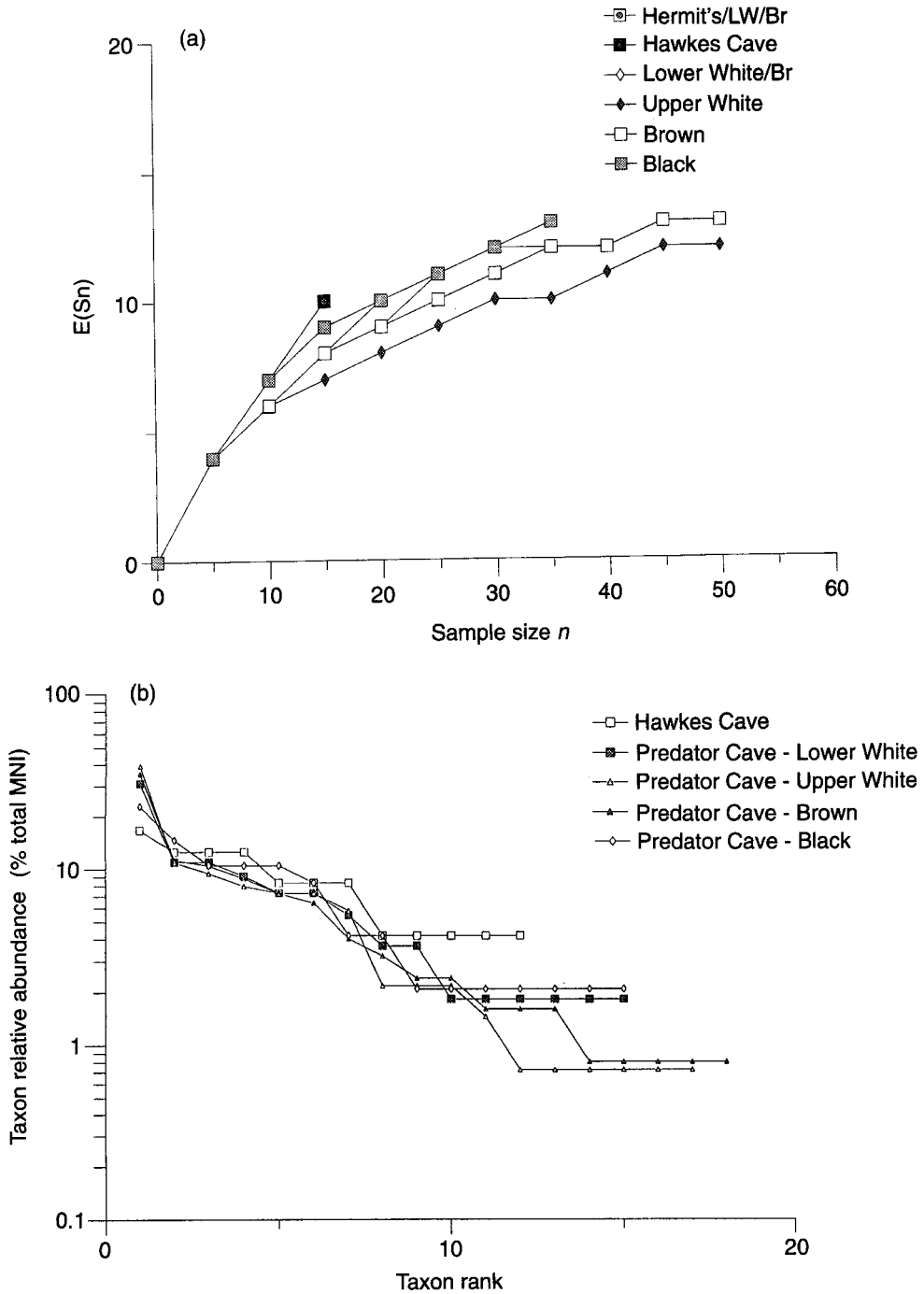
FIG. 5. (a) Rarefraction curves for samples from Hermit's, Hawkes, and Predator Caves. E(Sn), expected number of taxa for given sample size; (b) comparison of log abundance versus taxon rank for samples from Hawkes Cave and four layers from Predator Cave.

TABLE IV

Broad guilds of vertebrates on Takaka Hill during Holocene, before human intervention. Bold, globally extinct; *, locally extinct; ↓, reduced numbers locally; gp. species group

DIURNAL

TERRESTRIAL

Herbivore
Anomalopteryx didiformis
Dinornis novaezealandiae
Dinornis struthoides

Omnivore
Apteryx owenii *
Apteryx sp. (large)↓
Hymenolaimus malacorhynchos↓
Anas chlorotis*
Euryanas finschi
Gallirallus australis
Coenocorypha cf. aucklandica

Insectivore
Leiolopisma sp.
Leiolopisma sp.

ARBOREAL

Insectivore
Acanthisitta chloris
Gerygone igata
Mohoua novaeseelandiae

Insectivore-nectarivore
Anthornis melanura
Prosthemadera novaeseelandiae

Frugivore-folivore
Hemiphaga novaeseelandiae
Callaeas cinerea*
Nestor meridionalis↓

ARBOREAL-TERRESTRIAL

Insectivore
Xenicus longipes/gilviventris*
Pachyplichas yaldwyni
Traversia lyalli
Petroica macrocephala
Petroica australis↓
Mohoua ochrocephala*
Philesturnus carunculatus*

Frugivore-folivore
Cyanoramphus novaezelandiae*
Cyanoramphus auriceps↓
Strigops habroptilus*

Omnivore
Nestor notabilis
Turnagra capensis

AERIAL

Insectivore
Rhipidura fuliginosa

Predator
Circus eylesi
Falco novaeseelandiae↓

NOCTURNAL OR NOCTURNAL/CREPUSCULAR

TERRESTRIAL

Insectivore
Leiopelma hamiltoni*
Leiopelma markhami

ARBOREAL-TERRESTRIAL

Insectivore-nectarivore
Hoplodactylus maculatus gp
Hoplodactylus granulatus gp
Hoplodactylus duvaucelii*

AERIAL-ARBOREAL-TERRESTRIAL

Insectivore-nectarivore-frugivore
Mystacina tuberculata*
Mystacina robusta

AERIAL

Insectivore
Chalinolobus tuberculatus↓

Predator
Aegotheles novaezealandiae
Sceloglaux albifacies
Ninox novaeseelandiae

TABLE V

Changes in species richness (S) for broad guilds of vertebrates on Takaka Hill between pre-human (>800 years BP) and present faunas. H, herbivore; O, omnivore; I, insectivore; I-N, insectivore-nectarivore; F-F, frugivore-folivore; I-N-F, insectivore-nectarivore-frugivore; Nocturnal, includes crepuscular/nocturnal

Main activity height	Food	Species richness (S) Diurnal Pre-human	Present	% loss	Nocturnal Pre-human	Present	% loss
Terrestrial	H	3	0	100			
	O	7	3	57			
	I	2	2	0	2	0	100
Arboreal	I	3	3	0			
	I-N	2	2	0			
	F-F	3	1	67			
Arboreal-terrestrial	I	7	2	71			
	F-F	3	1	67			
	O	2	1	50			
	I-N				3+	2+	c. 30
Aerial	I	1	1	0	1	1	0
Aerial-arboreal-terrestrial	I-N-F				2	0	100
PREDATOR		2	1	50	3	1	67
TOTAL		35	17	51.4	11	4	63.6

and nocturnal aerial insectivores. All others have lost >30% of their species complement since humans arrived in New Zealand.

Discussion

Many recent fossil deposits excavated in New Zealand before 1990 were 'spring-sites', or swamps (e.g. Hutton, 1896; Worthy, 1989), whose taphonomies did not usually promote the preservation or recovery of small bones, particularly with the excavation techniques employed. Collections from caves were usually biased by the predominantly pitfall origin of the material. Preservation conditions in swamps and caves usually favour larger specimens (Scarlett, 1955; Worthy & Mildenhall, 1989; Worthy & Holdaway, 1993). Small (<100 g) species are usually rarely represented. Only in exceptional circumstances have smaller taxa been found abundantly in standard cave deposits (Worthy, 1993).

The rare rich deposits, such as those at Honeycomb Hill Cave (Worthy, 1993), provided the only tantalizing glimpses of the diversity and abundance of small birds, lizards, and frogs in the Holocene vertebrate faunas. The discovery of deposits containing large numbers of bones of the smallest vertebrates has allowed the first steps to be made in correcting the century-old bias towards the avian megafauna in Quaternary vertebrate studies in New Zealand.

The original biogeography, habitat preferences, and relative abundances of most New Zealand vertebrates are not well known. The environmental changes since humans arrived have been such, that even the species that survived into European times often did so as relict populations in marginal habitats. For example, *Traversia lyalli* was confined to Stephens Island (Oliver, 1955), *Strigops habroptilus* was almost entirely restricted to the mountainous areas of the South Island (Williams, 1956), and *Porphyrio mantelli* was confined to a few montane valleys in Fiordland

(Reid, 1974). Neither the distributions nor the habitats of these species in European times reflect fully their ecology in the undisturbed environment (e.g. Beauchamp & Worthy, 1988).

The gaps in biogeographical and palaeoecological knowledge of smaller vertebrates can only be filled by analysing rich, geographically separated, deposits of their remains. Fortunately, predator deposits are now known to be not uncommon in New Zealand (authors' unpubl. data). Predator Cave is the richest discovered so far.

Faunal change over time

Whereas the Hermit's Cave deposit has been dated to the coldest period of the Otiran glaciation [broadly contemporaneous with the height of the Wisconsin–Weichsel] (Williams *et al.*, 1993), the Predator Cave deposit was laid down under a warm temperate climate during the past 10,000 years. The presence in the black and brown sediments of vertebrates introduced by Europeans shows that deposition continued into the late 19th Century. The Predator Cave deposit therefore provides a more or less continuous record of the small vertebrate fauna on Takaka Hill for the entire Holocene. It provides a means of examining the diversity and composition of a vertebrate fauna through about 11,000 years of relative climatic stasis, including the most recent 800–1000 years when human influences have dominated the New Zealand environment (Anderson, 1991).

The major conclusion from analysis of the three lower parts of the deposit was that the composition of the fauna changed very little during the Holocene. Unfortunately, the nature of the deposit prevented a clear-cut distinction being made between pre-human and post-colonization phases of deposition. The rarity of introduced vertebrates in the lower and upper white and brown sediments, and the strong likelihood that material spilled from the black deposit, suggest that the black represented most, if not all, of the post-colonization period. If so, it records the sudden diminution of many taxa that had been abundant throughout the Holocene, coincident with the introduction of *Rattus exulans*.

Biology of the laughing owl *Sceloglaux albifacies*

The location and faunal composition of the Takaka Hill fossil sites provide new insights into the biology of *Sceloglaux albifacies*, a large owl which is now exceedingly rare, if not extinct (Turbott, 1990). From reports by European observers in the late 19th Century, the owl was thought to have preferred rocky areas in open country, or at the forest edge (Williams & Harrison, 1972). The prey of the Hermit's Cave owls included forest species, and those characteristic of open habitats, for example *Anthus*. The deposit was formed when the site surroundings were probably more open, with forest confined to sheltered river valleys, and quite different from the luxuriant Holocene podocarp-dominated rainforest of the present (Worthy & Holdaway, 1993, 1994*a*).

A reconstruction of the Holocene vegetation on Takaka Hill (Worthy & Holdaway, 1994*b*) shows that the owls in Hawkes and Predator Caves lived primarily in closed canopy forest, some distance from any clearings, or even expanses of lower shrublands. This was, however, *Nothofagus* forest that was relatively open beneath a 10–15 m canopy, and not the multi-tiered 30-m canopied podocarp forest. The preferred habitats of the extant vertebrates preserved in the deposits confirm that the owls hunted in forest. Most extant species in the prey assemblage lived in closed, continuous forest, and many are nocturnal.
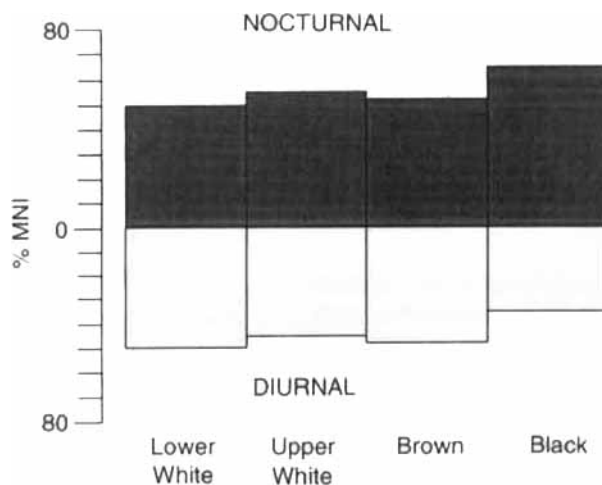
FIG. 6. Percentages of minimum numbers of individuals (MNI) in samples from Predator Cave, classified as primarily diurnal and nocturnal.

Hoplodactylus geckos, abundant in the Predator Cave deposit, are nocturnal (Whitaker, 1987; pers. comm., 12 Dec. 1993), whereas *Naultinus* geckos and *Leiolopisma* skinks are diurnal (Whitaker, pers. comm.). Nocturnal geckos were more numerous than the skinks, and *Naultinus* geckos were not identified among the remains. The laughing owl was largely nocturnal; 50% or more of the taxa in the prey assemblage were nocturnal (Fig. 6). Apart from the geckos, the nocturnal vertebrates included several birds (e.g. *Aegotheles novaezealandiae*, *Coenocorypha* cf. *aucklandica*, *Ninox novaeseelandiae*) and the leiopelmatid frogs and mystacinid bats.

There are few records of the diet of laughing owls. A captive bird in Christchurch in the 19th Century was fed on "mice, rats, and birds" (Potts, 1882). Buller (1888) listed earthworms, insects, lizards, small birds, and mammals (from the presence of fur in pellets). He drew on information provided by Smith (1884). Smith analysed recent pellets and gave the only record of the diet of living laughing owls. A mouse photographed in the beak of an owl, supposedly in 1916 (Anon., 1990), but actually between 1909 and 1912, was put there by the photographer (E. Parr, pers. comm., May 1995). The presence of invertebrates in the diet cannot be confirmed, because the sediments did not allow the preservation of cuticle.

Although laughing owls tended to take mainly the largest prey that could be easily subdued (such as prions at Hermit's Cave and parakeets and bats at Predator Cave), they took a diverse range of prey. The owl was an opportunistic predator that did not rely on one or a few species: any available vertebrate, below a maximum size, that presented itself at night, or in the late evening or early morning, within the forest, was taken. This agrees with studies of systems containing several taxa of owls where, although it might be expected that the raptors partition the resource by specializing on different species, most appear to be opportunistic and plastic in their prey choice (Marti, Korpimäki & Jaksić, 1993).

The opportunistic feeding behaviour of laughing owls means that deposits accumulated by them provided the best available evidence for the relative abundance of small vertebrates within 1–2 km of each deposit. In addition, extrapolation from the ecologies of extant taxa in the deposits may provide important clues to the habitat and behaviour of the extinct forms (Baird, 1989).

Analysis of the deposit can even shed light on the ecology of extant species. For example, little is known of the ecology of *Cyanoramphus novaezelandiae* on the mainland of New Zealand, where it is now extremely rare, if not extinct (Turbott, 1990). Early reports suggest that it was found in tall forest, usually at the tops of trees (Oliver, 1955). Where it survives on islands, however, it is more abundant at forest margins and in open country than in forests (Taylor, 1975). The diet of island populations suggests that *C. novaezelandiae* spends much more time on or near the ground than does *C. auriceps* (Taylor, 1975). The abundance of *C. novaezelandiae* in the Takaka Hill deposits shows that this species was formerly common in upland *Nothofagus* forests.

The apparent vulnerability of *Cyanoramphus* to *S. albifacies* does not necessarily indicate that the owl was active in daylight. Parakeets could have been active at dusk or at night as other New Zealand psittaciforms are, e.g. *Nestor meridionalis* (Potts, 1882: 179), and *Strigops habroptilus* (Merton, Morris & Atkinson, 1984). Parakeets nest and roost in holes in trees and cliffs, among rocks, or in burrows in the ground (Oliver, 1955). The owl could have taken parakeets as they returned to roosts at dusk.

Together, the two mystacinid bats comprised about 25% of the prey numbers, but only 8% of the biomass in the pre-rat fauna in the Predator Cave deposit. *Mystacina tuberculata*, the surviving mystacinid, is well known for its unusual—for bats—habit of spending much time foraging on the ground and on the trunks and branches of trees (Daniel, 1979). It flies a few centimetres above the forest floor (C. F. J. O'Donnell, pers. comm., 1994), and so would have been vulnerable to predation by laughing owls.

Bats are usually minor elements in owl diets (0.25–7.25% of small vertebrates in barn owl *Tyto alba* pellets in Poland [Ruprecht, 1979]). Bauer (1956) reported, however, that bats comprised 55.3% of all vertebrate remains in barn owl pellets in Austria. Ruprecht (1979) quoted other records of high representations of bats, including 12.5% in tawny owl *Strix aluco* and over 16% in eagle owl *Bubo bubo* pellets. Both owls are woodland birds, in contrast to the barn owl, which usually hunts in more open sites (Martin, 1990). Owls have been reported to take bats in flight, usually weaker-flying species (Bauer, 1956; Ruprecht, 1979), but most seem to be taken at the roost (Ruprecht, 1979). He concluded that the frequency of bat remains in owl pellets is a function of the exposure of the bats to the owls. Mystacinids, by invading niches occupied elsewhere by other mammalian groups such as rodents and shrews—mammals common in the diets of owls (Mayhew, 1977)—seem to have exposed themselves to additional predation pressure that most bats have avoided.

In Predator Cave, *M. tuberculata* was 2–3 times as abundant as the larger *Mystacina* cf. *robusta*. *M.* cf. *robusta* was apparently more susceptible to mammalian than owl predation or habitat loss and was extinct over most of New Zealand before European colonization. The last colonies of *M. robusta* were on islands off Stewart Island 800 km south of Takaka Hill and were destroyed by black rats (*R. rattus*) in the mid-1960s before they could be studied (Hill & Daniel, 1985). The vulnerability of the larger bat to predation by rodents suggests that it was probably at least as vulnerable to owl predation as was *M. tuberculata*. The differences in representation in the deposits may, therefore, reflect real differences in their abundance in the living fauna. The rarity of the vespertilionid *Chalinolobus tuberculatus* in the prey assemblage may be explicable, as it is an aerial feeder, and forages above the canopy, in contrast to the ground-feeding mystacinids.

Frogs and skinks were insignificant components of the diet of laughing owls on Takaka Hill, both in absolute numbers and in biomass. They were more common at Hermit's Cave, where the vegetation was probably more open, but still contributed very little to the prey biomass.

Leiopelmatid frogs have not been found live on the South Island mainland (Gill, 1986). Their fossils are, however, reasonably common in caves (Worthy, 1987*b*, *c*; Worthy & Holdaway, 1993). *Leiopelma hamiltoni*, *L. markhami*, and *L. hochstetteri* have been recorded from the Takaka area (Worthy, 1987*b*; Worthy & Holdaway, 1994*b*). The large total faunal samples from the predator deposits may indicate the relative abundance of native frogs on Takaka Hill.

Leiopelma hochstetteri was not found in the Takaka owl deposits, probably because it prefers to live in or near streams (Worthy, 1987*b*). There are no permanent streams within 2 km of Predator Cave. *L. hamiltoni* is known to be terrestrial and *L. markhami* has been characterized as a terrestrial frog (Worthy, 1987*b*, *c*). *L. hamiltoni* feeds on forest floor invertebrates, and is, like all extant *Leiopelma*, nocturnal. The relative rarity of these nocturnal animals in the fauna suggests either that they were not preferred prey of owls, or they were relatively less abundant near Predator Cave than they are now on Maud Island, where they are seen commonly at night (THW, pers. obs.).

Buller (1888) recorded lizards among the prey of the laughing owl. Lizard bones were abundant in the prey remains in Predator Cave, and all were determined to at least genus-level. Most belonged to nocturnal forest geckos. Geckos were equal in numbers to the bats in the older layers (geckos : bats—22 : 18, 73 : 62, 42 : 45), and did not differ significantly in abundance until the black deposit was laid down (27 : 18). Despite the parity in numbers, geckos other than *H. duvaucelii* still contributed much less than bats to the total prey biomass.

Although the large gecko *Hoplodactylus duvaucelii* was represented by few individuals, its presence was most interesting. Barwick (1982) suggested that the southern limit of its distribution was The Brothers Islands, in Cook Strait. There, individuals were active with body temperatures of 8 °C in mid-winter during a southerly gale. Animals live to at least 36 years of age on the islands (Thompson *et al.*, 1992). Worthy (1987*a*) found no evidence that *H. duvaucelii* was present formerly on the South Island. Worthy & Holdaway (1993) did not find it in caves on the West Coast, and it was not present in the extensive deposits of Honeycomb Hill Cave, west of Takaka Hill (Worthy & Mildenhall, 1989; Worthy, 1993). The samples from Predator Cave and the nearby Takaka Valley (Worthy & Holdaway, 1994*b*) are the first from the mainland of the South Island.

Hoplodactylus duvaucelii could have lived farther south than its present range before rats arrived, because it can tolerate low temperatures (Barwick, 1982). Whitaker (1987) reported that *H. duvaucelii* visit flowers to feed on nectar, and that they and other hoplodactylines are potentially important as pollinators and in seed dispersal. The former presence of these geckos on Takaka Hill was not suspected before the fossil evidence was found. They may have had a large influence on plant reproduction and demography in the South Island.

Several terrestrial taxa in the size range taken by *S. albifacies* are known from Hermit's Cave (Worthy & Holdaway, In press) were not found in the Takaka Hill deposits. *Anas chlorotis* (a duck of about the same size as *Euryanas finschi*, one individual of which was found at Hermit's Cave), the medium-sized rail *Gallirallus australis*, and the large parrot *Strigops habroptilus* were all absent from the predator deposits, although they were abundant in nearby pitfall trap sites such as Hobson's Tomo. The abundance of food in the preferred size range (50–150 g) may have meant that the Takaka Hill owls did not need to take the larger species (ducks, rails) that were taken as prey elsewhere.

Callaeas cinerea was not found in either predator deposit on Takaka Hill. It may have been too large to be regularly included in the laughing owl's diet there. It was, however, rare in pitfall sites (Worthy & Holdaway, 1994*b*), where other smaller prey was abundant, and may not have been

common on Takaka Hill in the Holocene. The one individual in Hermit's Cave was a juvenile (Worthy & Holdaway, 1994a).

Three other arboreal birds that were almost certainly present in the Holocene forests on Takaka Hill—*Halcyon sancta*, *Chrysococcyx lucidus*, and *Eudynamys taitensis*—were not represented in the prey samples. *H. sancta* and *C. lucidus* are mostly diurnal and frequent forest and shrubland (Falla, Sibson & Turbott, 1979). *E. taitensis* is perhaps too large and pugnacious to have been regular prey for *S. albifacies*, although its partly nocturnal habits (Oliver, 1955) would have exposed it to an increased risk. All three are rare in fossil sites elsewhere in New Zealand (Millener, 1991).

Although the deposit in Predator Cave accumulation did not contain the full range of small vertebrates present on Takaka Hill during the Holocene, it is still the best sample available to date from a single site in New Zealand. The assemblage contains only small, terrestrial, and nocturnal forest vertebrates but is as diverse as the entire surviving forest avifauna of New Zealand (McLay, 1974; Holdaway, 1990). The lower values of H' for Predator Cave than for some of the larger deposits elsewhere (Holdaway, 1990) reflects the lack of larger taxa in the prey accumulation. The value for a composite sample from Predator Cave, Hobson's Tomo, and other nearby Holocene pitfall traps (Worthy & Holdaway, 1994b) is as high as for any larger site.

The generally high values of the diversity measures reflect the wide range of prey taken by the owl, and the relatively even representation of many of the taxa. Atkinson & Cade (1993) obtained values for Hill's N1 of 6.3–11.8 and N2 of 4.0–7.9 (including insects) from pellet samples from northern shrikes in Idaho. The total vertebrate faunas in the laughing owl samples were (N1) 10.57–16.379 and (N2) 6.471–13.804.

The rarefraction curve estimates of species richness showed that the prey faunas in each of the four parts of the deposit were very similar. The differences of only one or two in the expected number of species for comparable sample sizes reflected both the owl's consistently broad choice of prey and the relative homogeneity of the available prey fauna through time and at different sites. The curve for Hawkes Cave was steeper than that for the larger samples, which indicates a greater evenness for that sample: each taxon was represented by only a few individuals. In contrast, the taxa were less evenly represented in the Hermit's and Predator Cave samples, emphasizing the predominance of a few main prey species. The rarefraction curves for the laughing owl were very similar to those for summer and adjusted winter pellet samples for northern shrikes (Atkinson & Cade, 1993), a passerine that preys on small vertebrates.

Atkinson & Cade (1993) suggested that, although small prey such as insects provided less energy than small vertebrates, insects allowed a greater rate of energy consumption because of the shorter handling time involved per item. It is possible that smaller vertebrates and insects are strongly under-represented in the laughing owl deposits considered here, the first because of greater loss rates and lower recovery rates for very small bones, and the second because the substrate pH was not conducive to the preservation of cuticle. The frogs, lizards, and small birds may represent more important dietary components than the biomass data suggest.

The wide range of prey taxa should indicate a situation of low prey abundance or availability, as pointed out by Atkinson & Cade (1993). Anecdotal reports suggest that many vertebrates were superabundant in New Zealand forests when Europeans arrived. It is reasonable to suppose that the same situation prevailed before humans arrived and introduced *Rattus exulans*. The abundance of many of the major prey taken by laughing owls, and the apparently wide choice of prey, would contradict the hypothesis that diet breadth is inversely related to prey availability,

unless the owl was primarily nocturnal rather than crepuscular. Prey availability would then be a function of activity time and the height stratum used by each species in the forest.

Indeed, the composition of the assemblage gives some clues as to the territorial and feeding behaviour of *S. albifacies*. Martin (1990) proposed a "nocturnal syndrome" that he suggested is characteristic of a minority of wholly nocturnal owls. These owls hunt regularly beneath a woodland canopy, and have a totally sedentary lifestyle that facilitates prey capture (by enhancing familiarity with the three-dimensional structure of the feeding range), so increasing breeding success, and individual survival.

Martin (1990) contrasted the behaviour of the wholly nocturnal owls with that of the majority, which are less strictly nocturnal. These use tree cover for roosting and nesting, but hunt along woodland edges and in clearings, and in open country away from trees, and may be sedentary at some times during the year. The Takaka Hill samples contained only one *Chalinolobus tuberculatus*, a bat which feeds over shrubland and along forest margins (C. F. J. O'Donnell, pers. comm. 1993), but many mystacinids. Surviving populations of *Mystacina tuberculata* forage mainly on the forest floor, and on the trunks and branches of trees (Daniel, 1979; Ecroyd, 1992, 1993; Higham, 1992; O'Donnell, pers. comm.).

Against the suggestion that the owls that inhabited Predator Cave lived within closed forest is that its main prey was *Cyanoramphus novaezelandiae*, whose extant populations prefer forest margins. In forested areas on the mainland, however, *C. novaezelandiae* may have fed on herbs and insects on the forest floor, especially the more open forest floors prevailing on Takaka Hill and in areas farther east. The evidence from island populations suggests only that *C. novaezelandiae* is more of a ground bird than *C. auriceps* (Taylor, 1975; Nixon, 1994). On the mainland, most of the eastern drier forests that could be expected to have had relatively open floors were destroyed by fire soon after human occupation began (McGlone, 1989).

Although strictly nocturnal owls are highly sedentary, they eat a wide range of prey and hunt by short flights from observation perches (Martin, 1990). Less nocturnal species take fewer prey taxa and hunt on the wing as well as from perches. The sedentary habit and strategy of hunting from a perch may reflect a need to "know" the area very well so as to be able to catch prey consistently. A wide range of prey suggests that the predator cannot, does not need to, or cannot afford to, discriminate between potential prey items. The diversity of prey in the deposits described here, coupled with the nocturnal, forest-floor-dwelling habits of many of them, suggest that the laughing owls, at least on Takaka Hill, were mainly nocturnal and sedentary birds that hunted from perches in stable and well-known territories.

The Predator Cave deposit and nest site was in a cave under (originally) closed forest. The owls must have been able and willing to fly at least short distances without visual clues (Martin, 1990). Although owls have sensitive vision that is close to the limits predicted for vertebrate eyes, the sensitivity "is insufficient to provide vision under all natural conditions" (Martin, 1990). Locating a nest in a cave, under forest, at night, was as close to operating without light as possible under natural conditions. The laughing owl's apparent ability to do this further supports the hypothesis that it was a sedentary, primarily nocturnal owl. However, the presence of some diurnal prey shows that, either the owl had a broad behavioural repertoire and was also crepuscular, taking birds as they went to roost, or that it could locate sleeping birds in the dark forest. The former is more likely, especially in an ecosystem where the more usually crepuscular owls, such as barn and short-eared owls, were absent.

Martin, Korpimäki & Jaksić (1993) concluded that raptors perceive prey resources differently in different regions and localities. They cautioned against extrapolating, even between adjacent

localities: "raptor guilds and assemblages may not be tightly coevolved systems". Hence, the species composition of the prey in a predator deposit cannot be taken as the sole evidence for the identity of the predator. But the prey characteristics of a fauna may well be similar, despite differences in species composition. Deposits in both Predator and Hermit's Caves were dominated by species active on the ground at night.

Taphonomic and other evidence must agree before the predator's identity can be predicted with confidence. The guild of nocturnal raptors in pre-human New Zealand included only two owls. The size difference between them (Worthy & Holdaway, 1994a) might suggest that there would be significant differences in prey size, especially where the owls were sympatric, but, as noted above, this may not always hold.

Raptors appear to choose prey on the basis of suitable size and availability (Marti *et al.*, 1993). The data for Hermit's Cave (Worthy & Holdaway, 1994a), and for Predator and Hawkes Caves, support this contention. The major prey items differ between the two areas, but given the absence of procellariids on Takaka Hill, the same size range was used. Jaksić & Braker (1983) concluded that raptors take all available prey from the largest they can subdue, to the smallest that gives a positive energy balance. The three owl deposits described to date support their hypothesis; the largest prey in the deposits (small ducks, medium-sized rails, large parrots) were very minor components of the total sample. Laughing owls could take prey up to c. 400 g, but they concentrated on species of 50–150 g, presumably because prey of this size was easier to handle.

The laughing owls at Predator Cave altered their diet in response to changes in prey availability. The proportion of endemic taxa was markedly lower in the most recent, black part of the deposit, which *R. exulans* dominated both in numbers and biomass.

Madagascar has a very similar history of human impact to that of New Zealand. Both land masses were settled very late in history and humans introduced exotic vertebrates and changed large tracts of vegetation on both, following which many vertebrates have become rare or gone extinct. The Madagascar long-eared owl *Asio madagascariensis* now includes large numbers of introduced rodents in its diet, both in terms of numbers (48.7%) and biomass (72.1%), despite the continued abundance of endemic rodents, bats, other small mammals, reptiles, and frogs (Goodman, Lagrand & Raxworthy, 1993). There the most common rodent in *A. madagascariensis*'s diet was *Rattus rattus*, which was introduced to Madagascar earlier in the 20th Century. *R. rattus* was introduced to New Zealand in the mid-to-late 19th Century (Atkinson, 1973). As the Madagascan owl apparently has a lower body weight than *S. albifacies*, *R. rattus* could also have become part of the New Zealand owl's diet in the brief period between the rat's arrival and the owl's near extinction.

The range of prey taken by *S. albifacies*, and the abundance of *R. exulans* in the 'black' deposit of Predator Cave may give some clue to the cause(s) of the owl's decline towards extinction in the late 19th and early 20th Centuries. So long as suitable prey was abundant, and there were no predatory mammals larger than *R. exulans*, *S. albifacies* had enough prey and was not subject to significant predation itself. The introduction of *Felis catus*, *Mustela erminea*, *M. nivalis*, *M. putorius*, and *Rattus norvegicus* and *R. rattus* in the second half of the 19th Century provided not only a new suite of predators and competitors for the owl, but also brought about the near extinction of *R. exulans* on the mainland.

Buller (1873) suggested that the laughing owl's disappearance was correlated with the rapid decline of *R. exulans*. Williams & Harrison (1972: 16) rejected Buller's hypothesis, on the grounds that the fur in the pellets could have come from bats and because they considered it "unlikely that an introduced mammal would become an essential item of diet". They questioned how, if the rat

had been important to the owl's diet last century, the owl had managed before the rat was introduced. Instead, Williams & Harrison (1972) suggested that a combination of introduced predators and destruction of its food supply by burning of the owl's supposed grassland habitat caused the bird's decline.

Although the fur in pellets inspected by Smith (in Buller, 1888) could have been bat fur, Buller may well have been correct in his surmise. The laughing owl was probably an opportunistic feeder and its acceptance of *R. exulans* shows that it could accommodate novel taxa in its diet as they became available. The owls in Predator Cave changed from a completely 'natural' diet, to one dominated by *R. exulans*. The Predator Cave deposit did not provide the stratigraphic resolution necessary to examine in detail the decline of either the indigenous fauna, or if *R. exulans* was displaced from the mainland by European rodents. Certainly, *contra* Williams & Harrison (1972), there was sufficient habitat (forest) left at the time of extinction.

It is likely that the laughing owl could have replaced *R. exulans* in its diet with European rodents, as the Madagascar long-eared owl did. Reasons other than the loss of potential prey are needed to explain the owl's decline to extinction. It is much more likely that other mammalian predators—*Felis catus*, and *Mustela erminea* and *M. putorius*—introduced by Europeans were responsible. *F. catus* was introduced in the 1840s. Mustelids were introduced in the 1880s to control introduced rabbits *Oryctolagus cuniculus* (King, 1990). In the South Island, the laughing owl rapidly became scarce after about 1880 (Williams & Harrison, 1972), which correlates well with the time of spread of mustelids, especially *M. erminea*. *M. erminea* had even spread to islands off the far south-west of the South Island by the turn of the century and was affecting ground-nesting birds (Henry, 1901, 1902).

Although Atkinson (1973) may have been correct in suggesting that the most important new predator was *R. rattus* for birds in general, we consider that the mustelids were more significant factors in the extinction of the laughing owl, because the owl could prey on any of the rats. Indeed, Atkinson could find no evidence that *R. rattus* was widespread in the South Island until the 1890s, 10 years after the owl had started to decline.

Ecology of extinct species

A simple picture can be constructed of the possible ecological relationships of the Takaka Hill fauna. In their discussion of the pre-human ecology of birds in various areas of New Zealand, Atkinson & Millener (1991) were hampered by having to use uncorroborated species lists from many sites. Temporal and altitudinal differences in species distributions were also not appreciated at that time, so Pleistocene and Holocene, and upland and lowland, components of the regional faunas were confounded. The use of presence/absence data, rather than relative abundance, further obscured the underlying patterns in the faunas.

The broad guilds of birds identified in the composite Holocene fauna of Takaka Hill (Table IV) are the first to be based on a large data set with close age control for any area of New Zealand. Most of the putative guilds have suffered losses since humans reached New Zealand; two guilds no longer exist (Table V). The surviving taxa are generally small and arboreal and at least partly insectivorous. Most surviving taxa are also relatively recent immigrants, or at least are taxonomically less differentiated from relatives elsewhere than were most of the extinct taxa (Fleming, 1962; Holdaway, 1989).

Beech (Nothofagus) forest birds

The Holocene vertebrate faunas from Takaka Hill include the first comprehensive record of a New Zealand *Nothofagus* forest avifauna undisturbed by the effects of human colonization. Contrary to present perceptions that had to be based on the limited, biased samples available from archaeological sites (e.g. Morrison & Anderson, 1991), it appears that the pre-human avifauna in *Nothofagus* forest was species-rich, although it may not have contained many taxa attractive as food sources for humans. The Takaka Hill avifauna cannot alone fill the gaps in our knowledge of *Nothofagus* forest avifaunas (Vuilleumier & Kikkawa, 1991). More sites deposited under *Nothofagus* elsewhere are needed before at least the Holocene and late Pleistocene distributions of New Zealand birds can be clarified, and any community that may have been unique to *Nothofagus* forest may be characterized. While not elucidating the course of evolution of *Nothofagus* faunas, that would at least allow the proper appreciation of one of the end-points, such as the limited diversity apparent today (McLay, 1974).

Conclusions

Many New Zealand vertebrates had relict distributions when Europeans arrived over 200 years ago (Holdaway, 1989; Millener, 1991; Worthy & Holdaway, 1993). The gross extent of the retraction in ranges from some of the larger species, and for the tuatara and some lizards and frogs is reasonably well known (e.g. Millener, 1991; Beauchamp & Worthy, 1988; Worthy, 1987*a*, *b*, *c*), but little is known about the former distributions of many of the smaller birds. In the absence of evidence to the contrary, it has been tacitly assumed that either the past distributions were the same as the present distributions, or that species had been more or less evenly distributed throughout the archipelago. These models are not tenable now, but more data are needed before former distribution patterns that account for relative abundance can be understood. Predator sites have the greatest potential for elucidating the pre-human distributions of vertebrates and large invertebrates in New Zealand.

The abundant remains of many indigenous taxa in the rich Predator Cave deposit, plus those of mammals introduced by Polynesian and European settlers, provide the most complete record available so far of changes in the indigenous fauna resulting from the effects of human colonization of New Zealand. Before the discovery of these deposits, it was possible only to compare what was present formerly to what existed when Europeans arrived, and to speculate as to what happened in between (Cassels, 1984; Holdaway, 1989). Therefore, in the past, only circumstantial evidence had been used to link the effects of humans and rats to faunal changes in New Zealand (e.g. Atkinson, 1977, 1985; Holdaway, 1989). This, the first description of a natural deposit that accumulated before and throughout the period of faunal change, is therefore the first demonstration of the changes in the indigenous fauna of New Zealand that coincided with the arrival of a rodent.

REFERENCES

Anderson, A. J. (1991). The colonization of New Zealand. *Antiquity* **65**: 767–795.

Anon. (1990). New light on extinct owl. *Otago Mus. newsl.* **14** (December 1990).

Atkinson, E. C. & Cade, T. J. (1993). Winter foraging and diet composition of northern shrikes in Idaho. *Condor* **95:** 528–535.

Atkinson, I. A. E. (1973). Spread of the ship rat (*Rattus r. rattus* L.) in New Zealand. *J. R. Soc. N. Z.* **3**(3): 457–472.

Atkinson, I. A. E. (1977). A reassessment of factors, particularly *Rattus rattus* L., that influenced the decline of endemic forest birds in the Hawaiian Islands. *Pac. Sci.* **31**(2): 109–133.

Atkinson, I. A. E. (1985). The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. *Int. Counc. Bird Preserv. Tech. Publ.* **3:** 35–81.

Atkinson, I. A. E. & Millener, P. R. (1991). An ornithological glimpse into New Zealand's pre-human past. *Acta XX Congr. Int. Orn.* **1:** 129–192.

Baird, R. F. (1989). Fossil bird assemblages from Australian caves: precise indicators of late Quaternary palaeoenvironments? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **69:** 241–244.

Bartle, J. A. & Sagar, P. M. (1987). Intraspecific variation in the New Zealand Bellbird *Anthornis melanura. Notornis* **34**(4): 353–306.

Barwick, R. E. (1982). The growth and ecology of the gecko *Hoplodactylus duvaucelii* at The Brothers Islands. New Zealand Wildlife Service, Department of Internal Affairs. *Occas. Publ.* **2:** 377–391.

Bauer, K. (1956). Schleiereule (*Tyto alba* Scop.) als Fledermausjäger. *J. Ornithol.* **97:** 335–340.

Beauchamp, A. & Worthy, T. H. (1988). The takahe's decline in distribution—a re-examination. *J. R. Soc. N. Z.* **18:** 103–112.

Buller, W. L. (1873). *A history of the birds of New Zealand.* London: Van Voorst.

Buller, W. L. (1888). *A history of the birds of New Zealand.* 2nd edn., 2 vols. London: The author.

Cassels, R. (1984). The role of prehistoric man in the faunal extinctions of New Zealand and other Pacific islands. In *Quaternary extinctions: a prehistoric revolution*: 741–767. Martin, P. S. & Klein, R. (Eds). Tucson, Arizona: University of Arizona Press.

Daniel, M. J. (1979). The New Zealand short-tailed bat, *Mystacina tuberculata*; a review of present knowledge. *N. Z. J. Zool.* **6**(2): 357–370.

Daugherty, C. H., Gibbs, G. W. & Hitchmough, R. A. (1993). Mega-island or micro-continent? New Zealand and its fauna. *Trends Ecol. Evol.* **8**(12): 437–442.

Ecroyd, C. (1992). Bats and wood rose. *For. Bird (Wellingt.)* (August 1992): 26.

Ecroyd, C. (1993). In search of the wood rose. *For. Bird (Wellingt.)* (February 1993): 24–28.

Falla, R. A., Sibson, R. B. & Turbott, E. G. (1979). *The new guide to the birds of New Zealand.* Auckland & London: Collins.

Fleming, C. A. (1962). The extinction of moas and other animals during the Holocene Period. *Notornis* **9**(8): 113–117.

Gill, B. J. (1980). Abundance, feeding, and morphology of passerine birds at Kowhai Bush, Kaikoura, New Zealand. *N. Z. J. Zool.* **7**(2): 235–246.

Gill, B. J. (1986). *Collins handguide to the frogs and reptiles of New Zealand.* Auckland: Collins.

Goodman, S. M., Langrand, O. & Raxworthy, C. J. (1993). Food habits of the Madagascar Long-eared Owl *Asio madagascariensis* in two habitats in southern Madagascar. *Ostrich* **64**(2): 79–85.

Henry, R. (1901). Report on Resolution Island. *NZ House of Representatives, Appendix to the Journals* **C.1:** 132–136.

Henry, R. (1902). Report on Resolution Island. *NZ House of Representatives, Appendix to the Journals* **C.1:** 84.

Higham, T. (1992). Pekapeka: New Zealand's secretive bats. *For. Bird (Wellingt.)* (August 1992): 21–26.

Hill, J. E. & Daniel, M. J. (1985). Systematics of the New Zealand short-tailed bat *Mystacina* Gray, 1843 Chiroptera: Mystacinidae. *Bull. Br. Mus. (Nat. Hist.) Zool.* **48**(4): 279–300.

Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology* **54:** 427–432.

Holdaway, R. N. (1989). New Zealand's pre-human avifauna and its vulnerability. *N. Z. J. Ecol.* **12** (Suppl.): 11–25.

Holdaway, R. N. (1990). Changes in the diversity of New Zealand forest birds. *N. Z. J. Zool.* **17:** 309–321.

Hutton, F. W. (1896). On a deposit of Moa-bones at Kapua. *Trans. Proc. N. Z. Inst.* **28** (1895): 627–644.

Jaksić, F. M. & Braker, H. E. (1983). Food-niche relationships and guild structure of diurnal birds of prey: competition versus opportunism. *Can. J. Zool.* **61:** 2230–2241.

James, F. C. & Rathbun, S. (1981). Rarefraction, relative abundance, and diversity of avian communities. *Auk* **98:** 785–800.

King, C. M. (Ed.) (1990). *Handbook of New Zealand mammals.* Auckland: Collins.

Ludwig, J. A. & Reynolds, J. F. (1988). *Statistical ecology: a primer on methods and computing.* New York: John Wiley & Sons.

Marti, C. D., Korpimäki, E. & Jaksić, F. M. (1993). Trophic structure of raptor communities: a three-continent comparison and synthesis. *Curr. Ornithol.* **10**: 47–137.

Martin, G. (1990). *Birds by night.* London: T. & A. D. Poyser.

Mayhew, D. F. (1977). Avian predators as accumulators of fossil mammal material. *Boreas* **6**: 25–31.

McGlone, M. S. (1989). The Polynesian settlement of New Zealand in relation to environmental and biotic changes. *N. Z. J. Ecol.* **12** (Suppl.): 115–129.

McLay, C. L. (1974). The species diversity of New Zealand forest birds: some possible consequences of the modification of beech forests. *N. Z. J. Zool.* **12**: 179–196.

Merton, D. V., Morris, R. B. & Atkinson, I. A. E. (1984). Lek behaviour in a parrot: the Kakapo *Strigops habroptilus* of New Zealand. *Ibis* **126**(3): 277–283.

Millener, P. R. (1988). Contributions to New Zealand's Late Quaternary avifauna. I: *Pachyplichas*, a new genus of wren (Aves: Acanthisittidae), with two new species. *J. R. Soc. N. Z.* **18**(4): 383–406.

Millener, P. R. (1991). The Quaternary avifauna of New Zealand. In *Vertebrate palaeontology of Australasia*: 1317–1344. Rich, P. V., Monaghan, J. M., Baird, R. F. & Rich, T. H. (Eds). Clayton, Victoria, Australia: Pioneer Design Studios and Monash University Publications Committee.

Millener, P. R. & Worthy, T. H. (1991). Contributions to New Zealand's Late Quaternary avifauna. II: *Dendroscansor decurvirostris*, a new genus and species of wren (Aves: Acanthisittidae). *J. R. Soc. N. Z.* **21**(2): 179–200.

Morrison, K. & Anderson, A. J. (1991). Lee Island and its Environment. In *Beech Forest Hunters*: 3–8. Anderson, A. J. & McGovern-Wilson, R. (Eds). *N. Z. Arch. Assoc. Monogr.* **18**: 1–88.

Nixon, A. J. (1994). Feeding ecology of hybridizing parakeets on Mangere Island, Chatham Islands. *Notornis* (Suppl.) **41**: 5–18.

Oliver, W. R. B. (1955). *New Zealand birds.* Wellington: A. H. & A. W. Reed.

Potts, T. H. (1882). *Out in the open.* Christchurch: Lyttelton Times.

Reid, B. (1974). Sightings and records of the Takahe (*Notornis mantelli*) prior to its 'official rediscovery' by Dr G. B. Orbell in 1948. *Notornis* **21**(4): 277–295.

Ruprecht, A. J. (1979). Bats (Chiroptera) as constituents of the food of Barn Owls *Tyto alba* in Poland. *Ibis* **121**(4): 489–494.

Scarlett, R. J. (1955). Further report on bird remains from Pyramid Valley. *Rec. Canterbury Mus.* **6**(4): 261–264.

Scarlett, R. J. (1968). An owlet-nightjar from New Zealand. *Notornis* **15**(4): 254–266.

Smith, W. W. (1884). *Sceloglaux albifacies* (laughing owl). *N. Z. J. Sci.* **2**: 86–88.

Taylor, R. H. (1975). Some ideas on speciation in New Zealand parakeets. *Notornis* **22**(2): 110–121.

Thompson, M. B., Daugherty, C. H., Cree, A., French, D. C., Gillingham, J. C. & Barwick, R. E. (1992). Status and longevity of the tuatara, *Sphenodon guntheri*, and Duvaucel's gecko, *Hoplodactylus duvaucelii*, on North Brother Island, New Zealand. *J. R. Soc. N. Z.* **22**(2): 123–130.

Turbott, E. G. (Convener). (1990). *Checklist of the birds of New Zealand and the Ross Dependency, Antarctica.* 3rd edn. Auckland: Random Century and Ornithological Society of New Zealand.

Vuilleumier, F. & Kikkawa, J. (1991). Reconstructing the history of *Nothofagus* forest avifaunas. In *Acta XX Congressus Internationalis, Ornithologici* **2**: 578–586. Bell, B. D., Cossee, R. O., Flux, J. E. C., Heather, B. D., Hitchmough, R. A., Robertson, C. J. R. & Williams, M. J. (Eds). Wellington: New Zealand Ornithological Congress Trust.

Whitaker, A. H. (1987). The role of lizards in New Zealand plant reproductive strategies. *N. Z. J. Bot.* **25**: 315–328.

Williams, G. R. (1956). The Kakapo (*Strigops habroptilus* Gray). A review and reappraisal of a near-extinct species. *Notornis* **7**: 29–56.

Williams, G. R. & Harrison, M. (1972). The laughing owl *Sceloglaux albifacies* (Gray, 1844): a general survey of a near-extinct species. *Notornis* **19**(1): 4–19.

Williams, M. A. J., Dunkerley, D. L., De Decker, P., Kershaw, A. P. & Stokes, T. (1993). *Quaternary environments.* London: Edward Arnold.

Worthy, T. H. (1987a). Osteological observations on the larger species of the skink *Cyclodina* and the subfossil occurrence of these and the gecko *Hoplodactylus duvaucelii* in the North Island, New Zealand. *N. Z. J. Zool.* **14**: 219–229.

Worthy, T. H. (1987b). Osteology of *Leiopelma* Amphibia: Leiopelmatidae and descriptions of three new subfossil *Leiopelma* species. *J. R. Soc. N. Z.* **17**(3): 201–251.

Worthy, T. H. (1987c). Palaeoecological information concerning members of the frog genus *Leiopelma*: Leiopelmatidae in New Zealand. *J. R. Soc. N. Z.* **17**(4): 409–420.

Worthy, T. H. (1989). An analysis of moa bones Aves: Dinornithiformes from three lowland North Island swamp sites: Makirikiri, Riverlands and Takapau Road. *J. R. Soc. N. Z.* **19**(4): 419–432.

Worthy, T. H. (1993). *Fossils of Honeycomb Hill*. Wellington: Museum of New Zealand, Te Papa Tongarewa.

Worthy, T. H. & Holdaway, R. N. (1993). Quaternary fossil faunas from caves in the Punakaiki area, West Coast, South Island, New Zealand. *J. R. Soc. N. Z.* **23**(3): 147–254.

Worthy, T. H. & Holdaway, R. N. (1994a). Scraps from an owl's table—predator activity as a significant process newly recognised from New Zealand fossil deposits. *Alcheringa* **18**: 229–245.

Worthy, T. H. & Holdaway, R. N. (1994b). Quaternary fossil faunas from caves in the Takaka area, northwest Nelson, South Island, New Zealand. *J. R. Soc. N. Z.* **24**(3): 297–391.

Worthy, T. H. & Holdaway, R. N. (In press). Taphonomy of two Holocene microvertebrate deposits, Takaka Hill, Nelson, New Zealand, and identification of the avian predator responsible. *Hist. Biol.*

Worthy, T. H. & Mildenhall, D. C. (1989). A late Otiran-Holocene paleoenvironment reconstruction based on cave excavations in northwest Nelson, New Zealand. *N. Z. J. Geol. Geophys.* **32**: 243–253.

Appendix 1

Names of vertebrates mentioned in text

Scientific name	Common name
Anomalopteryx didiformis	Little bush moa
Dinornis novaezealandiae	Large bush moa
D. struthoides	Slender bush moa
Hymenolaimus malacorhynchos	Blue duck
Apteryx sp.	Kiwi species
Euryanas finschi	Finsch's duck
Anas chlorotis	Brown teal
Porphyrio mantelli	Takahe
Gallirallus australis	Weka
Sceloglaux albifacies	Laughing owl
Ninox novaeseelandiae	Morepork (owl)
Aegotheles novaezealandiae	New Zealand owlet-nightjar
Cyanoramphus novaezelandiae	New Zealand red-crowned parakeet
C. auriceps	New Zealand yellow-crowned parakeet
Nestor meridionalis	Kaka (parrot)
Strigops habroptilus	Kakapo (parrot)
Coenocorypha cf. *aucklandica*	New Zealand snipe
Hemiphaga novaeseelandiae	New Zealand pigeon
Circus eylesi	Eyles's harrier
Falco novaeseelandiae	New Zealand falcon
Pachyptila turtur	Fairy prion
Pelecanoides urinatrix	Diving petrel
Puffinus sp.	Scarlett's petrel
Fregetta sp.?	Storm petrel
Acanthisitta chloris	Rifleman [Acanthisittidae]
Xenicus sp.	Rock and/or bush wren [Acanthisittidae]
Traversia lyalli	Stephens Island wren [Acanthisittidae]
Pachyplichas yaldwyni	South Island thick-thighed wren [Acanthisittidae]
Petroica australis	New Zealand robin [Petroicidae]
P. macrocephala	New Zealand tomtit [Petroicidae]
Mohoua ochrocephala	Yellowhead [Pachycephalinae]
M. novaeseelandiae	Brown creeper [Pachycephalinae]
Rhipidura fuliginosa	New Zealand fantail [Dicrurinae]
Gerygone igata	Grey warbler [Acanthizinae]
Prosthemadera novaeseelandiae	Tui [Meliphagidae]
Anthornis melanura	Bellbird [Meliphagidae]
Anthus novaeseelandiae	New Zealand pipit
Alauda arvensis	European skylark
Philesturnus carunculatus	Saddleback [Callaeatidae]
Callaeas cinerea	South Island kokako [Callaeatidae]
Turnagra capensis	South Island piopio [Turnagridae]
Chalinolobus tuberculatus	New Zealand long-tailed bat
Mystacina tuberculata	Lesser short-tailed bat
Mystacina cf. *robusta*	Greater short-tailed bat
Rattus exulans	Kiore or Polynesian rat
R. rattus	Black or Ship rat
R. norvegicus	Norway or Brown rat
Mus musculus	House mouse
Hoplodactylus cf. *granulatus*	Brown forest gecko assemblage
H. cf. *maculatus*	Common brown gecko assemblage
H. duvaucelii	Duvaucel's gecko
Leiolopisma sp.	New Zealand leiolopismatid skinks
Leiopelma hochstetteri	Hochstetter's frog [Leiopelmatidae]
L. markhami	Markham's frog [Leiopelmatidae]
L. hamiltoni	Hamilton's frog [Leiopelmatidae]