Change in the diet of sooty owls (*Tyto tenebricosa*) since European settlement: from terrestrial to arboreal prey and increased overlap with powerful owls

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Abstract. The current diet of the sooty owl (*Tyto tenebricosa*) was determined by analysing freshly regurgitated pellets collected beneath their roosting sites in East Gippsland, Victoria. Comparisons were then made to: i) prehistoric and historic diet from bone deposits found in cave roosts, and ii) diet of a sympatric owl species the powerful owl (*Ninox strenua*). Sooty owls consumed a large array of terrestrial mammal species prior to European settlement, however, only three terrestrial species were detected in their current diet, a reduction of at least eight species since European settlement. To compensate, sooty owls have increased their arboreal prey consumption from 55% to 81% of their diet. Arboreal species are also a major component of the powerful owl diet and this prey shift by sooty owls has increased dietary overlap between these two species. Predation by foxes (*Vulpes vulpes*), and other feral species, is likely to have reduced the amount of terrestrial prey available to sooty owls since European settlement. Investigation of sooty owl diet changes may offer a unique monitoring system for evaluating the ability of fox control strategies to influence increases in critical weight range mammals.

Key words: sooty owl; powerful owl; diet shift; competition; fox control

Running title: Dietary change of the sooty owl

Introduction

Since European settlement in Australia, many non-volant mammals within the critical weight range of 35g to 5500g have suffered major declines in abundance and distribution, while some have become extinct (Burbidge and McKenzie 1989; Dickman *et al.* 1993; Short and Smith 1994). The exact reasons for these declines are issues of dispute, with attributing factors appearing to include clearing and alteration of habitat, disease, altered fire regimes and the introduction of feral mammals that both compete with and consume native mammals (Burbidge and McKenzie 1989; Dickman *et al.* 1993; Wilson and Friend 1999).

Although it is difficult to prove the direct historic effect of predation on critical weight range mammals by feral species, there seems to be sufficient evidence for the decline of some mammal species with the introduction of the fox (*Vulpes vulpes*) and cat (*Felis catus*), in addition to the effects previously mentioned (Dickman *et al.* 1993; May and Norton 1996; Smith and Quinn 1996; Wilson and Friend 1999). What is certain is that, in forested systems, there continues to be high levels of predation on native mammals, particularly by foxes (e.g. Triggs *et al.* 1984; Wallis and Brunner 1987; Brown and Triggs 1990; Lunney *et al.* 1990).

Although foxes are recognized as a major threatening process on small mammal communities in Australia, their impact on other species within the ecosystem is virtually unknown. Introduced predators such as foxes have severely depleted, and are continuing to deplete, a terrestrial prey base that was once available to, and relied upon, by native predators such as Tytonidae owls. In heavily forested areas where introduced species such as European rabbits (*Oryctolagus cuniculus*) and black rats (*Rattus rattus*)

are low in abundance, the effects of a depleted terrestrial food source on native predators are virtually unknown.

One such predator is the sooty owl (*Tyto tenebricosa*) which is a large forest owl occurring in rainforest and wet eucalypt forests in south-eastern Australia (Blakers *et al.* 1984). It is a top order carnivore consuming large numbers of both arboreal and terrestrial mammal species (e.g. Hollands 1991; Lundie-Jenkins 1993; Debus 1994; Kavanagh 2002). The sooty owl often roosts in caves, where regurgitated prey remains can accumulate over thousands of years (Hollands 1991; Morris *et al.* 1997). These accumulations of prey remains provide the opportunity to assess the dietary change of the sooty owl since European settlement, by comparing prey items contained in cave roosts to prey items found in current regurgitated pellets. This not only provides us with information about dietary change in a top order predator, but also about the terrestrial mammals that once occurred in the area and their possible abundance.

A sympatric owl species, the powerful owl (*Ninox strenua*) is also a top order carnivore, however, this species has a diet consisting almost exclusively of medium-sized arboreal, marsupial prey (e.g. Cooke *et al.* 1997; Kavanagh 2002; Kavanagh 2004). Although the powerful owl does not roost in caves it has the potential to become a main competitor of the sooty owl if the sooty owl undergoes a dietary shift away from terrestrial mammals to a diet consisting more of arboreal species.

The overall aim of this study is to assess the sooty owls current diet in East Gippsland, Victoria. With this dietary information two further aims can be assessed: i) to compare the sooty owls current diet to their prehistoric diet (pre European settlement), and historic diet (post European settlement) from cave roosts in the Mitchell River National Park, and ii) to compare the sooty owls current diet to that of a sympatric owl species, the powerful owl where both species occur in the same habitat.

Materials and Methods

Study sites

This study focuses on 11 different sites that contain sooty owl populations within the Mitchell River National Park, the Nicholson River catchment and Lake Tyers Forest Park, in East Gippsland, Victoria (Figure 1). Sooty owl pellets were collected from nine territories within these sites. Powerful owl pellets were also collected from six territories within these sites. Prehistoric and historic diets were determined by analysing bone remains from two cave sites within the Mitchell River National Park. All study sites are located within communities of Warm Temperate Rainforest, Gallery Rainforest and Dry Rainforest, located in ephemeral streams. As rainforest takes centuries to form (Peel 1999), it is likely to have been a similar vegetation type for several hundred years, particularly given the size of many of the rainforest trees in the area (Melick and Ashton 1991).

(Insert figure 1 here)

Cave deposits

Sooty owls currently occupy both caves where bone deposits were collected and were identified as the predator responsible for these bone deposits. The deposits were different to characteristic prey assemblages attributed to barn owls (*Tyto alba*) and masked owls (*Tyto novaehollandiae*) which are two species also known to roost in caves (Baird 1996).

Barn Owls generally consume small terrestrial mammals less than 200 grams (Baird 1996) whereas these deposits contain larger mammals with body weights over 1000 grams. The prey body weight does fall within the range of the masked owl, however, during our study the cave deposits were all located in rainforest, a preferred habitat of sooty owls (Blakers *et al.* 1984).

Prehistoric diet

Mammalian prey species in the prehistoric diet of the sooty owl from the Mitchell River National Park were determined by analysis of a core sample excavation of bone material from the floor of a cave roost. This cave is still used by a sooty owl, which has been observed on numerous occasions. The core sample was approximately 20cm in diameter and 20cm deep, from a bone deposit 450cm in length, 850cm wide and up to 25cm in depth (Figure 2a). As it was a small sample, percentages of each species were not determined nor were they allocated to a stratified layer. The prey remains were sieved to remove the bones from the soil with all visible cranial material being used for identification, including mandibles, maxilla and teeth.

Historic diet

All visible mandibles were removed and identified from the surface of a bone deposit within a cave roost now rarely used by sooty owls in the Mitchell River National Park (Figure 2b). This deposit is referred to as their historic diet, as it represents a time post European settlement. The surface of two deposits within the cave have been analysed and one is 150cm in length, 125cm wide and approximately 10cm deep (Figure 2c), the other deposit is 110cm in length, 95cm wide and approximately 6-7cm deep. This deposit is 4 km south from the bone deposit where the prehistoric diet was determined. The minimum number of individuals present was determined by counting the number of left or right mandibles, with the most numerous side representing the number of individuals.

(Insert figure 2 here)

Pellet collection

Current owl diets were determined by analysis of freshly regurgitated pellets collected beneath roosting sites of both sooty owls and powerful owls. Pellet collection dates

varied between sites, with sooty owl pellets initially being collected from the Mitchell River National Park in summer 2002/2003, with collections continuing every three to six months until September 2004. Collections from the Lake Tyres Forest Park occurred fortnightly from March until September 2004. When the owl was absent from the roost at the time of collection, the owl species could be determined by analysing the type or position of the roost, the colour and shape of the pellets, the degree of bone fracture within the pellets, the colour of the whitewash and occasionally the presence of feathers. Sooty owl pellets are generally tightly packed and dark in colour, usually containing unbroken bones. Powerful owl pellets (although dark/grey) can be lighter in colour often with broken bones of larger prey, and not as tightly packed (Hollands 1991; Kavanagh 1997). Sooty owl faeces are generally whiter than powerful owl (Kavanagh 1997), but with age, faeces can change colour, particularly after rain, so it was often inappropriate to determine the species on whitewash alone.

The sooty owls current diet was investigated in areas without fox control, and all sites were located at least 4 km from any area considered to have a fox control program in place. Sooty owl pellets were collected from nine sites, and powerful owl pellets were collected from six sites (Figure 1). All sites ranged from the Mitchell River National Park (37°41'S, 147°22'E) in the west, to Nowa Nowa (37°43'S, 148°05'E) in the east. Poisoned baits are laid periodically at the Mitchell River National Park, although it appears that populations of foxes are still relatively high (Glenn McLeod pers. comm.) and is therefore not regarded as having an effective predator control program for this study.

Prey identification

Individual pellets were collected separately and placed into labelled envelopes, with location, roost number, date and owl species being recorded. Each pellet was examined as an individual sampling unit. To identify pellet content, each pellet was soaked

individually in hot water until the pellet became soggy and bones began to separate from the hair with ease. Water was removed by pouring through a sieve and the remains were placed on a tray to manually remove bones from the hair for identification. Distinguishable bone material was used for identification and determining the number of individuals present. Bone material was compared to reference collections from Melbourne Museum and CSIRO, as well as photographs from Wakefield (1960a, 1960b, see 1967), Triggs (2001), and drawings from Green (1983). Some pellets contained insufficient or damaged bone for identification and therefore identification was undertaken using hair analysis. Hair analysis involved either making whole mounts or cross-sections of the hair in order to examine the medulla structure and the shape of the cross-section. These results were then compared with descriptions of hair in Brunner and Coman (1974).

Statistical analyses

To assess compositional differences between the diets of the two owl species, a similarity among species matrix was developed using a Bray-Curtis index based on the percentage of each prey species detected in the diet of each species. Gross differences between the diet of the species were compared by using ANOSIM (analysis of similarity). The SIMPER (similarity percentage) procedure was used to identify those prey species contributing most to the similarity within the two owl species, and the dissimilarity between groups. Both the ANOSIM and SIMPER procedures were conducted using the PRIMER software package (Clarke and Warwick 1994). Multi-dimensional scaling was used to generate an ordination of the similarity of diet (Bray-Curtis Similarity) among the two owl species.

Results

Sooty owl prehistoric and historic diet

The small core sample from the bone deposit in the Mitchell River National Park, representing the prehistoric diet, contained 20 species of small mammal, of which eight species were arboreal and 12 were terrestrial (Table 1). The more recent historic diet examination of the surface of cave deposits revealed a total of 129 prey items. Of these, six species were arboreal mammals and 11 species were terrestrial mammals. Overall, 55% of the diet consisted of arboreal mammals (Table 1).

Terrestrial prey constituted a significant proportion of the sooty owls historic diet representing 45% of prey items (Table 1). The two most abundant terrestrial species detected in the historic diet were the bush rat (*Rattus fuscipes*) and the southern brown bandicoot (*Isoodon obesulus*), representing 12% and 11% of the total terrestrial diet respectively. The eastern quoll (*Dasyurus viverrinus*) represented 7% of the total terrestrial diet and the remaining eight species comprised less than 4% of the overall total (Table 1). Interestingly, several of the species detected in the prehistoric and historic diet are now extinct or extinct from the area (e.g. white-footed rabbit rat (*Conilurus albipes*), eastern quoll and Hastings river mouse (*Pseudomys oralis*)).

(Insert Table 1 here)

Sooty owl current diet

A total of 972 individual prey items were detected in the 771 regurgitated pellets collected and analysed from areas without an effective fox control program. Of these prey items, 853 were detected in pellets collected from the Mitchell River National Park and 119 were detected in pellets collected within the Lake Tyers Forest Park. Seven different mammalian species were consumed in total, three arboreal species, three native terrestrial species and one introduced species (Table 2). When compared to the

historic diet a significant shift has occurred with 81% of the diet now derived from arboreal mammals as apposed to 55% in the historic diet (Tables 1 and 2). Arboreal prey species were detected in the pellets in larger quantities than terrestrial prey in eight of the nine sites investigated. At least four different mammalian species were consumed at each site with the sugar glider (*Petaurus breviceps*) and greater glider (*Petauroides volans*) representing the two most abundant species detected in the pellets at all sites (Table 2). An average of 2 ± 0.7 (mean ± 1SD) native terrestrial species were consumed at each site with the bush rat representing the most abundant terrestrial mammal detected in the pellets (Table 2). A total of three native terrestrial mammal species were detected in the sooty owls current diet, a reduction of eight species since European settlement (Tables 1 and 2). The second most common terrestrial species in the historic diet, the southern brown bandicoot, was not detected in the current diet. This shift towards mainly arboreal prey may be driving sooty owls into a competitive situation with powerful owls in East Gippsland.

Sooty owl and powerful owl dietary comparison

A total of 272 prey items were detected in the 253 powerful owl pellets collected during this study. Powerful owl pellets were collected from six different sites; one from the Mitchell River National Park, one from the Nicholson River catchment and four from the Lake Tyers Forest Park. A total of five mammalian species were detected in the pellets (Table 2). Of the mammalian prey consumed, all were arboreal species, with the greater glider, common ringtail possum (*Pseudocheirus peregrinus*) and sugar glider being the most abundant species detected in the pellets, representing 37%, 25% and 20% of the total diet respectively (Table 2).

(Insert Table 2 here)

Sooty owls were recorded in all six sites where powerful owl pellets were collected during this study. Based on Bray-Curtis similarity indices, there was a significant difference in the diet between sooty owls and powerful owls (ANOSIM), with two of the 999 random permutations exceeding the global R statistic (0.481, $p<0.01$) (Figure 3). The three main arboreal mammalian species detected in the sooty owl pellets were, however, also the main species detected in the powerful owl pellets. These three species, the sugar glider, greater glider and common ringtail possum represented over 81% of prey items detected in both owl species diet (Tables 2). Although both species consume the same three prey species, they do so in different quantities. Sooty owls consume more sugar gliders and terrestrial prey than powerful owls, which only consume arboreal prey and birds, preferring larger prey such as greater gliders and common ringtail possums (Table 3). The greatest degree of overlap occurred in consumption of greater gliders and sugar gliders whereas birds and terrestrial prey contributed to the dissimilarity between prey (Table 3).

(Insert Figure 3 here)

(Insert Table 3 here)

Discussion

Arboreal prey dominated the current sooty owl diet in both the Mitchell River National Park and Lake Tyers Forest Park, to a degree not previously recorded in other dietary studies (e.g. Hollands 1991; Holmes 1994; Kavanagh 1997). This high level of arboreal prey consumption appears to be a relatively recent occurrence as prior to European settlement large numbers of terrestrial prey were consumed. Thirteen species of terrestrial mammal were once consumed in the Mitchell River National Park, with eleven of these occurring on the surface of one bone deposit, indicating the vast array of terrestrial prey available to and consumed by sooty owls until soon after European

settlement. Of these eleven species, the white-footed rabbit rat is now extinct, the eastern quoll is extinct on mainland Australia, four species have not been recorded in the area, and only five species have been recorded in the immediate area of the Mitchell River National Park (Menkhorst 1995). Of these five species, only three are currently detected in pellets, and the other two are most likely in low abundances. The southern brown bandicoot and long-nosed potoroo (*Potorous tridactylus*) occur in the Lake Tyers Forest Park, but have not been recorded in the Mitchell River National Park. There has, therefore, been a major reduction of terrestrial prey species available to sooty owls since European settlement, with eight of the eleven species currently unavailable as prey.

A similar array of species was also consumed by sooty owls prior to European settlement from Marble Arch (Hall 1977 see Hollands 1991), Jenolan (Morris *et al.* 1997), and Buchan where the attributing *Tyto* owl species is unknown (Wakefield 1960a; 1960b; 1967; 1972), indicating the large number of terrestrial prey available to sooty owls prior to European settlement across their distribution.

Prey remains found in sooty owl cave roosts (including Buchan) indicate that the Conilurini tribe of rodents was one of the most consumed prey groups prior to European settlement. This group, however, has suffered the greatest decline of any terrestrial mammal group in Australia since European settlement (Smith and Quinn 1996) and are virtually non-existent in the current sooty owl diet (Smith 1984; Loyn *et al.* 1986; Hollands 1991; Lundie-Jenkins 1993; Holmes 1994; Kavanagh 2002).

Native terrestrial species less affected by European settlement, including the bush rat and *Antechinus* species, appear not to be consumed significantly more by sooty owls than they were historically. Introduced species including European rabbits and black rats occur in low abundances in undisturbed forested areas (Menkhorst 1995) and are therefore rarely consumed by sooty owls; when they do feature in the diet, it is in close proximity to human settlement and relatively disturbed environments (Lundie-Jenkins

1993; Kavanagh 1997). In most forested areas, there has been a reduction of terrestrial prey biomass that has not been supplemented by a dominant native species, or by introduced prey species. So without an alternative terrestrial food source in many forested areas, sooty owls have shifted their diet to consume more arboreal prey, rather than exploring alternative habitats where terrestrial species, such as introduced species are more abundant. Unlike the masked owl, which is more of a habitat generalist capable of occurring in areas where large numbers of introduced terrestrial prey are available, the sooty owl is a habitat specialist (Mooney 1993; Kavanagh 1997; 2002). Arboreal prey species are still in high abundance in most forested areas, and have been less affected since European settlement than many terrestrial species, and are therefore heavily consumed by sooty owls in areas where terrestrial prey are in lower abundance.

Where sooty owls currently consume large numbers of arboreal prey, they are possibly competing with a large sympatric owl species, the powerful owl, which almost exclusively consumes arboreal prey (e.g. Tilley 1982; Pavey 1994; Wallis *et al.* 1998; Cooke *et al.* 2002; Kavanagh 2002). The powerful owls distribution overlaps the entire range of the sooty owls (Blakers *et al*. 1984; Barrett *et al.* 2003), and they are known to often co-exist in the same habitat type (Hyem 1979; McNabb 1996; Kavanagh 1997; 2002). This study has shown that powerful owls still consume large numbers of arboreal prey in the same habitat where sooty owls occur. This high level of dietary overlap is unusual and probably did not evolve this way, instead increasing due to the reduction in terrestrial prey available for the sooty owl since European settlement.

Usually sympatric owl species differ in habitat selection if hunting aspects are similar, or they occur in the same habitat and consume different prey, resulting in low levels of interspecific competition (Lack 1946; Lundberg 1980; Hayward and Garton 1988; Kavanagh 2002). This shift towards a competitive system between sooty owls and powerful owls may have serious ecological consequences. Reduced reproductive output

could occur, as seen in competing tawny owls (*Strix aluco*) and long-eared owls (*Asio otus*) (Nilsson 1984), potentially affecting the population size. Increased predatory pressure on arboreal mammals may reduce their abundance and result in both powerful owls and sooty owls seeking to extend their home range size. Ultimately this may lead to a reduced density of both powerful owls and sooty owls in East Gippsland, increasing the risk to both species in the long term.

As the sooty owl is a generalist predator, potentially consuming all arboreal and terrestrial prey species available to them under 1500g, it is likely that their diet is an indicator to the current health of small mammal communities in an area. As it appears that they consume the most abundant mammal species available to them, sooty owls could offer an ideal model for monitoring post fox-baiting responses by terrestrial mammals. It would be expected that if significant changes occur in the availability of critical weight range mammals (the goal of fox baiting) these species will also start to appear more frequently in the sooty owl diet. Sooty owl populations may also exhibit a marked numerical response to an increase in the available terrestrial prey base.

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Table 1. Prehistoric and historic diet of sooty owls from the Mitchell River National Park

Numbers are in percentages, with (P) representing the presence of a species. Common names follow that of Strahan (1995). Historic diet is derived from 129 prey items.

Prey species	Prehistoric	Historic
Arboreal Mammals		
common ringtail possum	P	34
greater glider	P	10
sugar glider	P	8
eastern pygmy possum	P	1
yellow-bellied glider	P	1
leadbeater's possum	P	1
feathertail glider	P	-
Trichosurus sp.	P	-
Total Arboreal Species	8	6
Total Percentage Arboreal		**55**
Terrestrial Mammals		
bush rat	P	12
southern brown bandicoot	P	11
eastern quoll	P	7
broad-toothed rat	P	4
long-nosed potoroo	P	3
long-nosed bandicoot	P	3
Hastings river mouse	P	1
agile antechinus	P	1
dusky antechinus	P	1
swamp rat	-	1
white-footed rabbit rat	P	1
smoky mouse	P	-
brush-tailed phascogale	P	-
Total Terrestrial Species	12	11
Total Percentage Terrestrial		**45**

Table 2. Sooty owl and powerful owl diet within Mitchell River National Park and the Lake Tyers Forest Park
sd = 1 standard deviation

Prey species	Sooty Owl (972 prey items)				Powerful Owl (272 prey items)			
	Prey items	No. of territories	Mean occurrence (%)	sd	Prey items	No. of territories	Mean Occurrence (%)	sd
Arboreal mammals								
sugar glider	505	9	47	16.2	47	6	20	13.7
greater glider	210	8	23	14.0	112	5	37	25.0
common ringtail possum	92	8	11	11.9	75	6	25	20.5
yellow-bellied glider					3	1	1	1.4
common brushtail possum					2	1	1	1.6
Total Arboreal			**81**	**16.1**			**84**	**19.1**
Terrestrial Mammals								
bush rat	100	9	10	8.9				
agile antechinus	33	7	6	7.0				
dusky antechinus	4	2	1	1.3				
European rabbit	2	1	1	1.1				
Total terrestrial			**17**	**16.4**				
Birds	26	5	**2**	**2.1**	32	5	**16**	**19.1**
Insects					8	2	**3**	**4.9**

Table 3. Percentage contribution of species to similarities between the diet of sooty owls and powerful owls, and to dissimilarities between sooty owls and powerful owls based on Bray-Curtis indices (SIMPER).

Values are only provided for those prey species contributing to 90% of the similarity and dissimilarity of the owls diet.

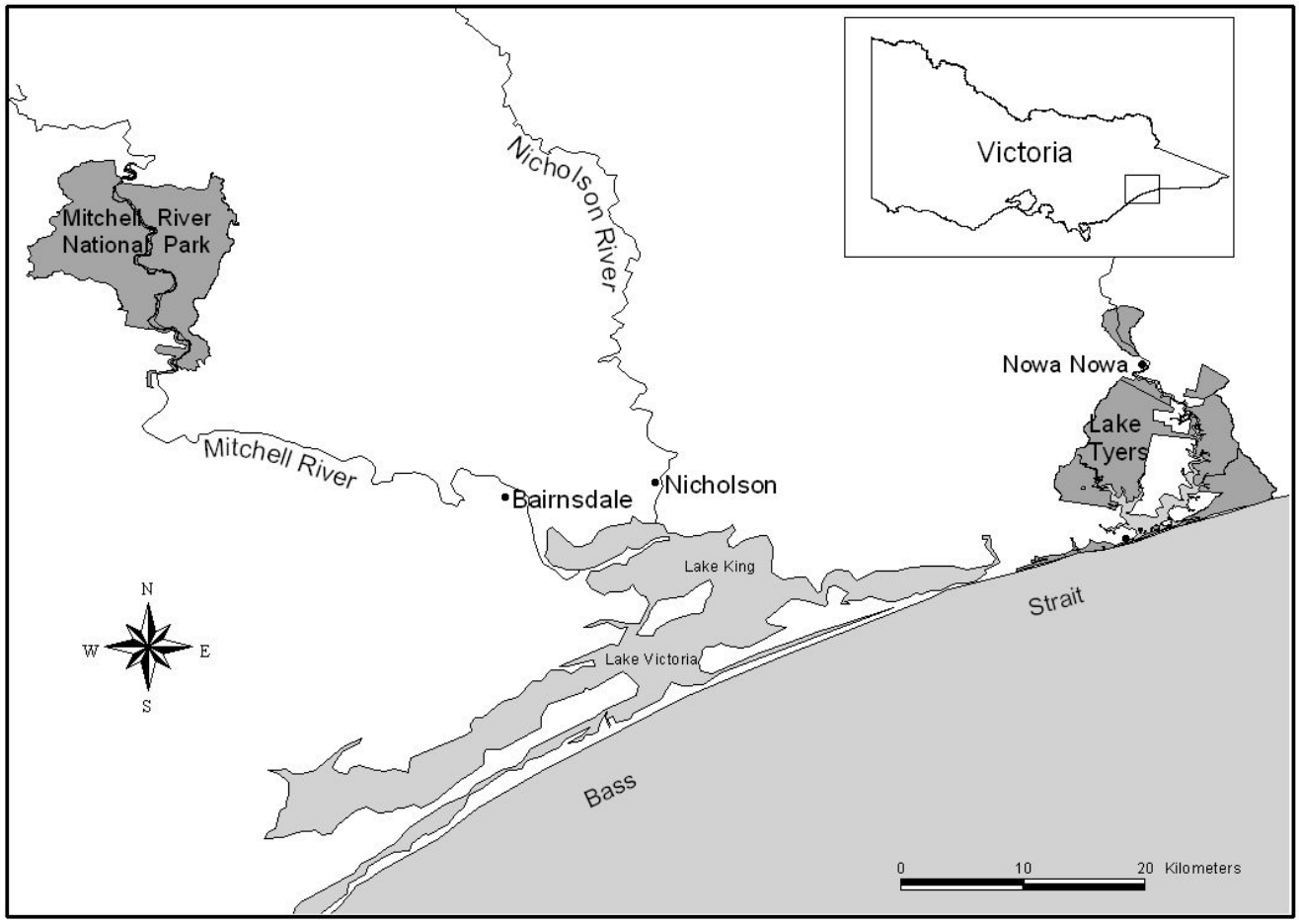
Prey species	**Similarity (% contribution)**		**Dissimilarity (% contribution)**	**Mean composition**	
	Sooty Owl	Powerful Owl		Sooty Owl	Powerful Owl
sugar glider	55.31	21.90	26.53	46.35	19.70
greater glider	21.75	42.06	22.78	22.76	37.00
bush rat	9.90	-	9.84	10.46	0.00
common ringtail possum	8.47	25.17	18.94	11.50	25.45
birds	-	10.88	14.38	2.14	16.61

Figure Headings

Figure 1. Locations of sooty owl and powerful owl pellet collection sites, in East Gippsland
Mitchell River National Park, Nicholson River Catchment and Lake Tyers Forest Park.

Figure 2. Cave roosts of sooty owls where prehistoric and historic diets were analysed.
a) the prehistoric diet cave, with the square indicating the excavation site, b) the historic diet cave, arrow pointing to cave entrance, c) part of the bone deposit in the historic diet cave, after the mandibles were removed.

Figure 3. Multi-dimensional scaling ordination of owl diets in East Gippsland, based on Bray-Curtis similarity measures of dietary composition.
▲= Sooty Owls; ■= Powerful Owls. (Stress = 0.11).


Victoria
Mitchell River National Park
Nicholson River
Mitchell River
Bairnsdale
Nicholson
Nowa Nowa
Lake Tyers
Lake King
Lake Victoria
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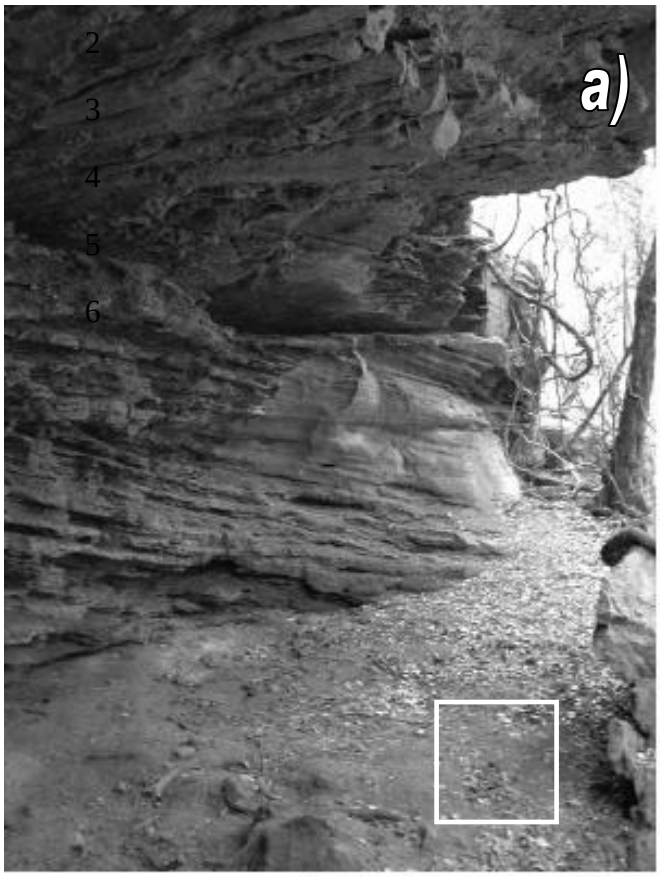

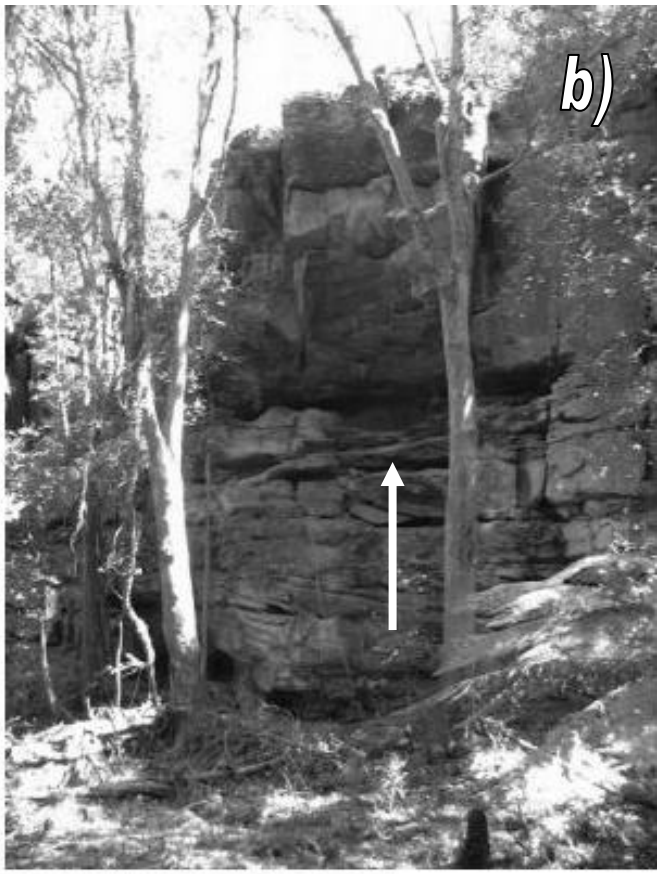

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