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COMPARATIVE DIETS OF THE POWERFUL OWL (*NINOX STRENUA*), SOOTY OWL (*TYTO TENEBRICOSA*) AND MASKED OWL (*TYTO NOVAEHOLLANDIAE*) IN SOUTHEASTERN AUSTRALIA

RODNEY P. KAVANAGH

Forest Research Division, State Forests of New South Wales, P.O. Box 100, Beecroft, NSW, Australia, 2119. Email: rodk@sf.nsw.gov.au

The three large forest owls of southeastern Australia, the Powerful Owl *Ninox strenua*, Sooty Owl *Tyto tenebricosa* and Masked Owl *T. novaehollandiae*, often occur sympatrically but little is known about how they partition their habitat. The places where owls obtain their food and what they eat may have a crucial bearing on our understanding of their habitat requirements. Totals of 1,672 prey items from 47 Powerful Owl territories, 1,466 items from 28 Sooty Owl territories, and 175 items from six Masked Owl territories (or locations) were analysed. There was virtually no overlap between the diets of the Powerful Owl and Masked Owl. The Powerful Owl preyed almost exclusively on arboreal mammals, most of which weighed 50–100% of adult owl body weight, supplemented by diurnal birds. In contrast, the Masked Owl preyed almost exclusively on small terrestrial and scansorial mammals, most of which weighed 3–20% of adult owl body weight, supplemented by diurnal birds. At any one site, both owls appeared to specialise on just one or two prey species. The diet of the Sooty Owl was strikingly different by its generalist nature, comprising, at any one site, a wide range of arboreal and terrestrial or scansorial mammals, mostly weighing 2–100% of adult owl body weight. The Sooty Owl appeared to take any available small and medium-sized mammals and foraged throughout its more limited habitat (rainforest, tall moist eucalypt forest) from the forest canopy to the ground. Geographical variation in owl diets was related to differences in the availability of potential prey. All three species were found to survive and breed successfully in the coastal and foothill forests of southeastern New South Wales on a diet composed principally of prey species that are not dependent on old-growth forest.

INTRODUCTION

Studies of resource partitioning among owls have generally emphasised the differences in food types between species (Lack 1946, Marti 1974, Herrara & Hiraldo 1976, Jaksic 1983, Korpimaki

1992, Marti *et al.* 1993). Relatively few studies have investigated resource use in terms of multiple niche dimensions, such as habitat use and time of activity in addition to food type (e.g. Korpimaki 1986, Hayward & Garton 1988). However, Lundberg (1980) explained the co-occurrence of the Ural Owl *Strix uralensis* and the Tawny Owl *Strix aluco*, which have a similar diet, by their different habitats. The suggestion from the above studies is that species with high dietary overlap co-exist either by differential habitat selection or by exploitation of super-abundant (non-limiting) food supplies, such as occur during peak vole years in the Northern Hemisphere. Hayward & Garton (1988) found that the largest and smallest sympatric owl species differed most in diet, whereas intermediate or similar-sized owls differed from one another most in habitat selection and use. Similar patterns of resource use have been described among other assemblages of carnivores (Schoener 1974), as well as among other trophic groups of vertebrates (Brown *et al.* 1986, Pianka 1986).

The vast differences in small mammal prey availability in many cool temperate areas of the Northern Hemisphere, which occur annually (often in 3–4 year cycles) and seasonally (in part due to snow cover), are well known and documented (Southern 1970, Krebs & Myers 1974, Hansson & Henttonen 1985, Houston 1987, Korpimaki 1992, Taylor 1992, Newton 2002). These fluctuations in prey abundance have powerful effects on the ecology and life history traits of some northern hemisphere owls (Korpimaki 1992, Newton 2002). Generalist predators tend to be resident while specialist predators tend to be migratory or nomadic. Such marked fluctuations in the abundance of small terrestrial mammals and arboreal marsupials do not occur in Australian temperate forests. However, the degree to which resident predators can switch to alternative prey (functional response) when favoured prey become unavailable is likely to influence the resilience of these species to habitat alteration, such as that caused by logging. Short-term population changes (numerical response) among Australian forest-dwelling predators are likely to occur infrequently unless, for example, habitat alteration results in a general depletion of prey.

The diets of Australian large forest owls are perhaps the best known aspect of their ecology, but most previous studies have been anecdotal, opportunistic, or limited to only one species within a given region. In this paper, I document the diets of the Powerful Owl *Ninox strenua*, Sooty Owl *Tyto tenebricosa* and Masked Owl *T. novaehollandiae* at a range of locations in southern New South Wales (NSW). I conclude that, despite the frequent co-occurrence of these three species, they frequently forage in different places and take different prey.

METHODS

Study animals

The Powerful Owl is Australia's largest owl, with males weighing approximately 1,700 g and females slightly less (approximately 1,600 g); the Sooty Owl is the largest mainland *Tyto*, and differs greatly in size between the sexes, with females up to 1,170 g and males approximately 650 g; and male mainland Masked Owls weigh approximately 670 g and females approximately 835 g (Schodde & Mason 1980, Hollands 1991, Kavanagh personal observations). All three owls are widespread throughout the forests of southeastern Australia, with the Sooty Owl favouring the taller, wetter forest types and the Masked Owl including drier woodlands among its habitat. Sympatry between the Powerful Owl and Sooty Owl, and between the Powerful Owl and Masked Owl, is common, but all three species occasionally co-occur in the same areas. Powerful Owls are

regular winter breeders, but the two *Tyto* owls are much less predictable, with Masked Owls possibly breeding mainly in autumn and Sooty Owls in spring.

Study areas

The ecology and behaviour of individual pairs of owls was studied from 1990 to 1996 at eight initially, then many other, locations near Eden, Bega and Bombala in southeastern NSW, and at more than ten locations near Newcastle, Sydney and Wollongong on the central coast of NSW. These study areas were centred on the territories of one or more species of large forest owls: for Powerful Owls, 28 territories in southeastern NSW plus 19 on the Central Coast; for Sooty Owls, 21 territories in southeastern NSW plus seven on the Central Coast; and for the Masked Owl, from one territory and the stomachs of three road-killed owls in southeastern NSW plus one territory and the stomach of one road-killed owl on the Central Coast. The approximate locations of the study territories were determined initially, either by the intensity and frequency of responses to call-playbacks made by owls detected during regional surveys (e.g. Kavanagh & Bamkin 1995), or by the chance discovery of an owl at its diurnal roost. A number of the areas were selected for study because the territories of different species overlapped.

In each study area, systematic searches were made to locate regular roost and nest trees, and to collect regurgitated pellets for analysis. All three owls nest inside large tree hollows; all three commonly roost among foliage, but the two *Tyto* owls also roost frequently inside tree hollows and occasionally in caves. The procedure for locating owl roosts, and subsequently nests, began with regular visits to each study area about one hour before dusk or dawn to listen for calls made by owls as they moved to and from their roosts. Areas where calls were heard were then searched the following day to locate the roost site, as indicated by the presence of the owl or of white-wash and pellets. The owls did not always call at dusk or dawn, and when they did vocalise the calls were often inaudible to an observer greater than 200m away. Thus, dusk/dawn listening was required at many locations before the general roosting areas were found. Furthermore, roost sites within hollow trees took longer to confirm because identification had to be done at night as the owls left or entered the hollows, and pellets deposited inside tree hollows were usually inaccessible. Often it was necessary to search systematically all likely areas in daylight, even at sites where owls were known to occur, because no calls were heard at dusk or dawn. Later, radio-tracking of owls at several locations led to the discovery of many new roost sites at which pellets could be collected.

Owl pellet identification and analysis

Owl diets were determined principally by analysis of regurgitated pellets collected from the ground below foliage roosts or from inside the tree hollows used as roost sites or nest sites. Occasionally, pellets and other prey remains were collected from below nocturnal perches.

If an owl was not present at the time of collection, pellets could usually be allocated to a particular species with confidence from the type of roost site (e.g. tree species and position in the landscape), and from the size, shape and colour of the pellets (Powerful Owl pellets were grey, while Sooty Owl and Masked Owl pellets were usually black and shiny; see König *et al.* 1999), and by the colour of the nearby whitewash (whiter in *Tyto* owls). Powerful Owl pellets were also distinguishable by the presence of broken skulls of prey species; both *Tyto* owls tended to regurgitate the entire, unbroken skulls of their prey. Also, Powerful Owl pellets rarely contained more than one prey item, but two or more items were common in Sooty Owl pellets.

Individual pellets are often used as the basic sampling unit in dietary studies, but this was not always appropriate in my study. Pellets tended to split into fragments when they landed on the ground, and began to degrade after several days owing to beetles (Leiodidae: *Pseudonemadus* sp.) and moth larvae (Tineidae: possibly *Monopis* sp.) consuming the mammalian hair which bound the pellets together, leaving a scattered pile of bones. This was the condition of most pellet material collected from inside caves and tree hollow roosts or nests. Several of the pellet 'samples' collected for the Sooty Owl and Masked Owl formed nest debris representing many pellets. Pellets were separated into different samples, where possible, according to the degree of weathering and decomposition, but there were many instances of multiple pellets bagged as one sample. The data are therefore presented mainly as the relative proportions by frequency of individual prey items. Mean liveweights of each prey species were determined from standard reference books so that contributions to total prey biomass could be calculated.

Pellet contents were identified by analysis of mammalian hair (Brunner & Coman 1974) and by comparison with reference bone material. The pellets were stored in a freezer to kill any moth larvae present, then prepared for analysis by washing in warm water to separate fur from bones followed by drying overnight in a warm oven. Cross-sections of hair samples permitted identification to genus and usually to species. Similarly, identification of animal bones was usually possible to species and counts of jaw bones, skulls, limb bones and pelvic girdles permitted assessment of the minimum number of individuals present in each pellet or pellet sample. Where analysis was based on the identification of hair only, the number of prey items was underestimated because two or more pellets were frequently bagged as one sample.

RESULTS

Powerful Owl

Almost all prey taken by the Powerful Owl were exclusively or primarily arboreal in habit (Strahan 1995), suggesting that this owl hunts only for animals that live in trees (Table 1; Fig. 1). Within the specialised arboreal food niche, the Powerful Owl appeared to be a dietary generalist that preyed opportunistically on the largest available prey, usually mammalian. Fifteen prey species or prey groups (including 'birds' and 'insects') were recorded in Powerful Owl diets across all sites (47), but only three of these were recorded at 23 or more sites, namely Common Ringtail Possum *Pseudocheirus peregrinus* (33 sites), Sugar Glider *Petaurus breviceps* (26 sites) and 'birds'. A regional comparison of Powerful Owl diets showed that birds were taken significantly less often in southeastern NSW compared to the Central Coast of NSW, with relatively minor differences between regions in the contribution of all species of arboreal mammals grouped together, and all insects ($\chi^2 = 44.8$, df. = 2, $P < 0.01$).

The Common Ringtail Possum (900 g; Strahan 1995) comprised 58% of prey items across all sites; however, in many coastal or low (<300 m) elevation forests (37 territories) this species comprised 65–95% of the diet, compared to 0–12% in higher (>300 m) elevation forests (10 territories). The Common Ringtail Possum constituted, numerically, 49% of prey items in southeastern NSW (28 territories), but 62% on the Central Coast (19 territories) (Table 1). The Sugar Glider (125 g; Strahan 1995) comprised only 7% of prey items across all sites, but appeared to be taken more commonly in southeastern NSW (9%) than on the Central Coast (6%). The Greater Glider *Petauroides volans* (1300 g; Strahan 1995) comprised 12% of prey items across all sites, but occasionally predominated at particular sites. For example, two sites (Nunnock Swamp

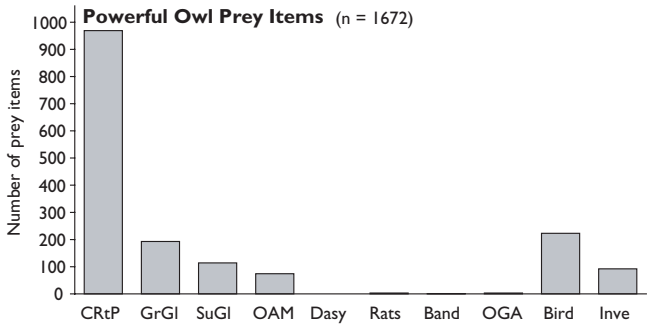
Table 1. Comparative diets of the Powerful Owl, Sooty Owl and Masked Owl in southeastern NSW and on the Central Coast of NSW.

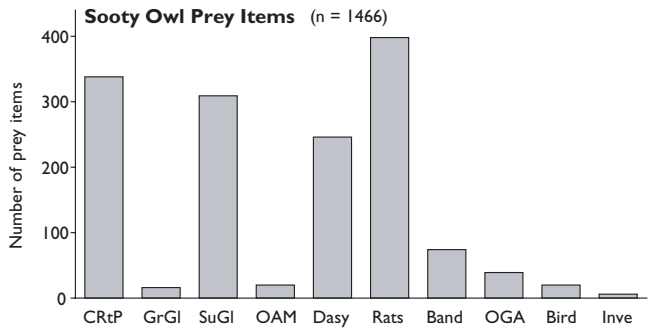
Data are the proportions by number (%) of each prey species taken across all study sites, using owl pellet data only.

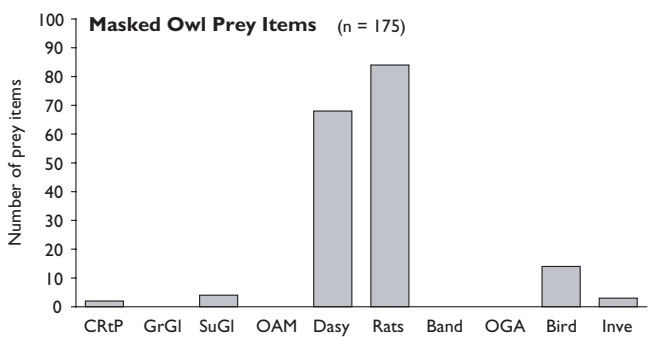
Prey item	Southeastern N.S.W.			Central Coast		
	Powerful Owl	Sooty Owl	Masked Owl	Powerful Owl	Sooty Owl	Masked Owl
Arboreal mammals	**91.2**	**47.6**	**4.6**	**76.5**	**44.3**	**0**
Common Ringtail Possum	48.6	23.0	1.5	61.6	23.3	0
Greater Glider	29.9	0.4	0	4.3	2.9	0
Yellow-bellied Glider	2.1	0.8	0	0	0	0
Sugar Glider	9.1	22.6	3.1	5.9	17.2	0
Mountain Brushtail Possum	0.2	0	0	0	0	0
Common Brushtail Possum	1.3	0.2	0	1.9	0.2	0
Eastern Pygmy Possum	0	0.6	0	0	0.5	0
Koala	0	0	0	0.3	0	0
Grey-headed Flying Fox	0	0	0	2.5	0	0
Micro-bat (*Nyctophilus*?)	0	0	0	0	0.2	0
Terrestrial mammals	**0**	**51.5**	**89.4**	**0.5**	**48.1**	**79.5**
Red-necked Wallaby	0	0	0	0.1	0	0
Long-nosed Bandicoot	0	4.6	0	0.1	3.9	0
Southern Brown Bandicoot	0	1.0	0	0	0	0
Brown Antechinus	0	10.6	29.0	0	10.9	0
Dusky Antechinus	0	8.2	22.9	0	0.2	0
White-footed Dunnart	0	0.2	0	0	0	0
Bush Rat	0	25.0	35.9	0	18.5	0
Black Rat	0	0	0.8	0.3	12.9	70.5
Swamp Rat	0	0.2	0	0	0	0
Broad-toothed Rat	0	0.1	0	0	0	0
House Mouse	0	0	0.8	0	0.7	9.1
European Rabbit	0	1.6	0	0	1.0	+
Other	**8.7**	**1.2**	**6.1**	**23.0**	**7.5**	**20.5**
Birds	5.5	1.0	3.8	16.4	2.2	20.5
Reptiles	0	0.1	0	0.2	4.1	0
Crustaceans	0	0	0	0.2	0.2	0
Insects	3.2	0.1	2.3	6.2	1.0	0
Total	471	1054	131	1201	412	44

and Blue Gum Swamp Creek) accounted for 86% of all records for this prey item. Both sites, and most other territories where the Greater Glider was recorded in owl diets, occurred in high elevation (>300m) forests where this species was usually abundant and the Common Ringtail Possum was rare or absent. No Greater Gliders were recorded in 17 of the 19 owl territories on the Central Coast of New South Wales, where low fertility soils do not support forests capable of providing habitat for this species (Braithwaite 1984, Kavanagh & Lambert 1990), although the Common Ringtail Possum may be abundant.

Birds comprised 13% of prey items across all sites but, as indicated above, differences between regions were apparent. In southeastern NSW, birds comprised only 6% of prey items across 28 territories of the Powerful Owl. This contrasts with 16% of prey items across 19 territories on the



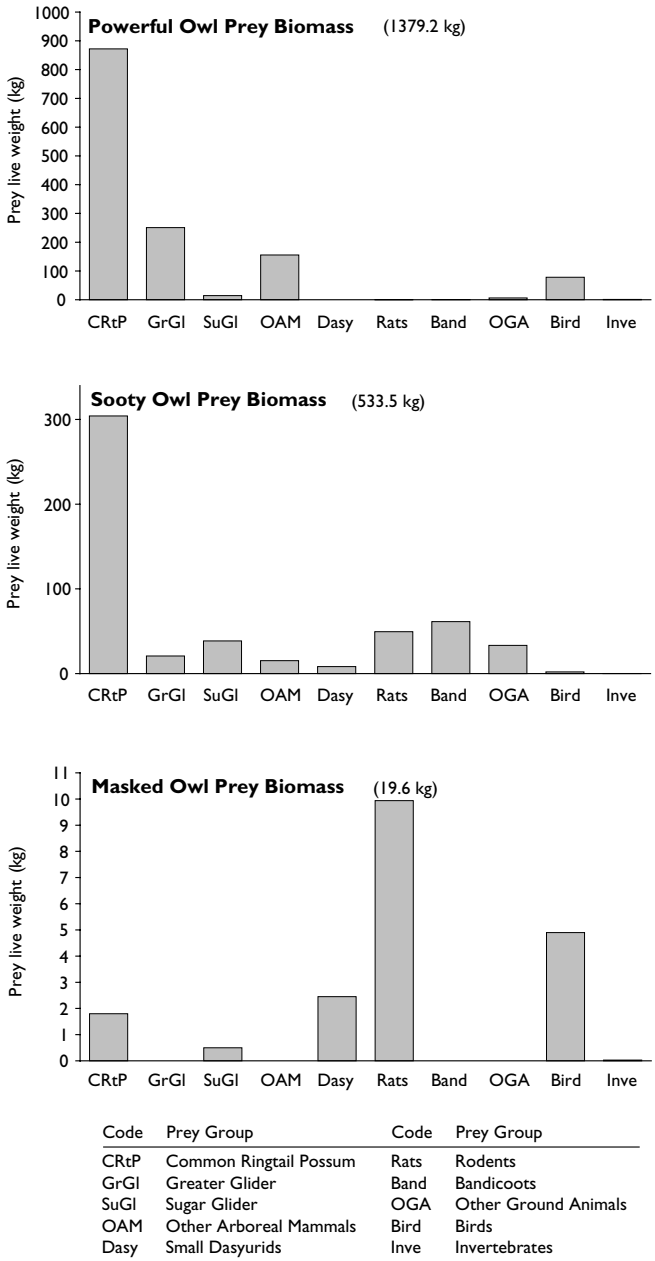




Code	Prey Group	Code	Prey Group
CRtP	Common Ringtail Possum	Rats	Rodents
GrGl	Greater Glider	Band	Bandicoots
SuGl	Sugar Glider	OGA	Other Ground Animals
OAM	Other Arboreal Mammals	Bird	Birds
Dasy	Small Dasyurids	Inve	Invertebrates

Fig. 1. Numbers of major prey items in owl diets in southeastern NSW and the Central Coast of NSW; (a) Powerful Owl (n = 47 owl territories); (b) Sooty Owl (n = 28 owl territories); (c) Masked Owl (n = 6 owl territories or locations).

Central Coast of NSW where many sites occurred in close proximity to urban areas and the forest habitat for owls was located on low fertility soils derived from Hawkesbury Sandstone geology. The bird species most commonly taken by the Powerful Owl were the Pied Currawong *Strepera graculina* (350 g; Strahan 1995) and Crimson Rosella *Platycercus elegans* (150 g; Crome & Shields 1992).



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OAM	Other Arboreal Mammals	Bird	Birds
Dasy	Small Dasyurids	Inve	Invertebrates

Fig. 2. Biomass contributions of major prey items in owl diets in southeastern NSW and the Central Coast of NSW; (a) Powerful Owl (n = 47 owl territories); (b) Sooty Owl (n = 28 owl territories); (c) Masked Owl (n = 6 owl territories or locations).

Also recorded were the Galah *Cacatua roseicapilla* (350 g; Crome & Shields 1992), Rainbow Lorrikeet *Trichoglossus haematodus* (130 g; Crome & Shields 1992), King Parrot *Alisterus scapularis* (225 g; Crome & Shields 1992) and Sulphur-crested Cockatoo *Cacatua galerita* (775 g; Crome & Shields 1992). The average prey weight for these birds was taken to be approximately 350 g.

Insects, mainly large arboreal Christmas Beetles (Scarabaeidae) and large Ghost Moths (Hepialidae), made up more than 5% of the diet of Powerful Owls (each pellet sample containing insects was given the value of one), but insects were used by owls at many (15) sites.

The Grey-headed Flying Fox *Pteropus poliocephalus* (mean weight 675 g; Strahan 1995) comprised 2% of the diet of the Powerful Owl across all sites, however, this prey item was recorded only at four territories, all on the Central Coast. One site, Rocky Creek, was responsible for 77% of records for this species. The main roosting area for the Rocky Creek owls was less than two kilometres from a large, traditional maternity camp of these fruit bats and the owls were often heard calling nearby. The Common Brushtail Possum *Trichosurus vulpecula* (3,500 g; Strahan 1995) comprised 2% of Powerful Owl diets but this species was recorded at 10 sites.

The remaining prey species each comprised numerically less than 1% of the overall diet. These were the Yellow-bellied Glider *Petaurus australis* (575 g; Strahan 1995), Mountain Brushtail Possum *Trichosurus caninus* (4,000 g; Strahan 1995) and Koala *Phascolarctos cinereus* (6,000 g; Strahan 1995). Adults of the two latter species are much larger than the Powerful Owl, but some adults were taken even though the majority were juveniles. The paucity of records for the smaller Yellow-bellied Glider is notable given the widespread distribution of this species in southeastern New South Wales (Braithwaite 1983, Davey 1984, Kavanagh 1984, Lunney 1987, Kavanagh & Bamkin 1995).

Only nine (0.5%) prey items were from species which are terrestrial in habit. These included one Long-nosed Bandicoot *Perameles nasuta*, one juvenile Red-necked Wallaby *Macropus rufogriseus*, three unidentified rats (possibly Black Rat *Rattus rattus*), two unidentified reptiles (possibly Eastern Water Dragon *Physignathus lesueuri*), and two unidentified crustaceans (possibly freshwater crayfish). Several of these unusual records may represent errors in pellet sample identification.

The numerical proportions of prey taken by the Powerful Owl across all 47 sites are summarised in Fig. 1. These data were converted, using the approximate liveweight of individual prey items (see above), to indicate the contribution of each species to total prey biomass (Fig. 2). The importance of the Common Ringtail Possum and the Greater Glider to the Powerful Owl is clearly illustrated.

Sooty Owl

The diet of the Sooty Owl across all sites was characterised by a much broader range of prey species or prey groups (22) than that of the Powerful Owl (Table 1; Fig. 1). In addition to all of the common arboreal prey species taken by the Powerful Owl, the Sooty Owl took large numbers of terrestrial mammals, ranging in size from the House Mouse *Mus musculus* (13 g; Strahan 1995) to the Long-nosed Bandicoot *Perameles nasuta* (mean weight 850 g; Strahan 1995) and European Rabbit *Oryctolagus cuniculus* (1,500 g; Strahan 1995).

The Sooty Owl appeared to be a dietary generalist that hunted throughout the vertical strata of its habitat from the tops of trees to the ground, taking mainly the largest available mammalian prey and those other smaller prey that were relatively abundant. Despite the diversity of prey types, four species were taken at almost every site, namely the Common Ringtail Possum, Sugar Glider, Brown Antechinus *Antechinus stuartii* and Bush Rat *Rattus fuscipes*. Relatively few birds or insects were taken, compared to the Powerful Owl. A regional comparison of Sooty Owl diets revealed no significant difference in the numbers of three main prey groups (all arboreal

mammals, all terrestrial mammals and birds) in southeastern NSW compared to the Central Coast of NSW ($\chi^2 = 3.31$, df. = 2, $P = 0.19$).

The Common Ringtail Possum comprised 23% of prey items across all sites, with no marked difference between southeastern New South Wales and the Central Coast (Table 1). This species was the most significant component by biomass in the diet of the Sooty Owl (Fig. 2). Only at three sites (where few pellets were collected) was the Common Ringtail Possum unrecorded. The Sugar Glider comprised 21% of prey items across all sites, but appeared to be taken more commonly in southeastern New South Wales (23%) than on the Central Coast (17%). The Sugar Glider formed a greater proportion of the diet of the Sooty Owl than of the Powerful Owl.

The Bush Rat (125 g; Strahan 1995) and the introduced Black Rat *Rattus rattus* (125 g) were occasionally difficult to distinguish in pellets, so the numbers of these two species were lumped in this analysis. The majority of confident identifications were attributed to the Bush Rat, while the Black Rat was reliably recorded in Sooty Owl pellets only near Sydney. Both rats together comprised 27% of prey items across all sites. Sooty Owl diets on the Central Coast appeared to consist of a greater proportion of rats (31%) than those in southeastern New South Wales (25%). Two additional rats (Muridae) were recorded occasionally in Sooty Owl pellets from southeastern New South Wales: the Swamp Rat *Rattus lutreolus* (125 g; Strahan 1995) and the Broad-toothed Rat *Mastacomys fuscus* (125 g).

The Brown Antechinus (25 g; Strahan 1995) and the Dusky Antechinus *Antechinus swainsonii* (50 g) comprised 11% and 6% of Sooty Owl diets across all sites. In southeastern New South Wales, where most records of the Dusky Antechinus were made, these two species together comprised 19% of the Sooty Owl diet. The Long-nosed Bandicoot and the Southern Brown Bandicoot *Isoodon obesulus* (700g; Strahan 1995) together comprised 5% of the recorded prey items but, because of their large size, they formed a substantial part of the overall prey biomass (Fig. 2). Birds were uncommon in Sooty Owl diets (1% of all prey items), and most of those taken were much smaller (approximately 100 g) than those taken by the Powerful Owl. Similarly, only few Greater Gliders (1% of all prey items) were taken by the Sooty Owl.

A wide range of additional prey was taken by the Sooty Owl, most of which were recorded only at a few sites. The European Rabbit comprised more than 1% of all prey items but nearly all records came from one location (Bodalla State Forest). Other species taken occasionally (each comprising less than 1% of the diet) included the Yellow-bellied Glider, Eastern Pygmy Possum *Cercartetus nanus* (25 g; Strahan 1995), Common Brushtail Possum, House Mouse and the White-footed Dunnart *Sminthopsis leucopus* (23 g; Strahan 1995). Insects (beetles) were recorded only in five pellet samples from three sites. Eighteen unidentified reptiles (possibly Eastern Water Dragon), one unidentified crustacean (possibly freshwater crayfish) and one micro-chiropteran bat (possibly *Nyctophilus* sp.) were also recorded.

The numerical and biomass proportions of prey taken by the Sooty Owl across all 28 sites are summarised in Fig. 1 and Fig. 2. The importance of the Common Ringtail Possum and the Bush Rat is clearly illustrated.

Masked Owl

The Masked Owl appeared to be a specialised predator of small terrestrial mammals although samples were limited. Four small terrestrial and scansorial (climbing) mammals numerically comprised 85% of the recorded diet. However, a small number of arboreal prey was also taken.

Arboreal marsupials comprised only 3% (Sugar Glider) and 2% (Common Ringtail Possum) of prey items, while birds comprised 8%. A regional comparison of Masked Owl diets showed that birds were taken significantly more often on the Central Coast of NSW than in southeastern NSW, with relatively minor differences between regions in the contribution of all species of arboreal mammals grouped together, and all terrestrial mammals ($\chi^2 = 13.6$, df. = 2, $P < 0.01$).

No prey species additional to those recorded for the Powerful Owl and Sooty Owl were recorded. The native Bush Rat (29% of prey items) and the introduced Black Rat (13%) together comprised 43% of the diet of the Masked Owl. The scansorial Brown Antechinus (24% of prey items) and the terrestrial Dusky Antechinus (19%) together comprised another 43% of the diet. The introduced House Mouse was also taken occasionally (>1% of prey items). Only trace quantities of beetles were recorded in some Masked Owl pellets.

An interesting contrast occurred between the mammalian prey of a pair of Masked Owls living within an entirely forested environment (Old Hut Creek near Eden in southeastern NSW), which included only native prey species, and the diet of another pair living in a highly fragmented semi-urban environment (Warners Bay near Newcastle on the Central Coast of NSW), which included only introduced species (Table 1). Additional prey remains found below regular nocturnal perches of the Masked Owls at Warners Bay suggested that these owls also consumed European Rabbits and a number of birds, including the Sulphur-crested Cockatoo and Tawny Frogmouth *Podargus strigoides*. The average prey weight for these birds, as for the Powerful Owl, was taken to be approximately 350 g.

The proportions of prey taken by the Masked Owl across all six sites are summarised by numbers and by biomass in Fig. 1 and Fig. 2. The importance in terms of biomass of the Bush Rat or the Black Rat, and also birds, to the Masked Owl is clearly illustrated.

Species comparisons

The diets of the three owls, assessed across all sites and in terms of the total numbers of arboreal mammals, terrestrial mammals, birds and insects recorded, were significantly different ($\chi^2 = 1429.0$, df. = 6, $P < 0.01$). Powerful Owls took more arboreal mammals, birds and insects and fewer terrestrial mammals than expected on the basis of comparisons with the other two species. Both the Sooty Owl and the Masked Owl took more terrestrial mammals and fewer arboreal mammals (less significant for the Sooty Owl) than expected, and the Sooty Owl took fewer birds and insects than expected on the basis of comparisons between all three owl species.

DISCUSSION

There was virtually no overlap between the diets of the Powerful Owl, assessed across all sites, and the Masked Owl. The Powerful Owl preyed almost exclusively on arboreal mammals, most of which weighed approximately 800–1,700 g, or 50–100% of adult owl body weight, supplemented by diurnal birds. In contrast, the Masked Owl preyed almost exclusively on small terrestrial and scansorial mammals, most of which weighed approximately 25–125 g, or 3–20% of adult owl body weight, supplemented by diurnal birds. At any one site, both owls appeared to specialise on just one or two prey species. The diet of the Sooty Owl was more diverse, including a wide range of both arboreal and terrestrial or scansorial mammals at any one site, most of which weighed approximately 25–900 g, or 2% to over 100% of adult owl body weight. The Sooty Owl appeared to take any available small or medium-sized mammal and foraged

throughout its more limited habitat (rainforest, tall moist eucalypt forest) from the forest canopy to the ground.

Studies of dietary overlap among raptor assemblages are usually undertaken at a regional scale, and are often taken to indicate the potential for competition (Lack 1946, Marti 1974, Herrera & Hiraldo 1976, Jaksic 1983, Korpimaki 1986, Hayward & Garton 1988). However, to understand whether competition is likely to affect raptor populations and distributions, comparisons need to be done at the local scale of overlapping pairs (Marti *et al.* 1993). According to these latter authors, only two studies (Nilsson 1984, Korpimaki 1987) had attempted to connect the breeding success of raptors with competition for food. Both showed reduced breeding success in the presence of a competitor.

The results of the present study are reported generally at the regional scale, although attempts were made in several localities to compare the diet and breeding success of overlapping species pairs. Only at one site (Bellbird Creek near Eden) was this achieved effectively. Of 12 prey types or prey groups (including 'birds' and 'insects'), only four (Common Ringtail Possum, Sugar Glider, Yellow-bellied Glider and 'birds') were taken by both the resident overlapping pairs of Powerful Owl and Sooty Owl. The Powerful Owl took an additional three prey types (Greater Glider, Common Brushtail Possum and 'insects'), two of which were very large items (>1500 g), while another five species were taken exclusively by the Sooty Owl (Bush Rat, Brown Antechinus, Dusky Antechinus, Eastern Pygmy Possum and Long-nosed Bandicoot). Despite these differences, one species, the Common Ringtail Possum, formed about 66% of the biomass taken by the Sooty Owl and more than 81% of the prey biomass taken by the Powerful Owl. This suggests that, unless the Common Ringtail Possum was in plentiful supply (as appeared to be the case), competition for food might occur between these two species at Bellbird Creek. Unfortunately, breeding could not be confirmed for the Sooty Owl pair during the study, although it may have occurred, while the Powerful Owl pair produced two young (the maximum number) in each of three consecutive years (1992–1994).

The range of prey species taken by the Powerful Owl, Sooty Owl and Masked Owl was generally as reported in the literature (Fleay 1968, Seebeck 1976, Hyem 1979, James 1980, Schodde & Mason 1980, Van Dyck & Gibbons 1980, Tilley 1982, Smith 1984, Loyn *et al.* 1986, Barker & Vestjens 1989, Hollands 1991, Chafer 1992, Debus 1993, 1994, Lundie-Jenkins 1993, Mooney 1993, Peake *et al.* 1993, Debus & Chafer 1994, Debus & Rose 1994, Holmes 1994, Lavazanian *et al.* 1994, Pavey 1994, 1995, Pavey *et al.* 1994, McNabb 1996). Differences in the recorded importance of particular prey species (the Greater Glider and the Common Ringtail Possum) to the Powerful Owl (Kavanagh 1992; Pavey 1992) simply reflect geographical variation.

The present study, like many others (e.g. Donázar 1987), found that geographical variations in owl diets were related to differences in the availability of potential prey. For example, the Greater Glider was abundant in the higher elevation forests of southeastern New South Wales (Kavanagh & Peake 1993, Kavanagh & Bamkin 1995; see also Kavanagh 1984, 1988) and formed more than 97% of total prey biomass for one pair of Powerful Owls (Nunnock Swamp pair). However, the Greater Glider was uncommon or absent in the lower elevation forests of the region where the Common Ringtail Possum formed the main component of Powerful Owl (and Sooty Owl) diets. On the Central Coast of New South Wales, the Greater Glider was absent at most sites, but at one site (Blue Gum Swamp Creek) this species formed nearly 68% of prey biomass and the Common Ringtail Possum, which was also present but not abundant, formed only 9% of prey biomass. Thus, the greater proportion of low elevation (<300 m) sites in this study (79%)

may have underestimated the overall importance of the Greater Glider in the diet of the Powerful Owl. Also, birds were taken more frequently by both Powerful Owls and Masked Owls living in bushland fragmented by urban and rural developments where arboreal marsupials are usually less abundant. Masked Owls preyed extensively on introduced species of small terrestrial mammals in highly disturbed environments but took only native species in less disturbed forests (see also Kavanagh 1996, Kavanagh & Murray 1996).

The general patterns of distribution, habitat and habits of arboreal marsupials and small terrestrial mammals in the forests of eastern Australia are summarised by Strahan (1995). Information about the susceptibility of the main prey species to habitat alteration is crucial for owl conservation. The marsupial gliders have been identified as potentially sensitive to a general reduction in the extent of old-growth forest due to their requirements for large hollows in old trees for shelter and breeding and their habit of foraging in the forest canopy (Tyndale-Biscoe & Calaby 1975, Kavanagh 1991, Scotts 1991). The two largest gliders, the Greater Glider and the Yellow-bellied Glider, are reported to have the closest associations with old-growth forest habitats (Kavanagh 1987, Lunney 1987, Macfarlane 1988, Lindenmayer *et al.*1990, Milledge *et al.*1991, Kavanagh & Bamkin 1995, Kavanagh & Webb 1998, Kavanagh 2000). The Sugar Glider, Feathertail Glider and Mountain Brushtail Possum use large old trees but are less demanding in their requirements, as shown by their varying associations with characteristics of the understorey (Smith 1982, Kavanagh 1984, 1987a, Seebeck *et al.* 1984, Lunney 1987, Lindenmayer *et al.*1990, 1996, Goldingay & Kavanagh 1995). The more adaptable and fecund Common Ringtail Possum and the Common Brushtail Possum use (but do not require) tree hollows for shelter. Both commonly utilise disturbed environments, and the Common Ringtail Possum forages extensively, and builds leaf shelters (dreys), among dense understorey and forest regrowth (Thomson & Owen 1964, Davey 1984, How *et al.* 1984, Kerle 1984, Pahl 1987, Lunney 1987, Macfarlane 1988).

Many species of small ground-dwelling mammals also use trees as nesting or foraging sites (Wood 1970, Dickman 1991), making use of hollows, loose bark on the trunk and upper branches, leaf and bark litter around the base of trees and logs on the ground. However, the composition of the ground-dwelling mammal fauna in southeastern New South Wales is determined principally by the structural complexity of the understorey and ground layer (Catling & Burt 1995a). Logging and prescribed burning result in dynamic changes to understorey conditions that are tracked rapidly by populations of small ground mammals (Recher *et al.* 1980, Lunney *et al.* 1987, Macfarlane 1988, Catling 1991, Kavanagh & Webb 1998). Logging is generally not regarded as having a long-term (>10 years) deleterious effect on populations of most small ground mammals but frequent, low-intensity prescribed burns can simplify forest structure.

Owl prey (arboreal and terrestrial mammals) in southeastern New South Wales tend to be most abundant in gully or riparian forests on lower slope topography and, except for the Greater Glider, at lower elevations in the region (Kavanagh & Peake 1993, Catling & Burt 1995b, Kavanagh & Bamkin 1995, Kavanagh 1997). However, the structural characteristics of the vegetation in many gully forests, and potentially also in forests regenerating after logging, could reduce the availability of prey for the owls (e.g. Southern & Lowe 1968). Thus species such as the Masked Owl, which prey almost exclusively on small terrestrial mammals, may hunt most efficiently in open forests where the ground cover is patchy or sparse, but close to dense cover which provides good habitat for small ground mammals.

The degree of resilience by owls to habitat disturbance may be predicted by their ability to switch to alternative prey (Korpimaki & Norrdahl 1989) and by the population responses of their

prey species to disturbance. The Sooty Owl is a dietary generalist compared to the Powerful Owl and the Masked Owl and may therefore be better adapted to habitat alteration. The Powerful Owl and the Masked Owl have more specialised but different diets due to vertical partitioning of the forest as foraging habitat. Owing to its specialisation on arboreal mammal prey, the Powerful Owl is predicted to be more sensitive to habitat disturbance by logging than either the Sooty Owl or the Masked Owl. This sensitivity is likely to be most acute in the higher elevation forests where the Greater Glider forms the main prey of the Powerful Owl.

Despite the overall differences in diet between the three owls, the overlap was considerable. Both Powerful Owl and Sooty Owl took many Common Ringtail Possums, and similarly the Sooty Owl and Masked Owl took many Bush Rats and Antechinuses. In a review of the mechanisms involved in resource partitioning in ecological communities, Schoener (1974) regarded habitat differences to be more frequent than diet differences, which in turn were more frequent than temporal differences in feeding. Clearly, food competition between forest owls is possible, especially where prey abundance is reduced by disturbance. However, differences in habitat may reduce this competition.

The Powerful Owl is widespread throughout most forest environments east of the Great Dividing Range from wet to dry forest types, including some woodlands (e.g. Kavanagh & Peake 1993, Kavanagh & Bamkin 1995, Kavanagh *et al.* 1995). The Sooty Owl, which overlaps in diet most with the Powerful Owl (arboreal marsupials), was almost confined to the wettest forests but occasionally ventured into drier forests where cave-roosting sites were available (Kavanagh & Jackson 1997). The Masked Owl, which overlaps in diet most with the Sooty Owl (small terrestrial mammals), appeared to avoid the wetter forests and to exploit only the drier, more open forests. While the Powerful Owl and Masked Owl may occur together in drier forest types, the diets of these two species were almost mutually exclusive.

ACKNOWLEDGMENTS

All pellet samples collected in southeastern New South Wales were analysed by Barbara Triggs (the acknowledged Australian expert on identification of mammalian hair and bones), as were some of the samples collected from all other study sites. Mark Chidel analysed most of the remaining pellets using reference samples provided by Barbara. Tony (A.B.) Rose and Chris-Anne Urquhart identified the beetles and moth larvae responsible for consuming the mammalian hair within owl pellets. A number of colleagues collected owl pellets within the study sites, including Khia Atkins, David Coombes, Richard Jackson, Michael Murray, Sandy Sansom, Matthew Stanton, Dick Turner and Judy Wiles. I am most grateful to all of the above for their assistance. Very helpful comments on the manuscript were provided by Ian Newton and an anonymous referee.

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