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Distribution of Nocturnal Forest Birds and Mammals in North-eastern New South Wales: Relationships with Environmental Variables and Management History

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Abstract

A regional survey of the forests in north-eastern New South Wales recorded eight species of nocturnal forest birds and nine species of arboreal marsupials from 291 sites. These forests are an important source of diversity for nocturnal bird and mammal species compared with the two other regions in south-eastern Australia (south-eastern New South Wales and the Central Highlands of Victoria) where similar studies have been undertaken.

Three major environmental gradients accounting for the distribution of these species in north-eastern New South Wales were identified. The dominant gradient contrasted higher-elevation forests in the western half of the region with lower-elevation forests nearer the coast. The second gradient contrasted wet forest types having a dense mesic understorey with dry forest types having an open or sparse understorey. The third gradient represented logging intensity. Characteristic assemblages of species were associated with each end of these three gradients. A core group of species occurred across a wide range of environmental conditions, including logged and unlogged forest.

Most species occurred with similar frequency in logged and unlogged forest. However, limitations in the design of this study, which reflect regional land-use patterns, restrict the untangling of interactions between forest type, elevation and management history. The more disturbed, lower-elevation forests appeared to be the most species-rich environments but the greatest numbers of animals were recorded in the highland forests of the region. The greater glider (*Petauroides volans*), whose stronghold is the higher-elevation forests, was identified as the species most sensitive to heavy logging, although numbers of this species were similar in selectively logged and unlogged forests.

Many of the species recorded in this study are known to use hollows in large old trees for breeding and diurnal shelter. Management attention needs to be directed towards establishing the threshold levels of retention for hollow-bearing trees and for patches of undisturbed vegetation. The establishment of a comprehensive network of retained undisturbed vegetation along most gully systems in the region would seem to be a prudent course of action to maintain biological diversity. As more of the landscape in the region becomes altered by intensive logging or clearing for agricultural and urban land uses, it will be necessary to carefully plan and refine management prescriptions to maintain wildlife habitat components.

Introduction

Large forest owls and marsupial gliders are among the species regarded as having the closest associations with old-growth forest environments in eastern Australia (Tyndale-Biscoe and Calaby 1975; Kavanagh 1991; Scotts 1991) and their conservation needs have a critical bearing on the outcome of land-use decisions. Regional surveys are the first step in assessing conservation options. No published accounts exist concerning the distribution of this fauna in north-eastern New South Wales. A comparative survey in south-eastern New South Wales found clear patterns in the distribution of nocturnal forest birds and arboreal marsupials (Kavanagh and Peake 1993*a*). The abundance of many species in south-eastern New South Wales differed from that recorded by a similar survey in an area of mountain ash (*Eucalyptus*

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regnans) forest in Victoria (Milledge *et al.* 1991). Logging was considered to have a greater influence on the distribution of species in the Victorian study (Milledge *et al.* 1991) than that in south-eastern New South Wales (Kavanagh and Bamkin 1995), but this may have been related to the more intensive silvicultural systems (clearfelling) employed in the mountain ash forests. No other studies on the effects of logging on nocturnal forest birds have been published in Australia. Numbers of arboreal marsupials occurring across a sequence of forest-age or logging-intensity classes were reported by Recher *et al.* (1980), Davey (1984), Meredith (1984), Lunney (1987), Macfarlane (1988), Smith and Lindenmayer (1988), Lindenmayer *et al.* (1990, 1991) and Traill (1991). The larger, tree-hollow-using species were identified as the most sensitive to logging. Tyndale-Biscoe and Smith (1969) demonstrated that one such species, the greater glider (*Petauroides volans*), had a poor ability to re-establish itself in nearby suitable habitat following displacement caused by total clearfelling.

The general patterns of distribution, habitat and habits of nocturnal forest birds are given by Fleay (1968), Schodde and Mason (1980), Blakers *et al.* (1984) and Hollands (1991). Recent reviews for the three largest forest owls occurring in New South Wales, the powerful owl (*Ninox strenua*), the sooty owl (*Tyto tenebricosa*) and the masked owl (*Tyto novaehollandiae*), were provided by Garnett (1992), Davey (1993), Debus (1993, 1994), Peake *et al.* (1993), Debus and Rose (1994) and Debus and Chafer (1994). All species occur more widely in eastern Australia. Broad vegetation community, stand structure and fragmentation, and topography appear to be aspects of habitat important for most species. The general patterns of distribution, habitat and habits of arboreal marsupials in the forests of eastern Australia are given by Strahan (1983). Recher *et al.* (1980), Braithwaite (1983), Davey (1984), Kavanagh (1984), Mackowski (1986), Lunney (1987) and Bennett *et al.* (1991) have highlighted the importance of broad vegetation community and topography (in particular the relationship between these factors and site productivity) and stand structure (which includes the availability of old hollow trees) as influences on habitat suitability for arboreal marsupials. The mammal fauna of north-eastern New South Wales has been identified as one of the richest of any region in Australia (Calaby 1966).

The objectives of this study were to document the pattern of distribution of nocturnal forest fauna in north-eastern New South Wales, to investigate the role of several environmental variables such as broad vegetation type, stand structure and topography in determining this pattern, and to provide a preliminary assessment of the impact of logging on this fauna. About half of the original forest cover in the region has been cleared for agriculture but most of the remainder occurs as large, continous areas of forest. The region is topographically and floristically diverse, and the forests in the eastern half of the region have had a long history of logging.

Methods

The study design and methodology were chosen to duplicate as far as possible an earlier survey in south-eastern New South Wales by Kavanagh and Peake (1993*a*), so that regional comparisons could be made.

Stratification

Numbers of nocturnal forest birds and mammals were estimated at 291 sites distributed throughout the Glen Innes, Grafton, Dorrigo and Coffs Harbour Forestry Management Areas in north-eastern New South Wales (Fig. 1). Sites were located in a total of 41 State forests, three national parks and one nature reserve. Between three and twelve sites were surveyed in each of 53 localities distributed evenly throughout the region. Sampling stratification was based primarily on topography, with one-third of sites located on ridges and upper slopes, and two-thirds located on lower slopes and in gullies. Efforts were made to locate sites in approximately equal proportions within areas either 'generally unlogged' or 'generally logged', including eucalypt plantations. Logging history maps maintained by local Forestry District Offices were used to identify the locations of these areas. Sampling sites were classed as selectively logged if they were located in a coupe (30–100 ha) that had been cut only for fence posts or some sawlogs such that a substantial number of old, hollow trees remained. Sites were classed as heavily logged where several more intensive cutting cycles had occurred after which few or no old, hollow trees remained. The long history and variable intensity of disturbance (logging, fire, grazing) in many forested areas of north-eastern New South Wales made it impossible to achieve a fully balanced research design. The mean distance between adjacent survey sites was 2037 m (range 599–8471 m).

Survey Methods

Each site was surveyed once in winter 1991 (23 July–6 September) and again during the following summer (4 November–21 December). The numbers of all species encountered were estimated on variable-radius plots centred on each site. On each visit, 1 h was spent listening for the unelicited vocalisations and non-vocal cues indicating the presence of animals, followed by 15 min (5 min for each species) of broadcasting the pre-recorded vocalisations of the sooty owl, the powerful owl and the masked owl and waiting for a response. A Toa ER-66 megaphone, with power output rated at 10 W, was used to broadcast

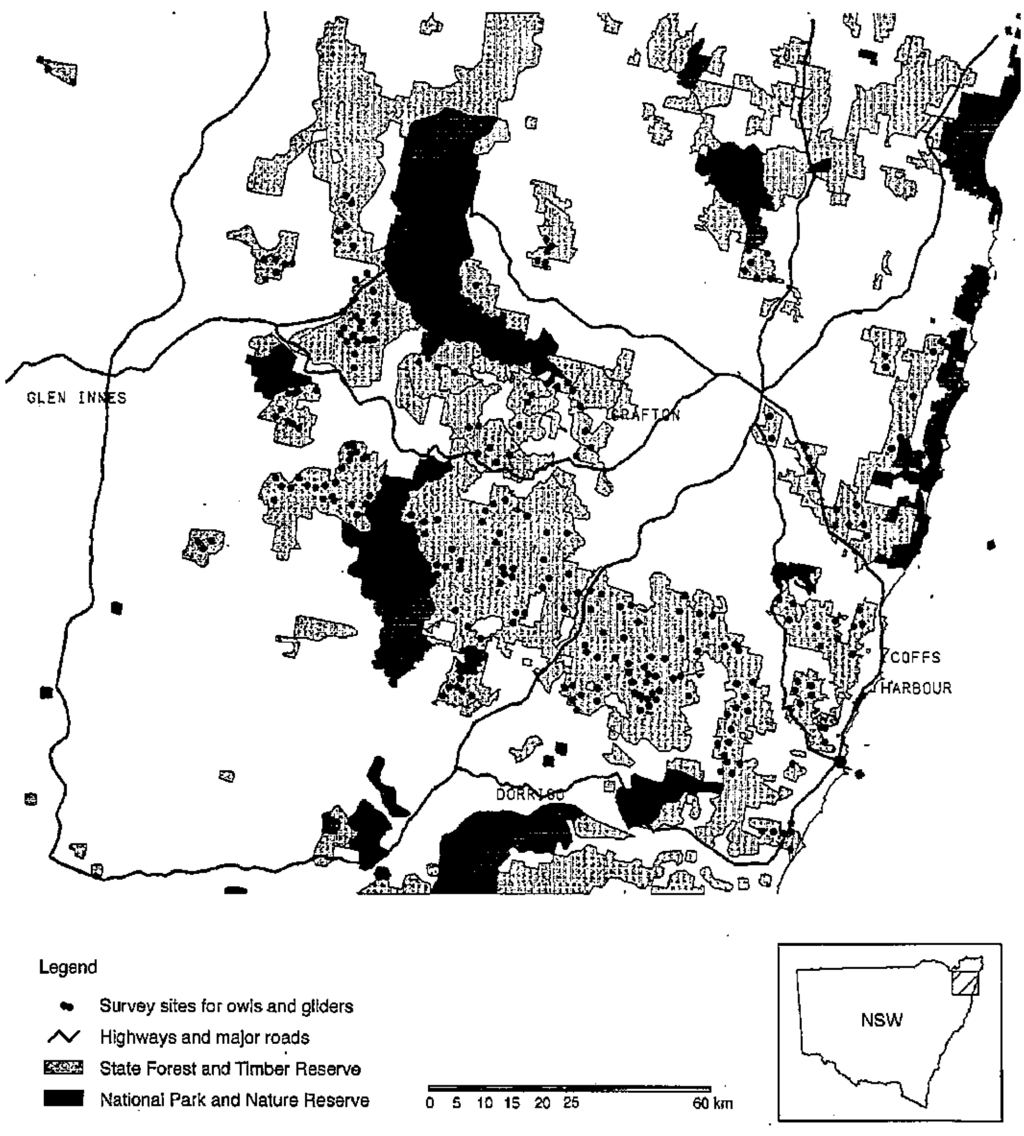

Fig. 1. Distribution of survey sites by State forest and national park in north-eastern New South Wales.

owl vocalisations. These call playbacks were effective (audible to the human ear) for a distance of at least one km. Finally, 5 min were spent searching with a 100-W spotlight for any nocturnal birds or mammals present at the site. The 1-h listening period was done either directly by an observer (64% of counts) or remotely, using a cassette recorder, an omni-directional microphone and a 1-h cassette tape. All tapes were replayed the following day and any vocalisations recorded were noted. Further details of the survey procedures and the equipment used are given by Kavanagh and Peake (1993*b*).

The same four observers were used throughout the study, each of whom surveyed three sites per night beginning shortly after dusk. The second survey on each site was undertaken by a different observer. The survey procedure was designed to be effective in detecting the presence of the three species of large forest owls; however, the combination of methods used is effective for detecting a wide range of nocturnal fauna (e.g. Kavanagh and Rohan-Jones 1982; Kavanagh and Peake 1983*b*; Kavanagh 1984). Identification was normally taken to species level except in the case of the bandicoots, *Perameles nasuta* and *Isoodon macrourus,* and the microchiropteran bats where the numbers of all species were combined as an index of bat activity. The bandicoots and bats were included in the study to provide an assessment of any gross differences in the patterns of distribution for these poorly known groups.

A standard set of environmental variables was measured at each site or was obtained from topographic and vegetation maps. All field assessments of environmental variables were made by one observer. A list of the variables recorded together with a summary of the characteristics of the survey sites is presented in Table 1. The dominant forest type at each site was obtained from the unpublished vegetation maps held by the Northern Region Forestry Office in Coffs Harbour and confirmed using the records of plant species composition measured at the site. For analysis, individual forest types (39 categories) were grouped into one of five vegetation 'super-types' based on the floristic composition of the dominant overstorey tree species and characteristics of the understorey. These broad categories of vegetation type were rainforest

Table 1. Summary of environmental variables at each survey site
Data represent the percentage of sites ($n = 291$) scored in each category for environmental variables

Habitat variable	Category	%	Habitat variable	Category	%
Altitude (m above sea level)	10–400	23·7	Understorey height (m)	0–2·0	28·5
	401–800	37·5		2·1–4·0	32·0
	801–1280	38·3		4·1+	39·5
Landform	Creek flat-lowerslope	32·0	Understorey density	Sparse	26·1
	Gully head-midslope	32·0		Medium	25·8
	Ridgetop-upperslope	36·0		Dense	48·1
Topography	Flat-undulating	22·7	Tree basal area (m^2 ha^{-1})	4·6–20	29·4
	Moderate slope (7–15°)	63·9		20·1–30	42·1
	Steep slope (> 15°)	13·4		30·1–80	28·5
Aspect	Exposed (N–W)	32·3	Habitat trees (No. ha^{-1})	0–1	26·5
	Intermediate-indeterminate	29·9		2–5	44·7
	Sheltered (E–S)	37·8		6+	28·9
Land tenure	State Forest-multiple use	82·8	Logging history	Unlogged	37·5
	Secure reserves	17·2		Selective	22·0
				Heavy	40·5
Dominant vegetation class	Rainforest	9·3	Fire history	None recent	54·6
	Wet sclerophyll forest	24·1		Recent (< 5 years)	45·4
	Dry sclerophyll forest	30·9			
	Wet highlands forest	11·3	Crown dieback	No damage	99·7
	Dry highlands forest	24·4		Crown damage	0·3

(Forest Types 1, 2, 3, 10, 11, 12, 15, 17 and 21; see Anon 1989), wet sclerophyll forest (Forest Types 36, 46, 47, 48 and 53), dry sclerophyll forest (Forest Types 31, 37, 38, 39, 60, 62, 70, 72, 74, 80, 82, 92 and 97), wet highlands forest (Forest Types 152, 159, 160, 161 and 168), and dry highlands forest (Forest Types 122, 129, 140, 141, 162, 163 and 176).

Analysis

Field observations were collected to form a 291 × 33 partitioned data matrix whose rows corresponded to samples (sites) and columns to variables. Variables were animal species (16) and environmental variables (17). Of the entries within the 291 × 16 species' matrix, 69% were zeros. Given the sparse, multivariate categorical nature of the data for analysis, together with their partitioned form, the most obvious candidate methods for analysis were multiple correspondence analysis and canonical correspondence analysis (CCA). Our preference was for the latter on the grounds that CCA more directly focuses attention on relations between two sets of distinct but associated variables (R. Gittins, personal communication). CCA summarises relations between species and environmental variables graphically in the form of a biplot in which species are represented as points and environmental variables by arrows. The method is due to ter Braak (1986, 1987), who provides a full account of the associated biplot, its properties and interpretation.

Canonical correspondence analysis can be regarded as a special case of canonical correlation analysis (Gittins 1985) in which the quantitative nature of the response variables is relaxed. The technique aims to reveal the correlation structure of the data simply and clearly. Presentation of the results as a biplot enables an interpretation of the sample in terms of its own familiar observed variables rather than in terms of synthetic mathematical constructs, such as principal components or canonical variates (Gabriel 1981; ter Braak 1986).

The importance of environmental variables is proportional to the length of their arrows on the biplot, and variables inversely related point in opposite directions from the origin or grand mean of all variables. Correlated environmental variables are represented by arrows that form an acute angle. The degree of association between species and particular environmental variables is indicated by the distance along each arrow subtended by a perpendicular line leading to that species. Species occurring near the outer edges of the biplot display are likely to be strongly associated with one or more of the measured environmental variables. Conversely, species occurring near the centre of the biplot are less likely to have a strong association with any of the environmental variables measured, due partly to their widespread distribution.

Canonical variate analysis (CVA) was used to summarise the response of 16 animal species in relation to one particular environmental variable, the logging history of the sites. This analysis illustrates differences in the responsiveness of species to a gradient in logging intensity. Canonical variate analysis seeks to maximise the distance in multivariate space between treatment means (Gittins 1985). The axis between the centroids of the two logging treatment means indicates the direction of the logging intensity gradient. In this analysis species are represented by arrows, the length of which is indicative of the response of each species to the logging gradient. Species whose arrows are perpendicular to this gradient are likely to occur independently of logging history.

Prior to analysis, the joint distribution of species variables was examined by means of a normal probability Q–Q plot of the raw count data to reveal the occurrence of possible unusual sample points (outliers) or non-linearity in the sample. The plot indicated that one site (the only site at which no species were recorded) was separated from the remainder (Fig. 2*a*). This site was therefore deleted. Several transformation values were tried empirically. A cube-root transformation applied to each species was found to have the strongest linearising effect on the joint distribution of species (Fig. 2*b*). From the figure, the distribution is seen to be approximately linear, symmetric and without major outliers. This result provides an assurance that the analysis will not be unduly influenced by idiosynchracies in the data.

Comparisons between the mean number of species and individuals recorded per site in relation to elevation (height above sea level), one of the dominant environmental variables identified by the CCA biplot, were made using the Kruskal–Wallis test (Zar 1984, SAS 1986). All of the above analyses were performed using count data. However, because most species were recorded in low numbers (usually ≤ 2 per site) partly due to the behavioural characteristics of individual animals (i.e. some members of a species display their presence more readily than others), further analyses for individual species were done using presence–absence data. Thus, contingency chi-square analysis and Fisher's Exact Test (Zar 1984; SAS 1986) were used to determine the levels of association between species occurrence and two variables shown to be important in the biplots, namely elevation class and logging history. The 10% level of significance was accepted to compensate partially for the conservative testing provided by non-parametric procedures.

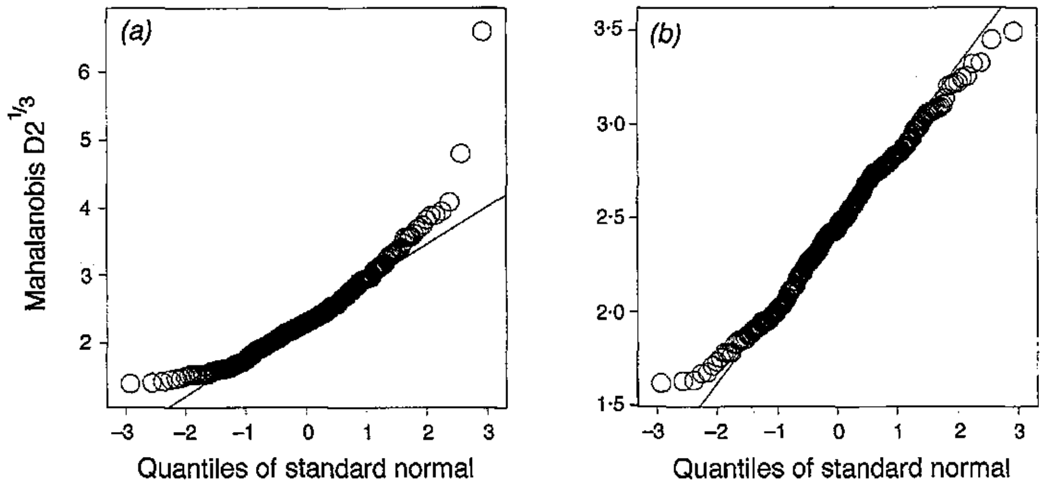

Fig. 2. *a*, Normal probability Q–Q plot showing the joint distribution of the variables (raw count data for all species) across all sites. One site is identified as an outlier. *b*, Normal probability Q–Q plot showing the joint distribution of the variables (data for all species) after cube-root transformation following deletion of one site (see Fig. 2*a*).

Results

Distribution

Eight species of nocturnal forest birds and nine species of arboreal marsupials were recorded, along with a number of other nocturnal mammals. The frequency of occurrence of the 16 most commonly recorded species or species groups by elevation class are presented in Table 2. About half of these species, including the greater glider, the yellow-bellied glider (*Petaurus australis*), the common ringtail possum (*Pseudocheirus peregrinus*), the common brushtail possum (*Trichosurus vulpecula*), the koala (*Phascolarctos cinereus*), the southern boobook (*Ninox novaeseelandiae*), the Australian owlet-nightjar (*Aegotheles cristatus*) and the white-throated nightjar (*Caprimulgus mystacalis*), showed particular clumping in their patterns of distribution in relation to elevation throughout north-eastern New South Wales (Table 2). However, the powerful owl, the sooty owl, the masked owl, the tawny frogmouth (*Podargus strigoides*), the sugar glider (*Petaurus breviceps*), the mountain brushtail possum (*Trichosurus caninus*), the bandicoots (both *Perameles nasuta* and *Isoodon macrourus* combined), and the microchiropteran bats (all species combined; i.e. an index of bat activity) appeared to be widespread and evenly distributed throughout the region, although very sparsely in the case of the masked owl and the mountain brushtail possum.

The widespread distribution of the three large owls is indicated by the geographical spread of the records. The powerful owl was recorded in at least 34 State forests, three national parks and one nature reserve in the region. Sooty owls were recorded in 23 State forests, three national parks and one nature reserve, while the masked owl was recorded in 20 State forests and one national park.

Other species recorded infrequently included the squirrel glider (*Petaurus norfolcensis*), the feathertail glider (*Acrobates pygmaeus*) and the barking owl (*Ninox connivens*). The squirrel glider was recorded at three sites from the Coast Range area east and south-east of Grafton (Candole, Pine Brush and Newfoundland State Forests). The barking owl was recorded at five sites, four in the Coast Range area (Pine Brush, Newfoundland and Orara East State Forests) and one at higher elevation near Dorrigo (Wild Cattle Creek State Forest). The feathertail glider was recorded at five sites within the Dorrigo and Grafton Management Areas. However, this small and cryptic species is certain to be more abundant and widely distributed throughout the region.

Table 2. Distribution by elevation class for nocturnal forest birds and mammals in north-eastern New South Wales

Data represent the percentage of sites where each species was recorded. The total numbers of animals observed are also shown. Probability values are those resulting from test of assocation using contingency chi-square analyses. n.s., not significant

Species	Elevation class (m above sea level)			Total No. of sites	Total No. of individuals	χ^2 value	*P*-value
	10–400	401–800	801–1280				
Powerful owl	37·7	32·1	46·0	113	157	4·57	= 0·1
Sooty owl	14·5	24·8	20·4	60	64	2·74	n.s.
Masked owl	13·0	11·0	10·6	33	35	0·27	n.s.
Southern boobook	59·4	75·2	85·8	220	407	16·23	< 0·01
Australian owlet-nightjar	82·6	64·2	27·4	158	214	59·47	< 0·01
White-throated nightjar	18·8	6·4	0·9	21	30	20·79	< 0·01
Tawny frogmouth	13·0	18·4	15·0	46	52	0·97	n.s.
Greater glider	21·7	37·6	82·3	149	376	75·77	< 0·01
Yellow-bellied glider	33·3	34·9	15·0	78	115	13·07	< 0·01
Sugar glider	44·9	39·5	36·3	115	151	1·34	n.s.
Common ringtail possum	0	14·7	23·0	42	66	18·37	< 0·01
Mountain brushtail possum	5·8	14·7	23·0	32	44	3·43	n.s.
Common brushtail possum	23·2	10·1	6·2	34	48	12·42	< 0·01
Koala	17·4	15·6	4·4	34	40	9·57	< 0·01
Bandicoots	40·6	39·5	31·9	107	129	1·94	n.s.
Microchiropteran bats	73·9	56·0	63·7	184	239	5·87	< 0·05
Total No. of sites	69	109	113	291			
% heavily logged	62·3	54·1	14·2				

Species richness per site appeared to be related inversely to elevation class, but this was not significant (H = 1·03, d.f. = 2; P = 0·60). Mean species richness was 5·1 for elevations below 400 m, 5·0 for elevations between 401 and 800 m and 4·8 for elevations above 800 m. However, the total numbers of animals recorded per site was positively associated with elevation (H = 10·19, d.f. = 2; $P < 0·01$). Comparative data for mean numbers of individuals recorded were 7·0, 7·0 and 8·3 for the three ascending classes of elevation.

Pattern in Relation to Logging

A significant association existed between elevation and logging intensity (χ^2=56·2, d.f. = 4; $P < 0·01$). Far more heavily logged sites were surveyed at elevations below 400 m (62·3%) compared with elevations above 800 m (14·2%). In the intermediate class 401–800 m, 54·1% of sites had been heavily logged.

No differences were found in the frequency of occurrence across unlogged, selectively logged and heavily logged sites for the powerful owl, the sooty owl, the white-throated nightjar, the tawny frogmouth, the yellow-bellied glider, the common ringtail possum, the common brushtail possum, the bandicoots (both species combined) and the microchiropteran bats (all species combined) (Table 3).

Species recorded at significantly ($P < 0·10$) lower frequency on logged sites were the masked owl, the southern boobook and the greater glider. There was no difference in the frequency of occurrence for the greater glider between unlogged and selectively logged sites. Greater gliders were more likely to be encountered on unlogged and selectively logged sites than on heavily logged sites ($P < 0·01$). Similarly, masked owls were more likely to be encountered on unlogged than on heavily logged sites ($P < 0·05$), but no difference was found in comparisons

Table 3. Distribution by logging-intensity class for nocturnal forest birds and mammals in north-eastern New South Wales

Data represent the percentage of sites where each species was recorded. Probability values are those resulting from test of assocation using contingency chi-square analyses. n.s., not significant

Species	Logging-intensity class			χ^2 value	*P*-value
	Unlogged	Selectively logged	Heavily logged		
Powerful owl	37·6	42·2	38·1	0·40	n.s.
Sooty owl	22·0	21·9	18·6	0·47	n.s.
Masked owl	16·5	9·4	7·6	4·77	< 0·10
Southern boobook	85·3	70·3	69·5	8·94	< 0·01
Australian owlet-nightjar	43·1	42·4	71·2	22·83	< 0·01
White-throated nightjar	4·6	6·3	10·2	2·75	n.s.
Tawny frogmouth	20·2	9·4	15·3	3·59	n.s.
Greater glider	67·0	62·5	30·5	34·34	< 0·01
Yellow-bellied glider	28·4	23·4	27·1	0·52	n.s.
Sugar glider	44·0	21·9	44·9	10·70	< 0·01
Common ringtail possum	13·8	10·9	17·0	1·28	n.s.
Mountain brushtail possum	7·3	18·8	10·2	5·50	< 0·10
Common brushtail possum	15·6	9·4	9·3	2·59	n.s.
Koala	6·4	1·6	22·0	21·53	< 0·01
Bandicoots	38·5	31·3	38·1	1·08	n.s.
Microchiropteran bats	64·2	56·3	66·1	1·81	n.s.
Total No. of sites	109	64	118	291	

between unlogged and selectively logged sites. In contrast, the southern boobook was recorded more frequently on unlogged sites than on selectively logged ($P < 0·01$) and heavily logged ($P < 0·01$) sites.

Species recorded with significantly greater frequency on logged sites were the Australian owlet-nightjar and the koala. Both species were recorded more frequently on heavily logged sites than on unlogged ($P < 0·01$) or selectively logged sites ($P < 0·01$).

The majority of species displayed no differences in occurrence between unlogged and selectively logged sites. The only exceptions were the southern boobook ($P < 0·01$), the tawny frogmouth ($P < 0·10$), the sugar glider ($P < 0·01$) and the mountain brushtail possum ($P < 0·10$). For this reason, selectively logged sites are included with unlogged sites to show the differentiation with heavily logged sites in the two ellipses showing the distribution of sites in multivariate space in Figs 3 and 4.

Occurrences of the sugar glider and the mountain brushtail possum were not significantly different between unlogged and heavily logged sites. However, both species appeared to respond to selective logging in unexpected but different ways. The sugar glider was recorded less frequently on selectively logged sites than on both unlogged ($P < 0·01$) and heavily logged sites ($P < 0·01$). The mountain brushtail possum was encountered more frequently on selectively logged sites than on unlogged sites ($P < 0·10$), but with frequency similar to that recorded on heavily logged sites.

Environmental Gradients and Species Assemblages

The two environmental variables accounting for most variation among the 290 sites were altitude and longitude, which were inversely related (Fig. 3). Other variables having a major contribution to the pattern of animal distribution, in order of importance, were dry sclerophyll

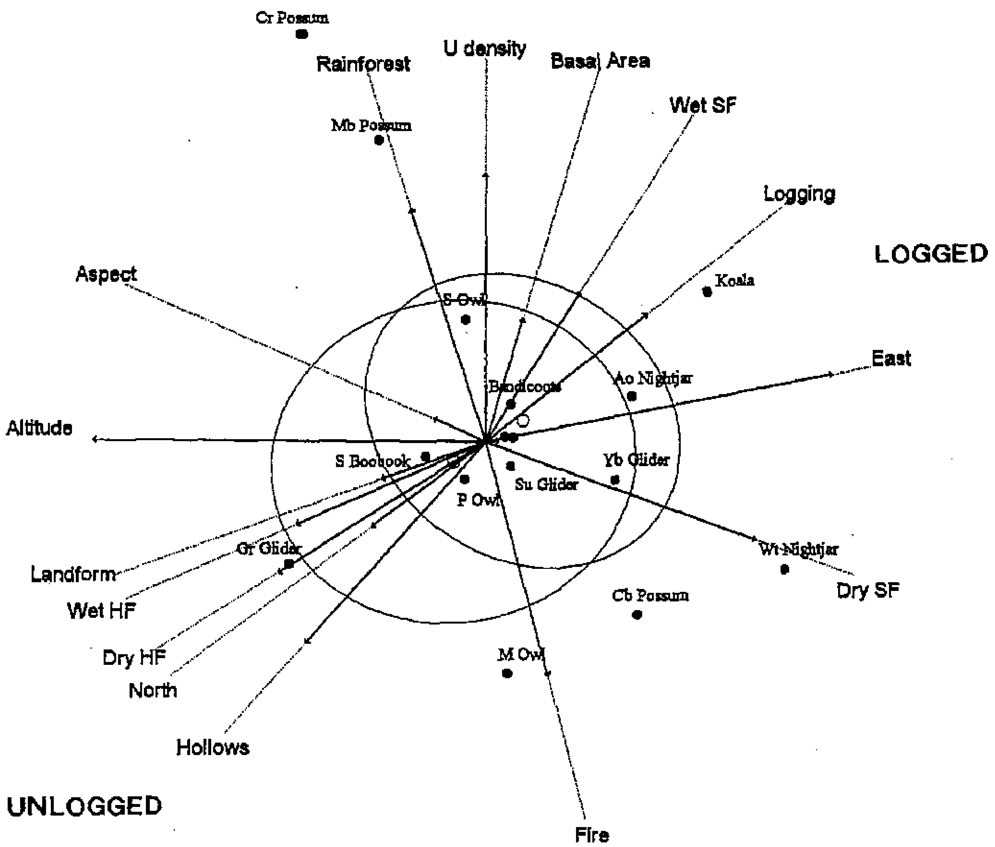

Fig. 3. Relations between 16 animal species or species groups (●) and 17 environmental variables (arrows) across 290 sites in north-eastern New South Wales using canonical correspondence analysis. The length of the arrows represents the variance explained by each variable and the distance along an arrow subtended perpendicularly by each species represents the degree of association with that variable. The two unlabelled species near the centre of the display are the tawny frogmouth and the microchiropteran bats (all species combined). Two environmental variables, topography (slope) and understorey height, had a minor contribution to the pattern summarised by the biplot and, for clarity, are not labelled. The ellipses summarise the distribution of unlogged and selectively logged sites (n = 173) and heavily logged sites (n = 117) within two standard deviations from the mean value (centroid) for each group. The centroids for each group (○) are aligned along the gradient in logging intensity. U, understorey; SF, sclerophyll forest; HF, highlands forest; East, longitude; North, latitude.

forest, numbers of trees with large hollows, understorey density, rainforest, dry highlands forest, fire frequency, logging intensity, wet highlands forest and wet sclerophyll forest (Fig. 3). Variables of lesser importance were latitude, tree basal area, landform and aspect. Topography and understorey height had little influence in the presence of the above variables. Various associations were evident between each species and these environmental gradients but the analyses do not imply causality, due to possible correlations with other unknown or unmeasured variables.

Three major environmental gradients accounting for the distribution of species in north-eastern New South Wales were identified (Fig. 3). The dominant gradient contrasted higher-elevation forests in the western half of the region with lower-elevation forests nearer the coast. Two groups of species were strongly associated with this gradient. The greater glider, the common ringtail possum and the mountain brushtail possum at higher elevations contrasted with the white-throated nightjar, the koala, the common brushtail possum, the yellow-bellied glider and the Australian owlet-nightjar at lower elevations. The second major environmental gradient contrasted wet forest types having a dense understorey with dry forest types having an open or sparse understorey. The two groups of species most closely associated with this gradient were the common ringtail possum, the mountain brushtail possum, the sooty owl and the koala at the wetter end, which contrasted with the white-throated nightjar, the common brushtail possum and the masked owl at the drier end of this gradient. The third major environmental gradient was represented by logging intensity. Again, two groups of species were contrasted along this gradient. The greater glider and the masked owl were the species most closely associated with unlogged forests, and the koala, the white-throated nightjar, the Australian owlet-nightjar, the common ringtail possum and the mountain brushtail possum were the species most closely associated with logged forests.

Species–Environment Relationships

The greater glider was strongly associated with altitude, and particularly forests containing many old, hollow trees within a range of forest types typical of elevations above 800 m above sea level (Fig. 3). These sites also tended to occur on mid-to-upper slopes [e.g. where New England blackbutt (*Eucalyptus campanulata*) and silvertop stringybark (*E. laevopinea*) were present]. The analysis suggests that these forests tended to have a sparse understorey, one that is possibly maintained by frequent fire (Fig. 3). Furthermore, the analysis indicates that the greater glider was strongly associated with unlogged sites (Fig. 3).

The common ringtail possum and the mountain brushtail possum (less so) were strongly associated with high-elevation forests, particularly the wetter forest types such as rainforest and wet sclerophyll forest where a dense understorey was present (Fig. 3). These species tended to occur on sites displaying little evidence of fire. The analysis suggests that both species may be either independent of logging history or associated with logged sites (Fig. 3).

The koala was strongly associated with logged forests (Fig. 3). Koalas were frequently recorded in eucalypt plantations and other forests with a long history of logging. They were also strongly associated with longitude and sites at low elevation in the region. Koalas were associated predominantly with the wet sclerophyll forest types, often those with a dense understorey, but containing few old hollow trees (Fig. 3).

The yellow-bellied glider, the common brushtail possum, the white-throated nightjar and the Australian owlet-nightjar were associated with longitude and the lower-altitude forests of the region (Fig. 3). All four species were strongly associated with dry sclerophyll forest, and all but the common brushtail possum also showed some affinity with wet sclerophyll forest and logged sites. The common brushtail possum and the white-throated nightjar were associated with forests having a history of fire and a sparse understorey.

The three large forest owls, the powerful owl, the sooty owl and the masked owl, showed no strong associations with the dominant environmental gradients of altitude and longitude, indicating their widespread distribution throughout the region (Fig. 3). However, these large owls appeared to respond differently to a gradient in forest type from wet to dry and in understorey characteristics from dense to sparse. The sooty owl was strongly associated with the wetter forest types, rainforest and wet sclerophyll forest, and those containing a dense understorey (Fig. 3). The analysis suggests that the sooty owl may be either independent of logging history or associated with logged sites and sites with relatively few old hollow trees. The masked owl appeared to be most responsive to the environmental gradient reflecting dry open forest with a sparse understorey, one that is possibly maintained by fire (Fig. 3). The masked owl was more likely to be associated with unlogged sites and sites with many old hollow trees. The powerful owl showed little association with any of the environmental gradients considered, as exemplified by its central position on the biplot and as demonstrated by its widespread and relatively even distribution in the region (Table 2). There was a slight tendency for the powerful owl to be associated with the unlogged, higher-altitude forests of the region (Fig. 3).

Like the powerful owl, the remaining species, including the southern boobook, the sugar glider, the tawny frogmouth, the bandicoots (both species combined) and the microchiropteran bats (all species combined), showed little association with any of the environmental gradients considered. This may be related to the widespread distribution for most of these species, as indicated in Table 2. Also, species with different ecological tolerances may be combined in the species groups represented by bandicoots and bats. The southern boobook was more likely to be associated with unlogged forests than the bandicoots (Fig. 3).

When the fauna were ordinated with each other in the presence of just one environmental variable, logging intensity, the greater glider was shown to be the species most responsive to this gradient (Fig. 4). The koala was the species associated most directly with the other (logged) end of this gradient. The Australian owlet-nightjar also showed a strong association with logged sites, whereas the sugar glider and the microchiropteran bats (all species combined) showed a weak association with logged sites. The southern boobook displayed a weak association with unlogged sites. The canonical variate analysis suggested the occurrence of the powerful owl in the region to be independent of logging intensity.

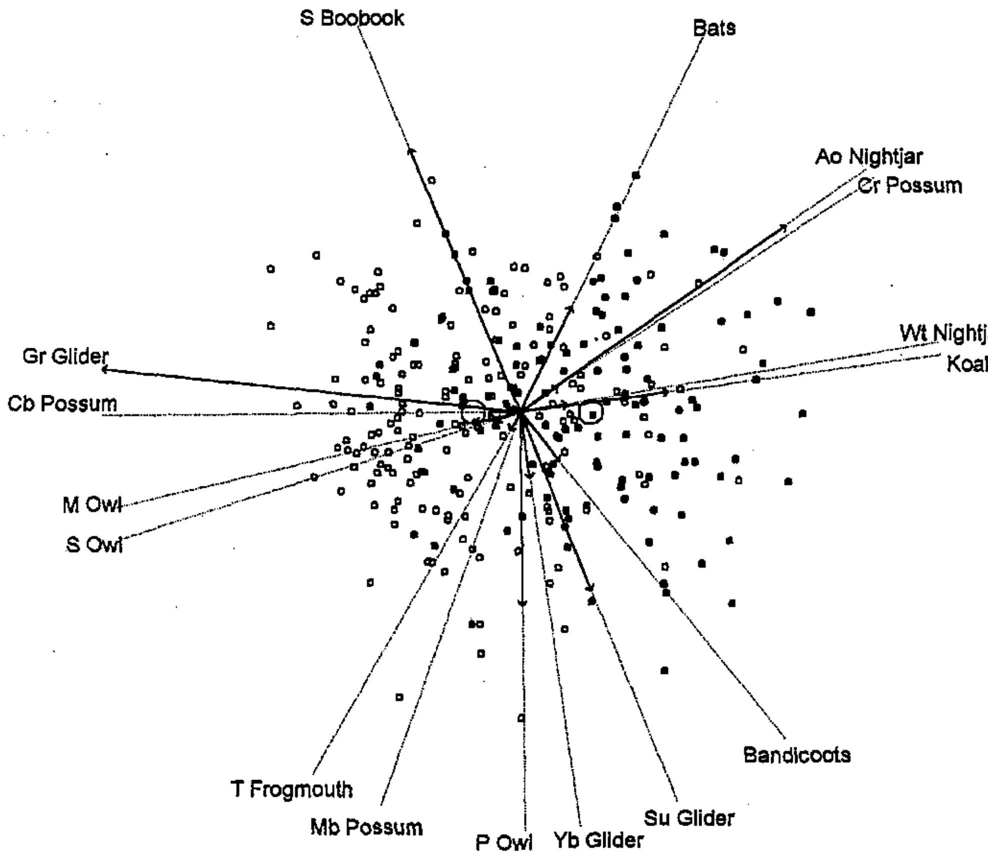

Fig. 4. Relations between 16 animal species or species groups and one environmental variable, logging intensity, across 290 sites in north-eastern New South Wales using canonical variates analysis. □, unlogged and selectively logged sites; ▪, heavily logged sites. The greater glider and the koala are plotted at either end of the gradient in logging intensity, which is indicated by the alignment of the centroids (○) or means for the two site-groups.

Discussion

Regional Differences

The survey recorded eight species of nocturnal forest birds and nine species of arboreal marsupials, together with a number of other nocturnal mammals. Most species were encountered more frequently than during an earlier, but comparable, survey in south-eastern New South Wales (Kavanagh and Peake 1993*a*; Kavanagh, unpublished data). The three large owls and the greater glider were two to four times more likely to be recorded (i.e. widespread) in north-eastern than in south-eastern New South Wales. Comparisons for these species between the mean numbers of individuals recorded per site showed greater differences between the two regions (all $P < 0 \cdot 01$, Mann–Whitney *U*-test). The koala and the bandicoots (two species combined) appeared to be 10 times more abundant in north-eastern New South Wales. Other species that were significantly more abundant in north-eastern New South Wales were the southern boobook, the tawny frogmouth, the mountain brushtail possum (all $P < 0 \cdot 01$), and the Australian owlet-nightjar ($P = 0 \cdot 07$). The barking owl and the squirrel glider were not recorded in south-eastern New South Wales. No differences in abundance between regions were observed for the sugar glider, the feathertail glider, the common brushtail possum and the common ringtail possum (all $P > 0 \cdot 10$). The feathertail glider may have been inadequately detected in both studies for reasonable comparisons. Species that were significantly more abundant in south-eastern New South Wales were the white-throated nightjar and the yellow-bellied glider, as was the index of bat activity (combined species of microchiropteran bats).

Several differences, three in relation to survey methodology and another in relation to regional logging history (see below), existed between the surveys in south-eastern and north-eastern New South Wales. The use of more powerful speakers to broadcast owl vocalisations in the latter survey could potentially account for the higher detectability of large owls in north-eastern New South Wales. Also, the playback component of the method used during the south-east study did not include broadcasting of masked-owl calls, although the presence of this species was recorded when it was detected by other means. Also, a higher proportion of the 1-h listening counts in the north-east survey was done using an experienced observer (64% compared with 36%), which has been shown to be more efficient in detecting the three large owls than the remote censusing equipment (Kavanagh and Peake 1993*b*) used for the balance of the listening counts in both studies. The extent of bias due to these factors was examined by comparing the probability of detecting each species based on the results of the listening counts alone (both remote and person), *before* the owl call playbacks were done. The same microphones and tape recorders were used in both surveys. These data confirmed that large forest owls were indeed more likely to be recorded in north-eastern New South Wales than in south-eastern New South Wales. In north-eastern New South Wales, 3·4% of remote-censusing counts detected the powerful owl compared with 0·7% of similar counts in south-eastern New South Wales. Powerful owls were also recorded on 11·6% of person-listening counts in north-eastern New South Wales compared with 4·1% of similar counts in south-eastern New South Wales. Comparative data for the sooty owl were 2·9% *v.* 0·7% for remote counts and 6·5% *v.* 0·6% for person-listening counts. Comparative data for the masked owl were 1·0% *v.* 1·0% and 3·5% *v.* 1·8%.

The results of a second, independent survey in south-eastern New South Wales support the contention that most species of nocturnal birds and nocturnal arboreal marsupials are either similar to or more widespread and/or abundant in north-eastern New South Wales (Kavanagh and Bamkin 1995). Direct comparisons with this survey, however, are not possible because of differences in methodology (only one visit was made to each site) and sampling season (all counts were completed in autumn). A third study, that by Lunney (1987) who also used different survey methods, reported the relative frequencies of arboreal marsupials observed along spotlighting transects in five of the coastal forests in south-eastern New South Wales. Broad comparisons with the data from these two studies also suggest that the abundance of arboreal marsupials is similar, or greater, in north-eastern New South Wales. The sugar glider may be the only exception as this species comprised nearly half of all Lunney's records. The explanation for these regional differences may be related to the wetter and more fertile (i.e. productive) forest environments, and the milder winters, found in north-eastern New South Wales (Turner *et al.* 1978; Turner and Kelly 1981), and thus in general terms support the nutrient hypothesis of Braithwaite *et al.* (1983, 1984, 1989).

Comparisons with the survey results of Milledge *et al.* (1991) from the mountain ash forests of Victoria indicate that the frequency of occurrence of species may be quite different between the three regions. Only one species, the mountain brushtail possum, appeared to be more widespread in the mountain ash forests than in either north-eastern or south-eastern New South Wales. The sooty owl, the greater glider and the yellow-bellied glider appeared to have a similar frequency of occurrence between the mountain ash forests and the forests of north-eastern New South Wales. However, the frequency of occurrence for the powerful owl, the masked owl, the southern boobook, the Australian owlet-nightjar, the white-throated nightjar, the tawny frogmouth, the sugar glider, the common ringtail possum and the common brushtail possum appeared to be much lower in the mountain ash forests than either region in New South Wales. Neither the powerful owl or the masked owl were recorded in sufficient numbers for analysis in Milledge's study. One species, Leadbeater's possum (*Gymnobelideus leadbeateri*), is endemic to the mountain ash forests, whereas the barking owl and the squirrel glider were recorded only in north-eastern New South Wales. Compared with the above studies, the koala appears to be most abundant in north-eastern New South Wales.

A survey of the distribution of arboreal marsupials in a fourth region, north-eastern Victoria, was conducted by Bennett *et al.* (1991) using a variety of survey methods. Broadly, these authors recorded much lower frequencies of occurrence for the yellow-bellied glider and the sugar glider than in each of the other three regions. The common brushtail possum, however, was recorded much more frequently. The forests and woodlands of north-eastern Victoria and north-eastern New South Wales differed most from the other two regions by the greater frequency of occurrence of the squirrel glider and the koala.

Relationships with Logging History

A potential bias in the data may be due to the capacity of the survey method to record all species at varying distances from the survey site, including from adjacent unlogged forest. This bias may be insignificant in the landscape context for species with large home ranges, because most logged areas are intersected by, or are surrounded by, a mosaic of relatively undisturbed forest that may provide a refuge for these species. Indeed, the ability of the method to provide comparisons at the landscape scale between large areas of logged–unlogged forest and large areas of unlogged forest should enable more biologically meaningful results for these species, particularly for the three large owls. The proximity of old-growth forest components or patches of undisturbed forest may be more important to species with smaller home ranges.

The degree of overlap between the ellipses on the CCA biplot summarising the distribution of unlogged and selectively logged sites and heavily logged sites suggests that most of the nocturnal fauna community occurred with a similar frequency across logging-history categories. Indeed, just two or three species (the greater glider, the koala and the Australian owlet-nightjar) appeared to be the major contributors to the observed logging effect. This was also suggested by the results of the CVA biplot.

The greater proportion of logged sites sampled in the northern survey (62·5% logged, including 40·5% heavily logged) than in south-eastern New South Wales (27·0% logged, including 10·1% heavily logged; Kavanagh and Peake 1993*a*) gives greater confidence in the finding that most species of nocturnal fauna are more abundant in north-eastern New South Wales, and that logging does not appear to have had a major impact at the regional scale. Whether the more benign influence of logging in north-eastern New South Wales than in south-eastern New South Wales and the mountain ash forests of Victoria (Milledge *et al.* 1991; Kavanagh and Bamkin 1995) is related to differences in habitat quality or differences in silvicultural practices, or both, poses an intriguing question. The clearfelling logging system applied in the mountain ash forests is likely to be more intensive than logging systems in the other two regions. All studies, however, including those of Recher *et al.* (1980), Lunney (1987), Macfarlane (1988), Smith and Lindenmayer (1988), and Lindenmayer *et al.* (1990), found the greater glider to be the species most sensitive to logging. The greater glider is a folivore that depends on a tall eucalypt canopy for the maintenance of its food supply (Kavanagh 1987*a*; Kavanagh and Lambert 1990). The faithful attachment of this species to its very small home range makes it vulnerable to heavy logging (Tyndale-Biscoe and Smith 1969; Henry 1984; Kehl and Borsboom 1984).

The sensitivity to logging displayed by the sooty owl and the yellow-bellied glider that was reported by Milledge *et al.* (1991) was not upheld by this study, nor were the conclusions of Milledge *et al.* supported by those of Lunney (1987), Goldingay and Kavanagh (1993) and Kavanagh and Bamkin (1995) in south-eastern New South Wales. Again, this was possibly an effect of the more intensive silvicultural treatment (clearfelling) of mountain ash forests in Victoria. Furthermore, environments that are richer floristically and more productive in terms of plant growth and potential prey availability, such as those in north-eastern New South Wales, may provide habitats for animals that are more resilient to perturbation caused by logging. The sooty owl has a broad and relatively unspecialised diet consisting mainly of arboreal marsupials and small terrestrial mammals (Schodde and Mason 1980; Hollands 1991; Kavanagh, unpublished data), most of which are known to have little dependence on undisturbed forest for habitat. Also, tree species diversity is an important component of habitat for the yellow-bellied glider because it generally results in a more complex pattern of forest phenology (flowering, bark-shedding, new growth flushes) so integral to the diet of this species (Kavanagh 1987*b*).

The powerful owl displayed an indifference to logging, found also by Kavanagh and Bamkin (1995), which requires two points of qualification. First, this species, like the sooty owl and the yellow-bellied glider, has a requirement for large, old trees for nesting (Schodde and Mason 1980; Hollands 1991); hence, it is important to retain adequate numbers of this resource near logged areas. Second, the powerful owl's sensitivity to logging may depend on the forest types that are logged and the effect that this may have on its potential prey species. For example, the powerful owl may be more sensitive to logging in areas where the greater glider forms its principal prey (e.g. Kavanagh 1988). Data for the higher-elevation areas of the region, where the greater glider was most abundant, suggested that the occurrence of the powerful owl was independent of logging intensity. However, only 14% of sites above 800 m were heavily logged. Accordingly, this hypothesis could not be addressed rigorously by the present study. Also, a broader view of the extent of logging in the landscape is required, one that is more appropriate to the home-range size of the owl (Kavanagh and Bamkin 1995).

The masked owl is an enigma. The masked owl could be expected to have a lower dependence on unlogged forest as the diet of this owl is composed principally of terrestrial mammals (Schodde and Mason 1980; Hollands 1991; Debus 1993; Peake *et al.* 1993; Debus and Rose 1994; Kavanagh, unpublished data). Yet this species was encountered less than expected in heavily logged forest compared with unlogged forest ($P < 0{\cdot}05$). A similar result was obtained for this species in south-eastern New South Wales (Kavanagh and Bamkin 1995). An explanation, as suggested by the CCA biplot, is the association of the masked owl with frequently burnt sites supporting dry open forest and a sparse understorey. Typically, forests regenerating after logging have a relatively dense understorey or ground layer and these conditions may be less conducive to successful hunting by the masked owl. The frequency of occurrence of the masked owl at ecotones between forest and agricultural clearings and in other lightly timbered areas (Debus and Rose 1994) suggests that more work is needed to determine the status of this species in non-forest habitats.

Several species, including the common ringtail possum, the mountain brushtail possum, the common brushtail possum, the Australian owlet-nightjar and the tawny frogmouth, which were distributed as frequently or more frequently than expected in logged forest, were also distributed independently of logging in south-eastern New South Wales (Kavanagh and Bamkin 1995). The common ringtail possum and the mountain brushtail possum are commonly encountered in young regrowth stands of eucalypts (Pahl 1984; Macfarlane 1988; Milledge *et al.* 1991). Both species appear to have strong associations with characteristics of the forest understorey (Davey 1984; Seebeck *et al.* 1984; Pahl 1984; Kavanagh 1987*a*; Lunney 1987; Macfarlane 1988; Lindenmayer *et al.* 1990).

The southern boobook has been shown to be associated variously with logged forest (Kavanagh and Bamkin 1995), unlogged forest (this study), or distributed independently of logging (Milledge *et al.* 1991). The white-throated nightjar and the sugar glider were also apparently indifferent to logging. Both species were recorded more commonly in unlogged forest in south-eastern New South Wales (Kavanagh and Bamkin 1995), but in the present study this was not the case, nor was it so for the white-throated nightjar in the earlier study by Kavanagh and Peake (1993*a*). The sugar glider is closely associated with characteristics of the forest understorey (Smith 1982; Kavanagh 1987*a*) and this species has proven to be highly successful in fragmented forest (Suckling 1984). Lunney (1987) reported the sugar glider to be more common in unlogged forest.

There are no published accounts of the association between koalas and logging. Too few records were available for analysis by Kavanagh and Bamkin (1995). Many records of the koala in this study were made from within even-aged stands of eucalypt regrowth or plantation forests, often those that had been planted 20–30 years ago. Koalas were widespread occurring in at least 15 State forests and one national park, but they were most commonly recorded at mid-to-low elevations (< 800 m). Koalas appeared to favour the wetter forest types, particularly those dominated by blue gum (*E. saligna*), tallowood (*E. microcorys*), flooded gum (*E. grandis*) and blackbutt (*E. pilularis*), often when few or no veteran trees were present.

The microchiropteran bats (all species combined) were included as a species variable to examine whether there were any gross differences in the pattern of distribution of this poorly known group. Bat activity was common and widespread throughout the region, and was independent of logging intensity. Although species with different ecological tolerances may have been combined, these results are consistent with those of Kavanagh and Bamkin (1995) in south-eastern New South Wales. In that study, bat activity appeared to be more concentrated at lower elevations and in logged forest. Also in south-eastern New South Wales, Lunney and Barker (1987) trapped most species of bats in both logged and unlogged forest. The radio-tracking studies of these authors indicated that two common species frequently roosted inside tree hollows in unlogged gully forests, but foraged more widely including in the more heavily logged part of the forest (Lunney *et al.* 1985, 1988).

Management Implications

The forests of north-eastern New South Wales are shown to be an important source of diversity for nocturnal bird and mammal species compared with two other regions in south-eastern Australia where similar studies have been undertaken. The findings of this study support the claims of Calaby (1966) made nearly 30 years ago that this region has exceptional significance for mammal fauna conservation.

There were characteristic species assemblages associated with each of the broad forest types considered in this study, suggesting that management efforts may need to be targeted differently depending on forest type. Also, potential may exist to manipulate the structure of the forest understorey layer to enhance the numbers of the common ringtail possum, the mountain brushtail possum, the sooty owl, the masked owl and the common brushtail possum. A core group of species, including the powerful owl, the tawny frogmouth and the sugar glider, as well as the bandicoots (both species combined) and microchiropteran bats (all species combined), were found across a wide range of environmental conditions, including logged and unlogged forest.

Most species appear to be relatively unaffected by logging. However, no data exist for the relative fecundity and survivorship of these species between logged and unlogged forests. Also, the limitations in the design of this study, which reflect regional land-use patterns, restrict the untangling of interactions between forest type, elevation and management history. The species-rich forests found at lower elevations have been subject to a long history of repeated cycles of logging. Whether the species in lower-elevation forests occur independently of logging intensity or because these forests represent their preferred habitats, could not be determined clearly by this study. However, many of the species recorded are known to use hollows in large old trees for breeding and diurnal shelter. Management attention needs to be directed towards establishing the threshold levels of retention for undisturbed vegetation and old hollow-bearing trees, particularly in the coastal forests of the region. The establishment of a comprehensive network of retained undisturbed vegetation along most gully systems in the region would seem to be a prudent course of action to maintain biological diversity.

The greater glider was identified as the species most sensitive to heavy logging, although numbers of this species were unaffected by selective logging. The stronghold of the greater glider is the higher-elevation forests of the region, as it is elsewhere in south-eastern Australia (Tyndale-Biscoe and Smith 1969; Braithwaite 1983; Kavanagh 1984; Milledge *et al.* 1991), little of which has been heavily logged in north-eastern New South Wales. Accordingly, conservation of the greater glider and possibly also its major predator, the powerful owl, in these higher-elevation forests may depend on the application of reduced levels of logging intensity in this environment. As more of the landscape in the region becomes altered by intensive logging or clearing for agricultural and urban land uses, it will be necessary to carefully plan (e.g. Recher *et al.* 1987) and refine management prescriptions to maintain wildlife habitat components.

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