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Scattered trees in rural landscapes: foraging habitat for insectivorous bats in south-eastern Australia

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Abstract

Scattered trees and small patches of vegetation among farmland are typical of rural landscapes throughout the world, often comprising a significant proportion of remaining habitats for native fauna. Insectivorous bats can use such isolated resources owing to the high mobility of most species, but little is known of the relationship between bats and tree density, or of the impact of incremental loss of trees in the landscape. Bats were surveyed at 30 sites in south-eastern Australia, in five habitat categories representing a range of tree densities from remnant woodland blocks (>35 trees/ha) to sparsely scattered trees (<1 tree/ha), and open paddocks devoid of trees. Sampling was undertaken by using harp traps and ultrasonic bat detectors. The abundance of potential arthropod prey was assessed by using light traps. Eleven species of insectivorous bats were recorded and bats were widespread in all habitat categories; all species were recorded around scattered trees. Overall activity, as revealed by detectors, did not differ significantly between the four treed categories, but in open paddocks there was a lower level of activity and a different community composition. However, a regression model revealed a significant quadratic relationship between activity of bats and tree density, with highest activity at 20–30 trees/ha. All species were recorded in open paddocks, but for eight of the ten species this represented <7% of their total activity recorded across all habitat categories. For six species, significant positive correlations were found between activity levels and the abundance of potential arthropod prey. In contrast to bat detectors, trapping results showed a significant difference in overall abundance of bats between wooded habitats, with decreased abundance as tree density declined. This study highlights the value of scattered trees as foraging habitat for bats, and emphasizes that, in rural land mosaics, such small and isolated habitat components have value for the conservation of biodiversity, and require greater recognition and protection.

Keywords: Scattered trees; Rural landscapes; Fragmentation; Isolation; Bats; Foraging habitat

1. Introduction

In countries throughout the world, land dedicated to the conservation of biodiversity is generally small in size compared with the extensive areas transformed to provide food, housing and other resources for human society. Consequently, the conservation of many species depends on their capacity to persist within modified landscapes, particularly rural environments dominated by production of livestock, crops and other agricultural products. A mosaic of natural, semi-natural and newly-established habitats typically occur in such landscapes, including patches of forest or woodland, tree plantations, hedgerows or fencerows, roadside and riparian vegetation, wetlands, gardens, and scattered or isolated trees within the farmland matrix (Forman, 1995;

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Warkentin et al., 1995; Verboom and Huitema, 1997; Daily et al., 2001). A pressing challenge is the need to understand which components of the flora and fauna can (and which cannot) persist within these landscapes, what factors influence their persistence in particular landscape elements, and how the land mosaic can be most effectively managed for both agricultural production and biodiversity conservation.

In this study our focus is on the value of scattered trees among farmland. In agricultural regions of southern Australia, scattered trees across cleared farm paddocks are a conspicuous component of the remnant natural vegetation (also referred to as isolated trees or paddock trees). Such trees are valued aesthetically for their scenic quality in the landscape (Hodgkins et al., 1999; Ozolins et al., 2001), but their role in biodiversity conservation has been largely neglected (Reid and Landsberg, 1999). Most attention has been given to intact stands of remnant forest or woodland, particularly larger patches (e.g. Loyn, 1987; Bennett, 1990; Hadden and Westbrooke, 1996; Major et al., 2001). Reid and Landsberg (1999) estimated that in the temperate zone of Australia there are ≈20 million ha of scattered trees on agricultural land, compared with 6.6 million ha of remnant forest or woodland. Due to selective clearing on the more-fertile soil types, some vegetation communities are now represented predominantly by scattered trees (Gibbons and Boak, 2002).

Despite legislated controls on tree clearing (e.g. Native Vegetation Retention controls under the *Planning and Environment Act 1987* in Victoria; the New South Wales *Native Vegetation Conservation Act 1997*), scattered trees in farmland continue to be lost during agricultural practices. 'Dieback' due to defoliation by invertebrates can also severely affect such trees, eventually resulting in their death (Landsberg et al., 1990; Reid and Landsberg, 1999). Dead trees are often removed for firewood, or due to a perception that they are an indication of poor agricultural practices. Natural senescence of trees is also prevalent because many are survivors from land clearing over 100 years ago, and now are reaching the end of their lives. In many farmland areas little natural regeneration is occurring (Bennett et al., 1994; Reid and Landsberg, 1999; Saunders et al., 2003). In central New South Wales there has been a 20% decline in scattered trees between the 1960s and 1990s (Ozolins et al., 2001), and it has been suggested that there may be a total loss of scattered trees from the intensively-managed agricultural zone of Australia over the next 40–185 years (Gibbons and Boak, 2002).

Recent research has begun to document the extent of use of trees in farmland by various faunal groups, including diurnal birds (Fischer and Lindenmayer, 2002a), owls (Law et al., 2000), and arboreal mammals (Law et al., 2000; van der Ree et al., 2001, 2003). A surprisingly diverse range of bats has been recorded foraging around scattered trees. For example, Law et al. (2000) recorded 20 species of bat, including seven threatened species, flying in close proximity to scattered trees in paddocks in northern New South Wales. Such trees are also known to provide roost sites for bats (Parnaby and Cherry, 1992; Law et al., 2000; Lumsden et al., 2002). The mobility shown by bats means that they have access to multiple areas within the landscape, and consequently they appear to be less affected by habitat fragmentation than some other faunal groups (Lumsden and Bennett, 2000).

Previous surveys of bats in northern Victoria (Lumsden et al., 1995; Lumsden and Bennett, 2000) have identified a wide range of species that forage among scattered trees. However, nothing is known of the relationship between the diversity and abundance of bats and changes in the density of tree cover. This is an important conservation issue because there is continued incremental loss of paddock trees, and sound knowledge is required to underpin guidelines for managing clearing applications. Consequently, the aim of this study was to investigate the use by insectivorous bats of scattered trees in rural landscapes, in order to determine:

- the relationship between tree density and bat activity;
- the relative importance of scattered trees as foraging habitat compared with cleared farm paddocks;
- the relationship between abundance of potential arthropod prey and tree density; and
- the relationship between bat activity and potential arthropod prey.

2. Methods

2.1. Study area

The Riverina region adjacent to the Murray River in northern Victoria and southern New South Wales consists of alluvial plains of Pleistocene origin with relatively fertile soils. Pastoral settlement commenced in the mid-1800s and since that time most native vegetation has been cleared and the land developed for agriculture. The region is now used predominantly for cropping and the grazing of sheep and cattle, and in most districts less than 5% tree cover remains (Bennett and Ford, 1997; Driver and Davidson, 2002). The region has hot summers and mild winters with a mean annual rainfall of 400–600 mm (Land Conservation Council, 1983).

Three study areas were selected to investigate the use of scattered trees by bats: Numurkah (36°02′S, 145°32′E) and Rutherglen (36°06′S, 146°31′E) in Victoria, and Savernake (36°43′S, 146°03′E) in New South Wales. Each location was >10 km from extensive forests of river red gum (*Eucalyptus camaldulensis*) along the

Murray River, to reduce any influence from this dominant landscape feature.

2.2. Site selection

Sites representing five categories of tree density were selected:

- remnant woodland blocks (>35 trees per ha; abbreviated as 'block');
- scattered trees – high density (10–34 trees per ha; abbreviated as 'dense scattered');
- scattered trees – moderate density (1–9 trees per ha; abbreviated as 'moderate scattered');
- scattered trees – low density (<1 tree per ha; abbreviated as 'sparse scattered');
- open paddocks devoid of trees, with the closest trees >200 m away (abbreviated as 'open paddock').

Six replicates of each category (two sites in each of the three study areas) were chosen, resulting in a total of 30 sites. Sites were initially selected by using aerial photographs (Fig. 1) and then examined on the ground. A 1 ha site was selected within a 4 ha stand of relatively uniform tree density. The remnant patches in which sites were located were all <10 ha in size, to minimise any confounding effects between patch size and tree density. All species of bats in the region roost predominantly in tree hollows (Menkhorst, 1995). Trees suitable for roosting were widespread across the study areas.

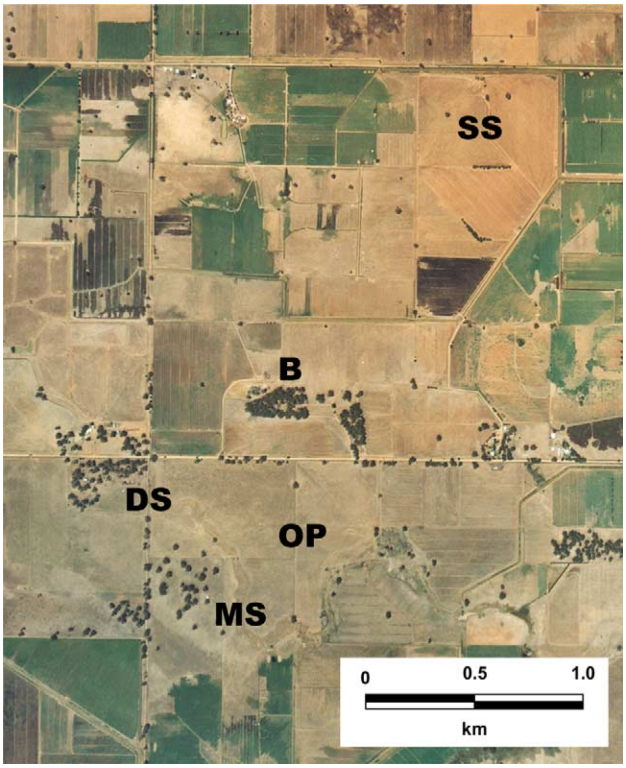


Fig. 1. Aerial photograph of half of the Numurkah study area showing sites in the five tree-density categories. B block; DS dense scattered; MS moderate scattered; SS sparse scattered; OP open paddock.

The dominant tree species at all sites was grey box (*Eucalyptus microcarpa*). This species comprised 83.7 ± 9.8% of the basal area of live trees at the block sites; 89.6 ± 10.4% at the dense scattered sites; 75.6 ± 13.8% at the moderate scattered sites; and 100% of trees at the sparse scattered sites. At Numurkah, small numbers of white cypress-pine (*Callitris glaucophylla*) and yellow box (*E. melliodora*) were also present; at Rutherglen there were also Blakely's red gum (*E. blakelyi*), river red gum, white box (*E. albens*) and yellow box; while at Savernake there were small numbers of white cypress-pine and buloke (*Allocasuarina luehmannii*) trees at some sites.

All sites were within active farming areas and most were unfenced and grazed by stock, predominantly sheep and cattle, at least periodically. There were few or no native plants in the understorey or ground layer. Sites were selected to be similar in tree species, ground cover composition and management history, with the main difference being the density of trees.

2.3. Bat census techniques

Bats were surveyed by using harp traps (Austbat, Bairnsdale, Victoria, modified from Tidemann and Woodside, 1978) and Anabat ultrasonic detectors (Titley Electronics, Ballina, New South Wales). These two techniques are complementary when used in conjunction (Duffy et al., 2000). Each site was sampled for four nights between January and April 2002 (2 nights in austral summer and 2 nights in autumn). In each study area, sites were grouped into two circuits each comprising one site in the five tree-density categories. Harp trapping was conducted at sites on one circuit for two nights with bat detectors and insect light traps employed at the other, and then the order was reversed. This resulted in sampling all tree-density categories simultaneously, and reduced interaction between techniques (i.e. so that trapping did not remove individuals that might otherwise be recorded by detectors). Sampling was restricted to nights with mild, fine and relatively calm weather conditions.

Two harp traps were set at each site on potential flight paths between or around trees. Open paddock sites were not trapped due to the low probability of catching animals. Traps were not set near water bodies, to prevent potential bias from individuals concentrating in the area to drink. Traps were checked once during the night and again in the morning. All bats were released at the point of capture, either during the night of capture or, to minimise predation risk (Speakman et al., 1994), the following night at dusk. The age, sex, reproductive condition, mass and forearm length of each individual was recorded. An index of body condition (BCI) was calculated by dividing body mass by forearm length. Females had recently ceased lactating and juveniles had commenced flying before the start of the study.

Individuals were identified to species level except for female freetail bats (*Mormopterus* spp.). Two genetically distinct forms of this genus are recognised in this region (Adams et al., 1988) which await formal description. Males were distinguished on penis length, but females could not be reliably identified from external examination and were combined as freetail bat (females) (*Mormopterus* sp.). The two taxa are referred to here as southern freetail bat (*Mormopterus* sp. southern) (species 4 in Adams et al., 1988) and eastern freetail bat (*Mormopterus* sp. eastern) (species 2 in Adams et al., 1988).

All trapped bats were marked so that the total number of individuals using a site over the four nights of sampling could be determined. Total number of individuals has been used in the results, rather than total number of captures, to eliminate the influence of any differences in retrap rates between tree-density categories. At the Numurkah sites, bats were banded as part of a larger mark-recapture study, with the exception of *Mormopterus* spp. which sustain high levels of band injuries (Baker et al., 2001). Bat bands were used, provided by the Australian Bird and Bat Banding Scheme (Department of Environment and Heritage, Canberra). At the other two study areas, bats were marked by fur clipping. This mark remained visible for several months and enabled retrapped animals to be recognised within and between field trips.

Ultrasonic echolocation calls were recorded at each site by linking an Anabat detector to a laptop computer (Toshiba Libretto 50CT) via an Anabat Zcaim (Titley Electronics, Ballina, New South Wales) (Chick and Lumsden, 1999). Each time a bat flew past the detector (defined here as a ‘pass’), a digital file was saved directly to the computer. This system enables high quality recordings of calls and complete nights of data to be collected. Detectors were set on the ground, ≈10 m from the base of a tree, with the microphone positioned at a height of 1 m facing upwards at an angle of ≈60° from horizontal. The detectors always pointed towards a tree (except for open paddock sites), with a different focal tree selected each night. Consequently, the data recorded are measures of activity by bats around a tree on a site having a particular density of trees, rather than being indicative of activity levels for the whole 1 ha site (as would be the case if detectors were located randomly in each site).

Echolocation calls were identified by using AnaScheme software (Matt Gibson, Ballarat University, Ballarat; Gibson and Lumsden, 2003) which automatically analyses Anabat files in a consistent, quantifiable way. A detailed description of the development of this system will be presented elsewhere, with only a summary here. We developed an identification key specifically for the Riverina region. Reference calls were collected from all species known from the region. Each call was examined and parameters extracted from search-phase pulses. A total of 2296 pulses from 106 reference calls was included in this analysis, with more than 200 pulses available for most species (Table 1). *Saccolaimus flaviventris* was included in the key despite there being no confirmed records from the region, because it has a patchy distribution and uncertain status in Victoria (Lumsden and Menkhorst, 1995a).

Table 1
The number of reference call sequences and pulses used to develop the AnaScheme key for the Riverina region, and the percentage of reference calls that were correctly identified

Species		Development of key		Testing of key			
		No. of call sequences	No. of pulses	No. of call sequences	% correctly identified	% mis-identified	% identified as unknown
White-striped freetail bat	*Tadarida australis*	2	52	2	100	0	0
Yellow-bellied sheathtail bat	*Saccolaimus flaviventris*	7	43	11	100	0	0
Southern freetail bat	*Mormopterus* sp.	9	191	10	80	0	20
Eastern freetail bat	*Mormopterus* sp.	12	216	14	100	0	0
Gould’s wattled bat	*Chalinolobus gouldii*	10	288	14	36	0	64
Chocolate wattled bat	*Chalinolobus morio*	12	230	21	90	0	10
Lesser long-eared bat	*Nyctophilus geoffroyi*	9	229	16	100[a]	0	0
Gould’s long-eared bat	*Nyctophilus gouldi*	7	158	9	100[a]	0	0
Inland broad-nosed bat	*Scotorepens balstoni*	10	211	22	32	0	68
Large forest bat	*Vespadelus darlingtoni*	11	219	16	38	0	62
Southern forest bat	*Vespadelus regulus*	8	223	11	82	0	18
Little forest bat	*Vespadelus vulturnus*	9	236	16	69	0	31
Total		106	2296	162	72	0	28

[a] Identified to genus level.

AnaScheme fits a modelled curve to each pulse and provides a range of parameters including various frequency and slope measures, duration and curvature of the pulse, and time between pulses. To distinguish species, mutually exclusive combinations of parameters were identified using two approaches. First, the parameters of the pulses from all reference calls were sorted into frequency ranges. Sub-sets were then sorted using other variables until a combination of variables, each within a specific data range, revealed a single species. This was repeated until all possible species identifications were recognised.

The second approach used discriminant function analysis for two groups of species for which pulse parameters overlapped extensively: (i) *Mormopterus* sp. (southern), *Mormopterus* sp. (eastern), *C. gouldii* and *Scotorepens balstoni*; and (ii) *Chalinolobus morio*, *Vespadelus darlingtoni*, *V. regulus* and *V. vulturnus*. Eleven pulse parameters from each of the reference calls were incorporated, and raw coefficients for canonical variables were calculated. The first two functions accounted for 94% of the variation within the first group of species, and 99% of the second. Discriminant function scores for the first two functions were plotted for all pulses. Clusters of pulses from a single species, with no overlap from another species, were used to determine the limits of each species. Steps in the classification key were developed that incorporated the weightings for each of the variables, and the limits represented by each species. Discriminant function analysis was conducted using Statistica Version 6.

The key was tested on reference calls of known species identity (the calls used to develop the key, plus additional reference calls for most species) and checked against unknown calls that had been manually identified. Many species overlap considerably in their echolocation call parameters and not all calls could be successfully identified. The key was refined until no reference calls were incorrectly identified and as many as possible were positively identified (Table 1). The remainder were identified as species complexes or recorded as 'unknowns'. The proportion of reference calls that could be correctly identified varied between species depending on the extent of overlap in pulse parameters with other species. All reference calls could be identified for some species (e.g. *Tadarida australis*, *Mormopterus* sp. eastern), whereas identification rates were less than 40% for others (*C. gouldii*, *S. balstoni*, *V. darlingtoni*; Table 1).

It was not possible to distinguish *Nyctophilus geoffroyi* and *N. gouldi* reliably by using AnaScheme (or manually). Therefore, for this genus identifications were made only to generic level. The form of *Vespadelus regulus* present in the Riverina has a higher echolocation call than in southern Victoria (characteristic frequency of 51–57 kHz, compared with 39–47 kHz in southern Victoria, Duffy et al., 2000; see also Law et al., 2002).

Once we were confident that the identification key was reliable, the calls recorded at study sites were analysed using the program. A minimum of five good quality pulses was required from a call sequence (i.e. a pass) for an identification to be attempted. The mean number of identified passes per night from four nights of sampling at each site, was then calculated for each species. In addition, the mean number of passes for all bats was recorded (irrespective of whether or not they could be identified).

2.4. Arthropod sampling

To assess prey availability, light traps were employed at each site in conjunction with bat detectors. The light trap consisted of a 20 l bucket in which was placed a white reflective cone leading down to a jar of 70% alcohol. A 12 V fluorescent light with dual tubes (a white and an ultraviolet black light), was positioned along the side of the cone, to attract photosensitive nocturnal, flying arthropods. Light traps were operated from dusk until dawn. They were positioned beneath the outer edge of a tree canopy on the treed sites, so that part of the cone of light shone into the canopy of the tree and part projected into space. For sites with dense vegetation a small canopy gap was selected so that the positioning was similar across all sites. The light trap was set distant (>20 m) from the detector to reduce any interaction between the two techniques.

Arthropods were sorted to ordinal level and into size-class categories based on the length of the body (0.1–2.0, 2.1–4.0, 4.1–6.0, 6.1–10.0, 10.1–14.0, 14.1–18.0, 18.1–24.0, 24.1–30.0, 30.1–36.0, 36.1–44.0, >44.0 mm). Results from the four nights of sampling at each site were averaged to provide a mean number of individuals per night in each size class for each order. Biomass was calculated using the generalised relationship for arthropods given by Rogers et al. (1976): $W = 0.0305L^{2.62}$, where W is dry mass in mg and L is length in mm. Previous studies of the diets of insectivorous bats in the Victorian Riverina (Lumsden and Wainer, unpublished data), revealed that the size range of prey items consumed was between 1 and 24 mm in length. Accordingly, biomass estimates were calculated only from potential prey items within this size range for comparison with total bat activity. To test for correlations between abundance of potential prey items and the activity levels of each bat species, the dominant sizes of the dominant prey types consumed by that particular species were used (Table 2; Lumsden and Wainer, unpublished data). Dominant prey types were defined as those orders constituting >10% by volume of the faecal remains. Dominant size classes were defined as those in which >10% of individuals from that order were present.

Table 2
Dominant prey types (orders constituting >10% by volume of faecal remains) and size classes (constituting >10% of individuals of that order) from diet analyses based on faecal samples of bats from 95 sites throughout the Victorian Riverina (Lumsden and Wainer, unpublished data)

Species	Dominant prey types and sizes (mm)
Tadarida australis	Hem (4–6), Lep (4–18)
Mormopterus sp. (southern)	Col (4–14), Hem (2–4)
Mormopterus sp. (eastern)	Hem (2–6), Hym (2–6[a])
Chalinolobus gouldii	Hem (2–6), Lep (4–10)
Chalinolobus morio	Lep (4–14)
Nyctophilus geoffroyi[b]	Col (6–14), Lep (4–14), Ort (4–14[a])
Nyctophilus gouldi[b]	Col (6–14), Lep (10–24)
Scotorepens balstoni	Col (6–14), Hem (2–6), Hym (2–14[a])
Vespadelus darlingtoni	Col (4–14), Dip (2–6), Hem (2–6), Hym (2–14[a])
Vespadelus regulus	Col (4–10), Dip (2–4), Lep (4–14)
Vespadelus vulturnus	Col (2–14), Dip (2–4), Hem (2–6), Hym (2–14[a])

Col – Coleoptera; Dip – Diptera; Hem – Hemiptera; Lep – Lepidoptera; Hym – Hymenoptera; Ort – Orthoptera.

[a] Data on body sizes were not available for Hymenoptera and Orthoptera, and so the overall size-range of prey taken by that species was used.

[b] As these two species could not be distinguished by their echolocation calls, the dominant prey types and sizes for these species have been combined for comparison with overall activity levels for *Nyctophilus* sp.

2.5. Habitat assessment

A 1.0 ha quadrat was marked out at the block and dense scattered tree sites by using a compass and range finder (Bushnell Yardage Pro 500). For sites with moderate and sparse scattered trees, assessments were made over 4 ha, which provided a more representative measure in these patchy habitats. Data were expressed as density of trees per ha at all sites. All trees (defined as stems with a diameter at breast height [DBH] $\geqslant$ 10 cm) were counted, and assigned to one of three size-class categories: small (10–30 cm); medium (31–70 cm); and large (>70 cm). Data were recorded separately for each tree species and for dead trees. Total basal area of trees was calculated for each site.

2.6. Statistical analysis

Data were analysed using SPSS for Windows (Version 11.0). Means are presented ± SE. Log_{10} transformations were used for data that were not normally distributed. To investigate differences between tree-density categories, 'two-factor mixed-effects ANOVAs' (Quinn and Keough, 2002) were used, with study area as the random factor and tree-density category as the fixed factor. Post-hoc tests were undertaken where significant differences were found, and homogeneous subsets were recognised when means within groups were not significantly different (Student–Newman–Kuels [SNK] tests). Pearson correlations on log-transformed data were used to test the relationships between bat activity and arthropod biomass.

Non-metric multi-dimensional scaling (MDS) was undertaken to investigate community structure based on species richness and abundance of bats (i.e. the number of identified detector passes and the number of individuals of each species trapped at each site). Detector data were non-normal and were square-root transformed. The Bray–Curtis similarity measure was used to create a matrix of similarities between sites, and this was then used as the basis for ordination. Analysis of similarity (ANOSIM) was used to investigate differences in the assemblages of bats between the sets of sites in the tree-density categories. SIMPER analysis identified the species that contributed most to differences between tree-density categories. MDS, ANOSIM and SIMPER analyses were conducted using Primer 5 for Windows (Version 5.2.4).

3. Results

3.1. Relationship between tree-density and bat activity

A total of 770 individuals of 11 species was caught during this study (Table 3), from a total of 814 captures (i.e. 5.7% were retrapped individuals). All 11 species of bats were trapped at Rutherglen, ten species were trapped at Numurkah (*T. australis* was not caught), and seven species were trapped at Savernake (no *Mormopterus* sp. eastern, *N. gouldi*, *V. darlingtoni* or *V. regulus*). Six species dominated the captures, together comprising 82% of individuals caught: *C. gouldii*, *V. vulturnus*, *Mormopterus* sp. (southern), *N. geoffroyi*, *C. morio* and *S. balstoni*.

All species were caught at sites among scattered trees in farmland. With the exception of *N. gouldi* and *T. australis*, which were infrequently trapped, all species were recorded in each of the tree-density categories (Table 3). There was a significant difference between categories in the total number of individuals trapped, with a reduction from a mean of 48.0 ± 6.3 individuals caught in blocks over the four nights to 11.5 ± 2.8 individuals caught in the sparse scattered category (Table 3). Species that showed significant differences in the number caught were *Mormopterus* sp. (southern), *Mormopterus* sp. (females; which, based on the relative abundance of males of the two forms, were likely to be dominated by the southern form), *C. gouldii* and *C. morio*, with capture rates highest in the denser vegetation. The other eight species did not show significant differences between tree-density categories, with capture rates in the sparsest sites not significantly different from capture rates in the denser blocks. Several species revealed significant differ-

Table 3
The total number of individual bats trapped during the study (with total captures in parentheses), and the mean number of individuals (±SE) recorded in each tree-density category

Species	Total no. individuals	Block	Dense scattered	Moderate scattered	Sparse scattered	Tree-density		Study area	
						F	*P*	*F*	*P*
Tadarida australis	14 (15)	0.7 ± 0.5	1.7 ± 1.7	0	0	1.04	0.440	1.09	0.396
Mormopterus sp. (southern)	110 (120)	8.3 ± 2.5	5.7 ± 1.5	3.3 ± 1.5	1.0 ± 0.8	9.54	**0.011**	13.69	**0.006**
Mormopterus sp. (eastern)	16 (18)	0.8 ± 0.4	1.0 ± 0.7	0.5 ± 0.2	0.3 ± 0.2	0.56	0.661	10.88	**0.010**
Mormopterus sp. (females)	47 (47)	3.2 ± 1.5	2.8 ± 1.4	1.5 ± 1.0	0.3 ± 0.3	4.99	**0.045**	11.67	**0.009**
Chalinolobus gouldii	160 (169)	13.3 ± 2.3	4.3 ± 1.4	7.5 ± 6.3	1.5 ± 0.7	14.43	**0.004**	5.39	**0.046**
Chalinolobus morio	73 (74)	3.8 ± 1.2	4.5 ± 3.2	3.3 ± 1.5	0.5 ± 0.5	5.25	**0.041**	0.61	0.574
Nyctophilus geoffroyi	100 (104)	6.2 ± 1.8	3.5 ± 0.7	4.0 ± 1.0	3.0 ± 1.2	0.81	0.535	2.75	0.142
Nyctophilus gouldi	2 (2)	0	0.3 ± 0.2	0	0	4.00	0.070	1.00	0.422
Scotorepens balstoni	66 (71)	2.7 ± 0.7	4.2 ± 2.2	2.8 ± 2.3	1.3 ± 1.0	2.87	0.126	17.33	**0.003**
Vespadelus darlingtoni	26 (26)	1.0 ± 0.6	2.2 ± 1.0	1.0 ± 1.0	1.7 ± 1.7	1.01	0.451	2.74	0.142
Vespadelus regulus	31 (32)	1.2 ± 0.8	2.3 ± 1.3	1.3 ± 0.8	0.3 ± 0.2	0.71	0.580	11.84	**0.008**
Vespadelus vulturnus	125 (136)	6.8 ± 1.4	7.5 ± 3.1	3.5 ± 0.9	3.0 ± 0.7	1.34	0.346	1.73	0.255
Total	770 (814)	48.0 ± 6.3	40.0 ± 11.8	28.8 ± 13.2	11.5 ± 2.8	7.70	**0.018**	8.09	**0.020**

Statistics are for two-factor mixed-effects ANOVAs conducted on log-transformed data, with *F* and *P* values given for tree-density categories (df = 3, 12) and study areas (df = 2, 12). Significant differences are highlighted in bold.

ences in capture rates between study areas (Table 3), with capture rates frequently higher at Numurkah than the other two areas. *V. regulus* was the only species for which there was a significant interaction effect between study area and tree density ($F = 4.432$, df = 6, 12, $P = 0.014$). For all others the pattern of differences between tree-density categories was consistent in all three areas.

A total of 29,628 passes was recorded during the 120 nights of detector recordings (246.9 ± 27.1 passes/night/site). There was a high level of variability, both between sites and between nights at the same site. The highest activity in a night was 913 passes at a dense scattered tree site at Rutherglen, and the lowest was six passes at an open paddock site at Savernake.

Using the AnaScheme program, 7991 (27.0%) passes were identified to species level (or to genus for *Nyctophilus* sp.). The remainder could not be identified either as a result of being a short sequence with insufficient good quality pulses to meet the minimum criteria, or having the majority of pulses with parameters that could not be distinguished between two species. The most commonly identified species were *Mormopterus* sp. (southern) and *V. vulturnus* (Fig. 2). In contrast to the trapping data, all ten taxa were recorded at each of the three study areas.

There were significant positive correlations between the measures of abundance obtained from the trapping and detector data for six taxa (*Mormopterus* sp. eastern, *Nyctophilus* sp., *S. balstoni*, *V. darlingtoni*, *V. regulus* and *V. vulturnus*; Table 4). The other four species showed no significant correlation between activity levels revealed by the two techniques.

The overall level of bat activity differed significantly between tree-density categories (two-factor mixed-effects ANOVA, $F = 71.386$, df = 4, 15, $P < 0.001$). There was significantly lower activity in the open paddock sites compared with the treed sites. There was no significant difference between any of the four categories of sites with trees (SNK test $P > 0.05$; Fig. 2), with activity levels of bats foraging around a single tree in a paddock similar to activity levels around a tree within a block. Significantly fewer passes were recorded at Savernake than the other two study areas ($F = 42.680$, df = 2, 15, $P < 0.001$). There was no interaction effect ($F = 0.288$, df = 8, 15, $P = 0.959$) indicating a consistent pattern of differences between tree-density categories in all three areas.

There were no significant differences in relation to tree-density category for several species (*T. australis*, *Mormopterus* sp. eastern, *Nyctophilus* sp., *V. regulus*; Fig. 2). *Mormopterus* sp. (southern) showed significant differences ($F = 7.280$, df = 4, 15, $P = 0.009$), but no homogenous subsets were revealed (SNK test $P = 0.136$). There were high levels of activity of this species in the dense and moderate scattered tree sites and low levels in blocks. This contrasts with trapping results for which the highest trapping success for this species was in blocks (Table 3). The highest levels of activity of *C. gouldii* were from the dense, moderate and sparse scattered tree sites with lower levels of activity in blocks and open paddock sites. Activity levels were significantly higher in treed sites than open paddock sites for *C. morio*, *S. balstoni* and *V. vulturnus*, with generally similar activity levels in the treed sites (Fig. 2).

Mormopterus sp. (southern) dominated activity in the open paddocks with 70% of all identifiable passes from these sites attributed to this species. This represented 14.5% of the total number of passes recorded for this species, while 17.3% of all *T. australis* passes were re-

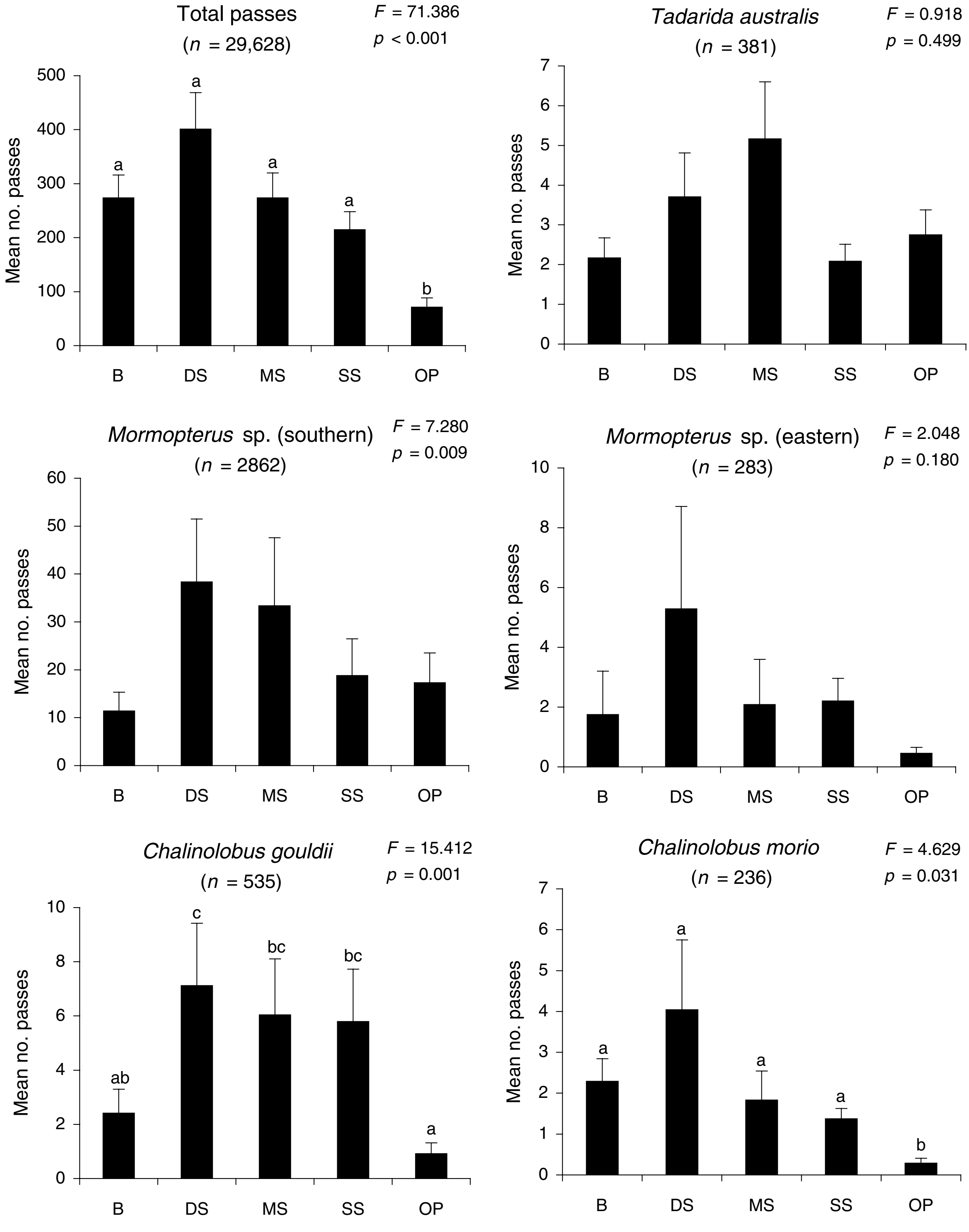


Fig. 2. The mean number (±SE) of detector passes of each species recorded in tree-density categories. B block; DS dense scattered; MS moderate scattered; SS sparse scattered; OP open paddock. n = total number of passes identified for each species. Statistics are for 'two-factor mixed-effects ANOVAs', with df = 4, 8 in each case, with F and P values given for the treatment factor, i.e. tree-density category. The letters, a–c, above the columns represent homogeneous subsets where means are not significantly different from each other, based on SNK tests with $P > 0.05$.

corded in open paddocks. Although all of the other eight taxa were also recorded in open paddocks, most of these spent little time in these habitats (<7% of passes). *V. vulturnus* and *S. balstoni* were the least frequently recorded with only 1.0% and 1.5%, respectively of their calls recorded from open paddock sites. *V. reg-*

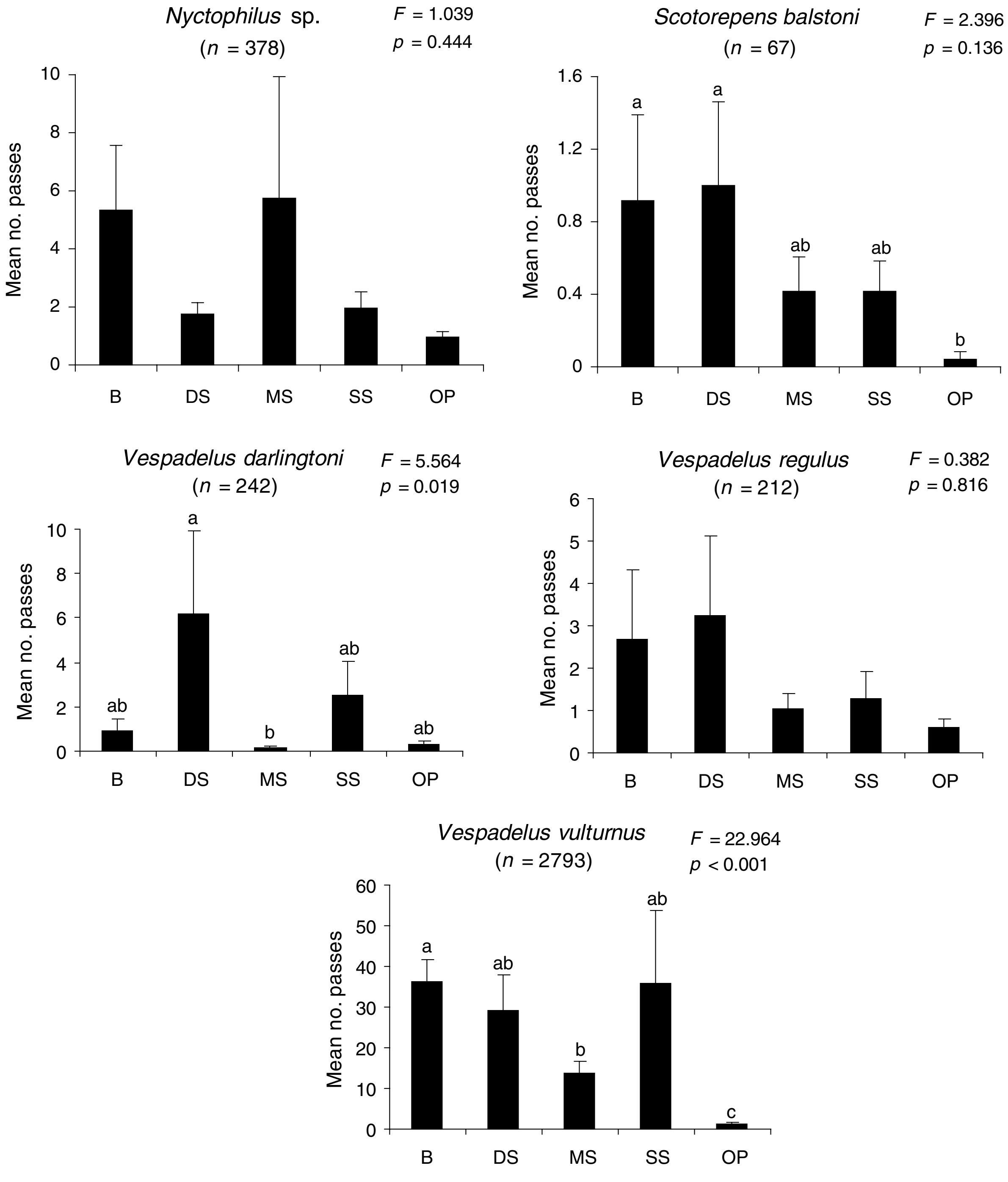


Fig. 2 (*continued*)

ulus (6.6%) and *Nyctophilus* sp. (6.1%) were recorded somewhat more often. To investigate if open paddock sites were used for foraging or as commuting routes, the detector files from these sites were examined manually in Anabat for characteristic feeding buzzes (these can not be distinguished in AnaScheme). Of the 594 identified passes from open paddocks, 56 (9.4%) contained feeding buzzes, the majority of which were from *Mormopterus* sp. (southern). Although based on small sample sizes, there is also evidence for some feeding in open paddocks by *T. australis*, *Mormopterus* sp. (eastern), *C. gouldii*, *Nyctophilus* sp. and *V. vulturnus*.

There were significant differences in activity levels between the three study areas for five of the ten taxa (*Mormopterus* sp. southern, *Mormopterus* sp. eastern, *C. gouldii*, *V. darlingtoni* and *V. regulus*; all $P < 0.05$). For all species, Numurkah had a greater mean number of passes per site than Rutherglen, which was greater

Table 4
Correlations between the mean number of individuals caught and the mean number of detector passes recorded per night at sites with trees (no trapping was undertaken at open paddock sites)

Species	Mean individuals caught/site	Mean detector passes/site	*r*	*P*
Tadarida australis	0.6 ± 0.4	3.3 ± 0.5	−0.176	0.412
Mormopterus sp. (southern)	4.6 ± 1.0	25.5 ± 5.4	0.357	0.087
Mormopterus sp. (eastern)	0.7 ± 0.2	2.8 ± 1.0	**0.492**	**0.015**
Chalinolobus gouldii	6.7 ± 1.9	5.3 ± 0.9	−0.053	0.805
Chalinolobus morio	3.0 ± 0.9	2.4 ± 0.5	0.220	0.301
Nyctophilus sp.	4.3 ± 0.6	3.7 ± 1.2	**0.507**	**0.011**
Scotorepens balstoni	2.8 ± 0.8	0.7 ± 0.2	**0.784**	**<0.001**
Vespadelus darlingtoni	1.1 ± 0.4	2.4 ± 1.1	**0.553**	**0.005**
Vespadelus regulus	1.3 ± 0.4	2.1 ± 0.6	**0.713**	**<0.001**
Vespadelus vulturnus	5.2 ± 0.9	28.8 ± 5.1	**0.628**	**0.001**

Statistics are Pearson correlations on log-transformed data, with $n = 24$ in each case. Significant correlations ($P < 0.05$) are indicated in bold. Trapping results from both species of *Nyctophilus* have been combined for comparison with detector results for this genus.

than Savernake. As found with the trapping results, *V. regulus* was the only species for which there was a significant interaction effect ($F = 3.148$, df = 8, 15, $P = 0.027$).

The total number of passes and the number of passes for each species were compared with the density and basal area of trees at each site. A quadratic relationship between the density of trees and total bat activity ($R^2 = 0.626$, $F_{(2,27)} = 22.571$, $P < 0.001$) provided the strongest relationship (Fig. 3). That is, total bat activity increased with increasing density of trees to ≈20–30 trees per ha and declined after this point. Consistent with their patterns for distribution among tree-density categories, the activity levels of *Mormopterus* sp. (southern), *C. gouldii*, *C. morio*, *S. balstoni* and *V. vulturnus* also showed significant quadratic relationships ($P < 0.05$) with the density of trees on sites. Comparisons with basal area revealed similar significant, although slightly weaker, relationships.

3.2. Community composition

There was a significant difference in the composition of bat assemblages between tree-density categories for the trapping data (ANOSIM global test statistic, $R = 0.129$, $P = 0.048$), primarily due to a difference between blocks and sparse scattered tree sites ($R = 0.544$, $P = 0.002$). The other five pair-wise comparisons were non-significant ($R < 0.187$, $P > 0.069$ for all). The relationships between sites in the four tree-density categories are shown in an MDS ordination plot in Fig. 4(a).

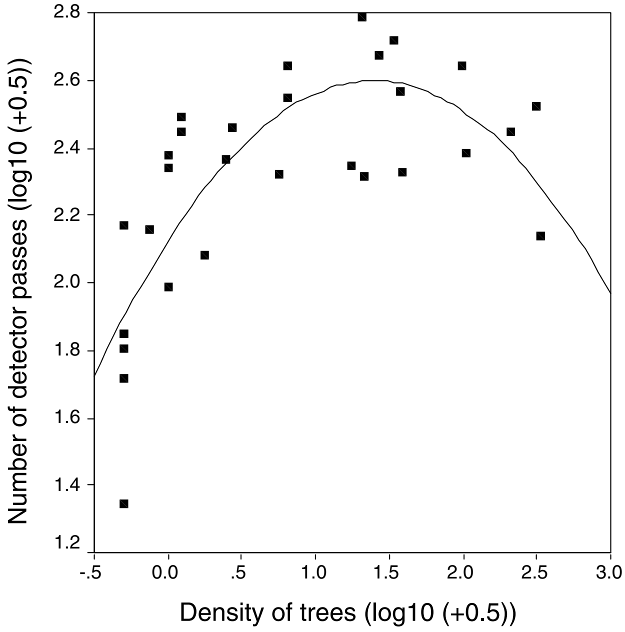


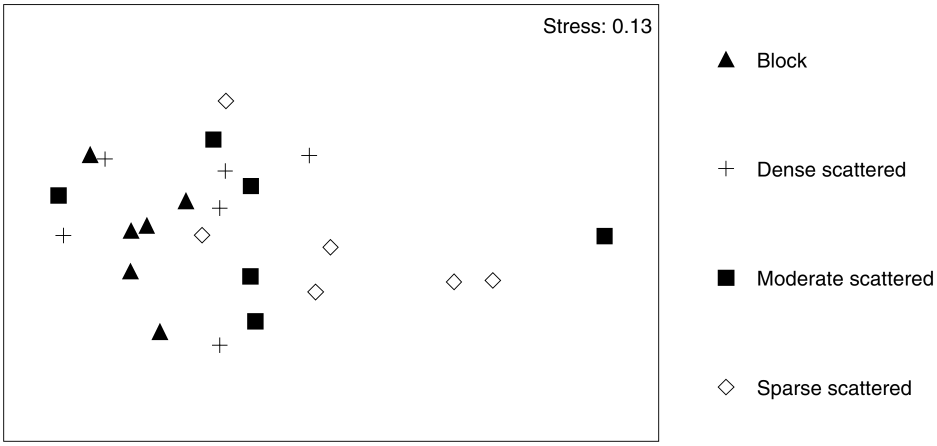
Fig. 3. The quadratic relationship between the total number of bat passes detected and the density of trees at sites (both variables are $\log_{10}(X + 0.5)$ transformed).

Data obtained by bat detectors also showed significant differences in the composition of assemblages between categories ($R = 0.309$, $P = 0.001$; Fig. 4(b)). There were significant pair-wise comparisons between each of the treed categories (block, dense scattered, moderate scattered and sparse scattered trees) and the open paddock sites ($R > 0.435$, $P < 0.006$ for each). The only significant pair-wise difference among treed categories was between blocks and moderate scattered trees ($R = 0.32$, $P = 0.022$). The abundance of *V. vulturnus* contributed 30% of the difference in composition between the open paddock sites and all treed sites combined (SIMPER analysis), with *Mormopterus* sp. (southern) and *C. gouldii* contributing a further 16% and 11%, respectively.

3.3. Demographic variation

To assess whether sites among scattered trees in paddocks were used by different components of the bat population to the denser sites, the age structure, sex ratio and body condition of individuals were compared. Juveniles were recorded in all tree-density categories. For most species there was either no significant difference (χ^2 tests, $P > 0.05$) in the proportion of juveniles recorded in the different tree-density categories, or small sample sizes of juveniles precluded comparisons. The only species that showed significant differences were *C. gouldii*, for which juveniles were more frequently recorded in the sparser sites compared to the denser treed sites ($\chi^2 = 9.345$, df = 3, $P = 0.025$), and *N. geoffroyi* for which there was a higher proportion of juveniles re-

(a) trapping



(b) detectors

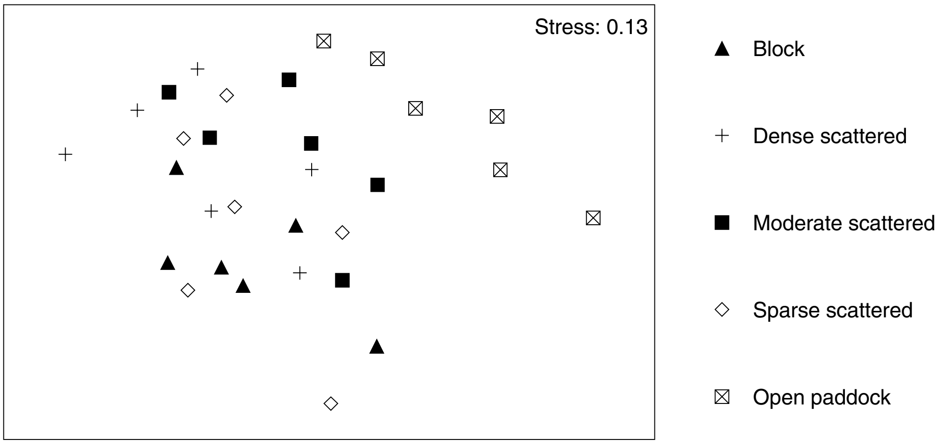


Fig. 4. Ordinations, using non-metric multidimensional scaling, of the composition of assemblages of bats at sites based on (a) trapping data; and (b) detector data.

corded in the block and sparse scattered sites than in dense and moderate scattered sites ($\chi^2 = 11.006$, df = 3, $P = 0.012$).

There were significant male biases in the overall sex ratio of trapped individuals for six species (Table 5): for example, 73% of *Mormopterus* sp. individuals trapped were males. Despite these overall differences, there were no significant differences in sex ratio between tree-density categories for any species (Table 5). Similarly, the body condition index (BCI) of species did not vary significantly between tree-density categories (two-factor mixed-effects ANOVAs, $P > 0.321$ for all species). There were no significant differences between the three study areas for any species except *V. vulturnus*, which had a higher BCI at Rutherglen than the other two areas ($F = 5.828$, df = 2, 70, $P = 0.023$). There was no significant interaction effect between tree-density categories and study area for any species ($P > 0.146$ for all species).

3.4. Arthropod sampling

More than 38,000 arthropods were collected using the light traps. The most abundant orders were Diptera, Coleoptera and Lepidoptera, which together comprised 77% of all individuals trapped. Five orders were represented by fewer than 20 individuals (Dermaptera, Isoptera, Mantodea, Ephemeroptera and Stresiptera). The number of individuals recorded for the other orders is shown in Table 6. There were no significant differences in the number of individuals between the tree-density categories for most orders sampled (Table 6). The orders that showed significant differences were Hemiptera, Hymenoptera, Trichoptera and Blattodea with abundances generally higher in the denser vegetation categories. Nine orders showed significant differences between the three study areas (Table 6), with Numurkah typically having the highest abundances and Savernake the lowest.

Table 5
Sex ratios for all individuals trapped and for individuals within each tree-density category

Species	% males (*n*)	Overall sex ratio		Block	Dense scattered	Moderate scattered	Sparse scattered	Comparison between tree-density categories	
		χ^2	*P*					χ^2	*P*
Tadarida australis	71.4 (14)	2.571	0.109	25.0 (4)	90.0 (10)	0 (0)	0 (0)		
Mormopterus sp. (combined)	72.8 (173)	36.075	**<0.001**	74.3 (74)	70.2 (57)	71.9 (32)	80.0 (10)	0.561	0.905
Chalinolobus gouldii	68.1 (160)	21.025	**<0.001**	70.0 (80)	69.2 (26)	66.7 (45)	55.6 (9)	0.843	0.839
Chalinolobus morio	64.4 (73)	6.041	**0.014**	56.5 (23)	63.0 (27)	80.0 (20)	33.3 (3)	4.032	0.258
Nyctophilus geoffroyi	62.0 (100)	5.760	**0.016**	56.8 (37)	81.0 (21)	66.7 (24)	44.4 (18)	6.210	0.102
Nyctophilus gouldi	50.0 (2)			0 (0)	50.0 (2)	0 (0)	0 (0)		
Scotorepens balstoni	81.8 (66)	26.727	**<0.001**	100 (16)	80.0 (25)	70.6 (17)	75.0 (8)	5.302	0.151
Vespadelus darlingtoni	50.0 (26)	0.000	1.000	83.3 (6)	53.8 (13)	16.7 (6)	0 (1)	6.410	0.093
Vespadelus regulus	48.4 (31)	0.032	0.857	71.4 (7)	57.1 (14)	12.5 (8)	50.0 (2)	6.045	0.109
Vespadelus vulturnus	63.2 (125)	8.712	**0.003**	61.0 (41)	60.0 (45)	81.0 (21)	55.6 (18)	3.583	0.310

Figures are the percentages that were males with the total sample size (*n*) in parentheses. The males of the two forms of *Mormopterus* have been combined to compare with female *Mormopterus*. Significant differences are highlighted in bold.

Table 6
The mean number of individuals (±SE) of arthropod orders in tree-density categories

Order	Total no. individuals	Block	Dense scattered	Moderate scattered	Sparse scattered	Open paddock	Tree-density		Study area	
							F	*P*	*F*	*P*
Diptera	12,457	171.4 ± 48.8	95.1 ± 34.4	92.4 ± 41.8	103.0 ± 50.0	57.2 ± 26.2	2.28	0.149	17.35	**0.001**
Coleoptera	8919	98.5 ± 32.9	49.0 ± 21.2	52.1 ± 24.2	59.3 ± 33.9	112.7 ± 62.7	1.44	0.306	17.66	**0.001**
Lepidoptera	8131	99.9 ± 23.1	58.6 ± 16.6	51.7 ± 17.3	49.8 ± 19.2	78.8 ± 33.5	2.38	0.138	18.76	**0.001**
Collembola	4251	0.4 ± 0.2	0.7 ± 0.4	1.2 ± 0.5	168.8 ± 167.8	6.1 ± 4.3	1.37	0.325	1.00	0.411
Hemiptera	2635	39.0 ± 21.1	15.1 ± 7.0	19.8 ± 9.7	11.1 ± 5.5	24.8 ± 11.6	5.15	**0.024**	78.64	**<0.001**
Hymenoptera	823	8.8 ± 2.3	8.0 ± 3.1	5.6 ± 2.3	8.0 ± 2.1	3.9 ± 2.0	3.82	**0.050**	14.37	**0.002**
Acarina	599	18.6 ± 17.7	2.9 ± 1.7	0.8 ± 0.6	0.9 ± 0.6	1.8 ± 0.6	0.81	0.550	3.13	0.099
Trichoptera	320	6.5 ± 2.5	2.5 ± 1.3	2.0 ± 0.7	1.1 ± 0.6	1.2 ± 0.8	5.70	**0.018**	14.41	**0.002**
Orthoptera	95	1.2 ± 0.6	1.1 ± 0.8	0.5 ± 0.4	0.4 ± 0.3	0.8 ± 0.3	0.96	0.478	12.65	**0.003**
Araneae	41	0.3 ± 0.1	0.6 ± 0.3	0.3 ± 0.2	0.3 ± 0.3	0.1 ± 0.1	0.73	0.595	2.02	0.195
Blattodea	35	1.0 ± 0.5	0.04 ± 0.04	0.2 ± 0.1	0.3 ± 0.1	0	14.10	**0.001**	6.32	**0.023**
Thysanoptera	29	0.1 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.3 ± 0.2	0.4 ± 0.1	0.76	0.580	1.06	0.391
Psocoptera	27	0.4 ± 0.2	0.04 ± 0.04	0.1 ± 0.1	0.3 ± 0.2	0.3 ± 0.3	1.26	0.360	5.32	**0.034**
Pseudoscorpionida	20	0.1 ± 0.1	0.5 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	2.85	0.097	2.51	0.142
Neuroptera	20	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.04 ± 0.04	0.94	0.489	2.59	0.136
Total	38,448	447.3 ± 115.2	235.0 ± 74.0	227.6 ± 93.0	403.9 ± 194.1	288.3 ± 136.5	1.40	0.317	14.71	**0.002**

Data are shown for orders represented by 20 or more individuals, while total and mean values include all orders. Statistics are for two-factor mixed-effects ANOVAs conducted on log-transformed data, with *F* and *P* values given for tree-density category (df = 4, 15) and for study area (df = 2, 15). Significant differences are shown highlighted in bold. The interaction effects were non-significant for all orders ($P > 0.05$).

There was a positive, but non-significant ($P = 0.07$), correlation between the total number of passes recorded by the bat detectors and arthropod biomass (within the size range of 1–24 mm) at the 30 sites (Table 7). Four species, *Mormopterus* sp. (southern), *Mormopterus* sp. (eastern), *S. balstoni* and *V. regulus*, showed significant positive correlations between bat activity and total biomass at sites (Table 7). For the other six taxa the correlation with arthropod biomass was not significant but the direction was positive for all but *T. australis*. When this comparison was restricted to the dominant size classes of the dominant arthropod orders found in the diet of each species (see Table 2), five taxa revealed significant positive correlations (Table 7): *Mormopterus* sp. (eastern), *C. gouldii*, *S. balstoni*, *V. darlingtoni* and *V. regulus*. In addition, the activity level of *Nyctophilus* sp. was marginally significantly correlated with the abundance of its prey ($P = 0.056$).

4. Discussion

4.1. Overall patterns and methodological considerations

The eleven species of bats recorded during this study represent most species known from the Riverina region of south-eastern Australia. Two species not recorded were the southern myotis *Myotis macropus*, a habitat

Table 7
Correlations between the activity of bats (mean number of detector passes at each site) and total arthropod biomass (within the range 1–24 mm), and with the biomass of dominant prey types and sizes for each bat species

Species	Correlation with total arthropod biomass		Correlation with dominant prey types and sizes	
	r	*P*	*r*	*P*
Tadarida australis	−0.113	0.551	−0.111	0.558
Mormopterus sp. (southern)	0.365	**0.048**	0.263	0.160
Mormopterus sp. (eastern)	0.375	**0.041**	0.521	**0.003**
Chalinolobus gouldii	0.258	0.168	0.383	**0.037**
Chalinolobus morio	0.129	0.499	0.040	0.835
Nyctophilus sp.	0.331	0.074	0.352	0.056
Scotorepens balstoni	0.477	**0.008**	0.374	**0.042**
Vespadelus darlingtoni	0.248	0.186	0.487	**0.006**
Vespadelus regulus	0.472	**0.008**	0.424	**0.020**
Vespadelus vulturnus	0.022	0.907	0.211	0.264
Total passes	0.331	0.074		

Statistics are Pearson correlations on log-transformed data, with $n = 30$ in each case. Significant correlations are indicated in bold.

specialist that forages exclusively over water (Lumsden and Menkhorst, 1995b), and the greater long-eared bat *Nyctophilus timoriensis*, a rare species in Victoria (Lumsden, 1994). The same suite of species occurred in the three study areas.

Bat detectors and trapping are complementary techniques, both having biases in the species most likely to be recorded (Duffy et al., 2000). Trapping rates are influenced by vegetation structure, with higher capture rates usually where there are well-defined flight paths in which to position traps. It may be expected therefore, that trapping rates would be proportionally higher in denser blocks. However, there may also be a counter effect in that isolated trees may be a focal point for activity. Trapping provides information on the number of individuals using a site, as well as facilitating collection of demographic data. In contrast, detectors provide a comparable index of activity that is not affected by trappability. However, they can not be used to estimate population numbers, because several individuals flying past a detector can not be distinguished from one individual repeatedly passing. Two main factors influence the perceived abundance of bat species as recorded by detectors (i.e. the index of bat activity). First, the detectability of each species varies depending on the height at which it flies and the strength of its call, and hence the distance over which it can be detected. Second, not all species are equally identifiable due to overlap of call parameters. The percentage of reference calls correctly identified using AnaScheme ranged from 32% to 100% for different taxa (Table 1). These two factors need to be considered when comparing activity levels between species, but as detection and identification rates are not likely to vary markedly between tree-density categories, intra-specific comparison of habitat use remains valid.

For six taxa there were significant positive correlations between trapping and detector data in estimating relative abundance. Most of these species typically forage below canopy height (≈20 m) (Lumsden et al., 1994), and hence fly within range of both traps and detectors. For most, their proportional occurrence among total trap captures was higher than their proportional occurrence in the total identifiable detector calls. For example, records of *Nyctophilus* sp. comprised 13.3% of total individuals trapped, but only 4.7% of identifiable detector passes. The three molossids (*T. australis*, *Mormopterus* sp. southern, *Mormopterus* sp. eastern), which are fast fliers with loud echolocation calls, and often fly higher than other species, were recorded with a greater relative frequency by detectors than by trapping (4.8% vs 1.8%, 35.8% vs 14.3% and 3.5% vs 2.1%, respectively). Two relatively fast, higher-flying species, expected to be more frequently recorded by detectors (*C. gouldii* and *S. balstoni*), were the species most difficult to distinguish by their echolocation calls (Table 1), and this may have influenced their perceived abundance.

4.2. Relationship between tree-density and bat activity

All species used scattered trees in farmland as a foraging resource. This contrasts with other faunal groups (e.g. arboreal marsupials, diurnal birds) where typically only a sub-set of the fauna have been recorded around scattered trees (e.g. Law et al., 2000; Fischer and Lindenmayer, 2002a). Other studies in south-eastern Australia have also revealed a high proportion of bat species using scattered trees in paddocks (e.g. Adams, 2000). Twenty of 21 species of bats recorded in northern New South Wales used isolated trees or small remnants for foraging or roosting (Law et al., 2000). In the Victorian Riverina, nine of 13 species were trapped at scattered trees (Lumsden et al., 1995): in one instance, a trap at an isolated tree resulted in the capture of 29 individuals of seven species in one night (Lumsden and Bennett, 2000). In contrast, in southern Africa Fenton et al. (1998) reported a significantly greater richness and abundance of bat species in intact woodlands compared with adjacent areas with a much reduced canopy cover.

There was a general trend for reduced activity or abundance of bats as tree density decreased. The trend was most clearly shown by trapping results, with a progressive decline in overall capture rates as tree density decreased (Table 3). Overall activity, as revealed by bat detectors, also differed significantly between tree-density categories, but the major differences were between each of the wooded habitats and open paddocks. Activity levels for most species were markedly lower in open farmland. There was also significant variation in the composition of bat assemblages, which showed similar patterns to that for indices of abundance. Based on detector records, the major compositional difference was between all wooded categories and open farmland, while for trap captures the greatest difference was between blocks and sparse treed sites.

The quadratic relationship between overall activity (based on detector records) and tree density showed that the highest level of activity corresponded with the category dense scattered trees; not, as might have been expected, with woodland blocks. Some blocks had a high density of relatively small trees due to regrowth from earlier disturbance, whereas dense scattered tree sites comprised mainly large old trees. These latter sites may be more representative of pre-European tree densities than the woodland blocks. Although the structure of woodlands prior to settlement is a contentious issue, Benson and Redpath (1997) argue that grassy woodlands of south-eastern Australia probably contained ≈30 large trees per ha, which corresponds well with the peak level of bat activity at 20–30 trees per ha (Fig. 3). Most individual species also followed this pattern, with the highest activity for seven of the 10 taxa in the dense scattered tree category (Fig. 2). This tree density may correspond with optimal foraging opportunities for most species because it contains sufficient space between trees for less-manoeuvrable species (such as *Mormopterus* spp.) but is sufficiently dense for species that prefer a more 'cluttered' environment (e.g. *Nyctophilus* spp., *Vespadelus* spp.). Species with wings adapted for cluttered environments are not precluded from flying in more open areas, whereas the converse is not the case (Fenton, 1990).

Use of open farmland by bats differed markedly from their use of wooded habitat, with significantly lower overall activity and a different bat assemblage. Trees in some form are necessary to provide foraging habitat for most species in this region (Lumsden and Bennett, 2000). Similar observations have been reported in Europe, where bat activity is low in open areas and dominated by a few species (Limpens and Kapteyn, 1991; Walsh and Harris, 1996; Russ and Montgomery, 2002).

It is important to recognise that activity of bats, as measured by bat detectors, is based on calls recorded at a single tree, and does not necessarily represent total activity across the site. Consequently, comparative results between tree-density categories (Fig. 2) should not be interpreted to mean that a 1 ha site with 1 tree per ha supports as many bats as a 1 ha site with 20 trees per ha, for example, despite a similar level of activity potentially being recorded around a single tree in each situation.

What then, is the impact on bats of the incremental loss of trees as tree density is reduced? Results from trapping may provide more useful insights. Based on four nights of trapping at each site, the mean number of individuals declined as tree density declined, from a mean of 48 individuals captured in blocks, to 40 in dense scattered, 29 in moderate scattered and 12 in sparse scattered trees (Table 3). This suggests that as tree density is reduced so too does the overall abundance of bats.

4.3. Demographic variation

If scattered trees in paddocks were less suitable as a foraging habitat than wooded blocks, it could be expected that there would be differences in sex ratios and population age structures. Females have higher energetic demands than males due to the cost of pregnancy and lactation (Thomas, 1988; Barclay, 1991). To compensate, females could forage in higher quality habitat to optimise food intake, although other potential strategies could include increased foraging time, increased feeding efficiency, or entering torpor (O'Donnell, 2002). The pooled data from this study revealed a significant male sex bias for many of the species trapped. This is consistent with results from a broad-scale survey across the Victorian Riverina that sampled 133 sites in a range of types of remnant vegetation (Lumsden, 2004). There is no evidence to suggest this bias is due to differential migration patterns, as for some northern hemisphere species (e.g. Cryan et al., 2000). All species (except possibly *T. australis*, Lumsden, 1999), are believed to be resident, and all breed in the region. However, despite an overall bias in the sex ratio for many species, comparisons across tree-density categories showed no differences in the sex ratio for any species.

A second indicator of marginal habitat may be low breeding success. Using relative abundance of juveniles as a measure of breeding success, for most species there were no differences between tree-density categories. The two species for which differences were evident showed a higher, rather than lower, proportion of young in sparsely treed sites. Juveniles often forage closer to their roost site than do adults (O'Donnell, 2001), but we do not know whether these sparsely treed sites are representative of their natal area or whether these results were influenced by juveniles dispersing. Little is known of dispersal patterns in these species.

A third potential indicator of marginal habitat is body condition, with individuals foraging in poor quality habitats possibly being in poorer condition than those foraging in optimal areas. There were no differences in the body condition index for any species across tree-density categories, again suggesting that sparser treed sites are not necessarily sub-optimal foraging habitat.

4.4. Relationships between bat activity and prey availability

Four taxa showed significant positive correlations between activity levels (as recorded by detectors) and availability of potential prey. We expected that greater resolution would be achieved when the prey biomass was reduced to the dominant types and sizes in the diet of each. Two additional species (*C. gouldii* and *V. darlingtoni*) were significantly positively correlated with prey availability when it was measured as the dominant dietary types, but *Mormopterus* sp. (southern) no longer showed a significant correlation. All but one of the remaining taxa were also positively (but non-significantly) correlated with prey availability. The light traps sampled the same arthropod orders found in the bats' diet, with five of the six numerically dominant orders in light trap samples also being the five dominant orders in the diets of the bats (Tables 2 and 6). Other studies have reported significant relationships between insect availability and bat activity based on temporal patterns within a night (e.g. Swift, 1980; Taylor and O'Neill, 1988), seasonal patterns (e.g. de Jong and Ahlén, 1991), and in relation to temperature (e.g. Richards, 1989) and habitat type (e.g. Arlettaz and Perrin, 1995; Warren et al., 2000). In contrast, Ekman and de Jong (1996) found no relation between insect abundance and bat distribution in fragmented and continuous forests in Sweden.

The species most strongly correlated with the abundance of preferred prey were typically the less common species (e.g. *Mormopterus* sp. eastern, *V. regulus*, *V. darlingtoni*). In contrast, the five taxa for which there were positive but non-significant correlations were mainly common species, including those with both generalist (e.g. *V. vulturnus*) and more-specific diets (e.g. *C. morio*). *T. australis*, the only species negatively correlated with arthropod biomass, generally flies above the canopy and it is likely that the arthropods on which it feeds are out of range of light traps on the ground.

While these results demonstrate a clear link between foraging activity and prey abundance, there are several possible reasons why the strength of this relationship was not greater. First, taxonomic resolution for both dietary items and arthropod availability was to ordinal level. A stronger relationship may have been apparent if it had been possible to identify potential prey items and prey remains to a finer level (Greene and Jaksic, 1983). Second, in this study it was only possible to measure overall activity, rather than specific foraging activity, and so a true measure of foraging was not available. However, other studies have found a strong correlation between the total number of passes and the number of feeding buzzes (Walsh et al., 1995; Law et al., 1998; O'Donnell, 2000), suggesting that overall activity reflects foraging activity. Third, food may not be limiting: if so, there would be less pressure to concentrate on areas of high arthropod availability. However, little is known about the distribution and extent of arthropod biomass in these rural landscapes, or the proportion taken by bats. Last, factors other than food availability may influence where bats forage, such as the risk of predation or the need to shelter from wind (Verboom and Spoelstra, 1999).

4.5. Implications for conservation

Scattered trees in farmland are used extensively by bats as foraging habitat. Although there was a general trend for a decline in abundance and activity of bats with declining tree density, no threshold level was revealed below which isolated trees were not used. Single isolated trees or small stands of sparsely scattered trees are unlikely to provide all the resources that an individual requires, but due to their mobility bats can traverse the rural landscape to exploit multiple patches of habitat. For most species, trees are a critical component of foraging habitat with little time spent in the open, but the ability to commute across open areas enables them to access sparsely scattered trees.

In a reciprocal relationship, insectivorous bats may contribute to the survival of scattered farmland trees through the ecosystem service they provide by consuming invertebrates. 'Dieback' of eucalypts in rural landscapes is often associated with high levels of defoliating insects (Landsberg et al., 1990). Discussion of biological processes associated with dieback often highlights the potential importance of insectivorous birds in regulating invertebrate abundance (e.g. Ford, 1985; Loyn, 1987; Landsberg et al., 1990; Reid and Landsberg, 1999), but the role that bats may play is usually overlooked. We suggest bats are likely to have an important role in regulating populations of herbivorous invertebrates around sparsely scattered trees, because woodland-dependent, insectivorous birds are often scarce in such habitats (Lumsden and Bennett, 2000).

Results from this study are widely applicable to agricultural landscapes across southern Australia, because many of the species recorded occur throughout these regions. These results also support the contention of others (e.g. Reid and Landsberg, 1999; Law et al., 2000; Fischer and Lindenmayer, 2002b; Gibbons and Boak, 2002), that while recognising the value of larger remnants for conservation, we must also acknowledge the values of scattered stands and even single trees. This is particularly important in extensively cleared rural landscapes where 95% or more of the vegetation has been removed. Conserving remaining vegetation is an essential component of landscape restoration.

A first step in improved protection and management of scattered trees in farmland is for their values to be recognised. There are potential economic benefits such as providing shade and shelter to stock, crops and pasture; lowering the risk of dryland salinity, reducing erosion and improving soil properties (Reid and Landsberg, 1999; Wilson, 2002). Greater awareness is also required of their role in biodiversity conservation. Many land managers are familiar with the beneficial role of birds as insectivores or pollinators. However, because insectivorous bats are small, nocturnal and hidden in roosts during the day, few people are aware of the diversity or abundance of bats that use trees in rural landscapes. Increasing the awareness of land managers and decision makers to the benefits of these species, will enhance knowledge of this faunal group in the community and provide further reasons for valuing scattered trees on farms.

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