

The effects of reducing bird predation on canopy arthropods of marri (*Eucalyptus calophylla*) saplings on the Swan Coastal Plain, Western Australia

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Abstract

The effect of bird predation on canopy arthropods inhabiting Marri (*Eucalyptus calophylla*) saplings was examined in *Banksia* woodland on the Swan Coastal Plain of Western Australia. Twenty pairs of saplings were selected and one of each pair was enclosed in bird-proof mesh to exclude foraging birds. Saplings were sampled in April 1998, prior to bird exclusion, and in August 1997, October 1997 and May 1998 after exclusion. Abundance, species richness and size of some arthropods increased on meshed saplings in certain months following bird exclusion. Spiders (Araneae) were most different between meshed and open saplings, with their abundance increasing on the saplings from which birds were excluded and remaining significantly more abundant after one year. The abundance of larger arthropods (in particular, spiders) increased and smaller animals decreased following bird exclusion, suggesting an interaction with birds on spiders as prey, and between spiders and their prey.

Additional evidence of an effect of bird predation on the arthropod fauna was found in the amount of arthropod-related damage to leaves on meshed and open saplings. Damage to leaves, recorded over an 8-week period in spring, on meshed saplings was 21% of total leaf area, compared with 6% on open saplings. These differences indicate that damage to canopy foliage is reduced by bird predation of herbivorous arthropods, and are consistent with trends in arthropod abundances between open and meshed saplings. We conclude that predation by birds affects the composition and size structure of canopy arthropod communities on eucalypts, and there is merit in initiating longer and more extensive studies.

Keywords: bird, predation, arthropods, Marri, Swan Coastal Plain

Introduction

Birds are arguably the most important visually-hunting predators of arthropod herbivores (Strong *et al.* 1983). Otvos (1979) and Holmes (1990a) suggest that birds suppress and delay the build-up of arthropod populations, thereby increasing the interval between arthropod outbreaks. Predation by birds may also accelerate the decline of arthropod populations after epidemics. Thus, the greatest influence of avian predation on arthropod populations may be exerted at endemic rather than epidemic levels (Holmes 1990a; Stephen *et al.* 1990).

Although there have been few studies on the interactions between birds and their prey, experimental and observational studies alike indicate a complex set of interactions affecting the abundances and community composition of both forest arthropods and forest birds (*e.g.* Holmes *et al.* 1979; Holmes 1990a;b; Loyn *et al.* 1983; Recher *et al.* 1996a). As well as affecting the population dynamics of individual species, birds may affect the taxonomic composition of the arthropod fauna and the size distribution of forest arthropods. In turn, the effects of avian predation on forest arthropods and the behaviour of birds may affect the species composition and abundance of both the forest avifauna and of other predators on forest arthropods. Such interactions may have important consequences for the health and sustainability of forest ecosystems (Loyn 1983;

Loyn *et al.* 1983). Loyn *et al.* (1983) demonstrated that colonial Bell Miners (*Manorina melanophrys*) excluded other passerines from eucalypt forest occupied by the colony. The consequence was an increase in insects, and the progressive degradation of the forest within the colony as a consequence of increased insect herbivory. When the miners were removed, other passerines returned and insect abundances were reduced. Marquis & Whelan (1994) found that the exclusion of birds from White Oak (*Quercus alba*) saplings increased numbers of arthropods and increased damage to foliage by grazing insects. They predicted that observed declines in North American populations of insectivorous birds could reduce forest productivity through increased abundance of arthropod herbivores and their subsequent impact on plant growth.

Despite the potential importance of birds as regulators of forest arthropod populations and of the composition of arthropod communities, few workers have attempted to measure the scale of avian predation on forest arthropods. Almost all such attempts have investigated bird predation on one or a few pest arthropods (*e.g.* Campbell *et al.* 1983; Kroll & Fleet 1979; Morrison *et al.* 1989; Solomon *et al.* 1976; Torgersen *et al.* 1990). Studies such as those of Loyn *et al.* (1983) and Marquis & Whelan (1994) are exceptional. Given the importance of forest arthropods as 'rate regulators' of ecological processes within forest ecosystems (Springett 1978), the richness of arthropod faunas in eucalypt forest canopies (Majer *et al.* 1994; Recher *et al.* 1996a),

and the importance of arthropods as food for eucalypt forest birds (Loyn *et al.* 1983; Recher *et al.* 1991, 1996a), we measured the impact of bird predation on the abundance, taxonomic composition and size structure of eucalypt canopy arthropods and the interactions of these variables with the amount of arthropod damage to canopy foliage. We report here the results of a one-year study on the exclusion of birds from Marri (*Eucalyptus calophylla*) saplings on the Swan Coastal Plain near Perth, Western Australia.

Site description and methodology

Study site

The study was conducted at Lowlands, a private property located 50 km south of Perth on the Swan Coastal Plain of Western Australia. Lowlands is a mosaic of fallow pasture and bushland that, unlike much of the bushland on the Swan Coastal Plain, has not been subject to periodic logging and fires (Keighery *et al.* 1995). A significant portion of the native vegetation on the property was never cleared and a core of native vegetation, broadly defined as *Banksia* woodland, dominates the property (Keighery *et al.* 1995; D van Gool, Agriculture WA, personal communication).

Experimental design

On the basis of similarities in location, height and canopy volume, 40 Marri saplings were selected and paired, giving two treatments with 20 replicates in each. Selected saplings were under 3 m in height. No flowering was recorded for saplings during the study.

Birds were excluded from one sapling of each pair by construction of a triangular cage around the sapling, using stakes and 25 x 25 mm polyethylene bird control mesh. No section of the canopy protruded outside the triangle. Cages were constructed in early May 1997. In the following, we refer to caged saplings as 'meshed' and to the uncaged saplings as 'open'. Prior to bird-exclusion, all 40 saplings were sampled for arthropods using the foliage beating and branchlet shaking method described by Majer *et al.* (1996).

A circular calico sheet, 100 cm in diameter with a single slit cut from the centre to the edge, was placed around the trunk of each sapling, giving a standard collection area for all saplings. Saplings were then shaken and beaten using a wooden pole to dislodge any arthropods from the canopy. Fast moving arthropods were collected immediately using forceps. The remainder of the collection was emptied from the sheet on to a piece of white cardboard and brushed into a collecting vial containing preserving fluid. The first sample was taken in April 1997. Post-exclusion samples were taken in August and October 1997, and in May 1998. All material was sorted and scored to the ordinal level.

Following log-normal transformation to stabilise variance and validate normality assumptions, a paired t-test was used to compare each ordinal taxa between saplings from open and meshed categories for each of the four sampling periods. The two-tailed probability was used. In order

to summarise the influence of bird exclusion on the arthropod fauna as a whole, each taxon was categorised in each sampling period on whether numbers were more abundant (+), less abundant (-) or equally abundant (=) on meshed as opposed to open saplings. The numbers of taxa in the '+' and '-' category were then compared with the expected score using a 'sign test' based on the binomial distribution. On the null hypothesis that bird exclusion had no effect on the fauna, each taxon was assumed to have an equal chance of being more or less abundant on the meshed trees. The '=' category was excluded from the analysis.

Material collected in April, August and October 1997, but not May 1998, was also sorted to morpho-species. Due to small size (generally less than 1.5 mm in length) and difficulties with identification, Psocoptera, Collembola, Acarina, Thysanoptera, Diptera adults (<3.0 mm) and larvae, early-instar Blattodea nymphs, Lepidoptera larvae, Coleoptera larvae, and Hymenoptera larvae and wasps were not assigned to morpho-species.

The diversity of a community comprises two characteristics; the total number of species (richness) and the relative abundance of individuals of each species (evenness). Arthropod species richness (S) was obtained by summing the number of morpho-species collected in a particular time and treatment. The cumulative number of morpho-species was also plotted against sapling numbers for both open and meshed categories. The diversity of arthropods was further investigated using the Shannon & Weaver (1949) H^1 index, which attempts to give a combined measure of richness and evenness. This was calculated by the following formula:

$$H^1(\text{decits}) = \frac{N \log N - \sum_i n_i \log n_i}{N}$$

where N = total number of individuals, and n_i the importance value of the i th morpho-species. This was then used to derive the evenness index (J^1), which was calculated as

$$J^1 = \frac{H^1(\text{decits})}{\log S}$$

The greater the value of J^1 , the more even is the relative abundance of individuals of each morpho-species.

Each arthropod was assigned to a length size-class; 1 is <0.5 mm; 2 is 0.51-1.0 mm; 3 is 1.01-2.0 mm; 4 is 2.01-3.0 mm; 5 is 3.01-4.0 mm; 6 is 4.01-5.0 mm; 7 is 5.01-10.0 mm; and 8 is >10.01 mm long. Differences in numbers of arthropods within each size class between meshed and open saplings for the pre-exclusion and post-exclusion samples were analysed using the Mann-Whitney U-test. This was used in preference to the t-test in view of the large number of zeros in the data. The two-tailed probability was used.

Foliage damage

Total height, mean crown diameter taken along two planes (east-west and north-south), and vertical depth of crown were measured for each sapling to outline its shape and size. Canopy measurements were repeated in October

1997. Differences in growth measurements between meshed and open saplings for the pre-exclusion and post-exclusion samples were analysed using the Mann-Whitney U-test. A non-parametric test was used because the data included negative values, which arose because canopies of some saplings had shrunk during the period between measurements. The two-tailed probability was used.

To quantify leaf damage caused by herbivorous arthropods, during August five undamaged leaves emerging from newly opened shoots were selected at random on each of a subset of paired saplings and a plastic coated wire band was used to secure a numbered 2.5 x 2.5 cm aluminium tag around the petiole of each leaf. All 40 saplings were inspected. Of these, 17 had experienced new leaf flush. This included six paired replicates (12 saplings, giving 60 leaves) which were used for the analysis. The subset represented a cross section of the different heights, canopy volumes, locations, surrounding vegetation types and bird exposure status of the saplings.

Damage to leaves was assessed by tracing tagged leaves from each sapling onto separate transparent plastic sheets. The extent of leaf damage was traced on two occasions over an 8-week period between August and October 1997. In October, individual leaves, together with any damage present, were outlined and damage was assigned to one of two categories as follows; leaf chewers (portions of the leaf lamina had been removed, either along the margins or within the lamina) and leaf miners (irregular shaped areas of raised necrotic leaf epidermis, also evident as narrow trails of damage). Where extensive damage had occurred to actively expanding leaves (generally by leaf chewing arthropods), estimation of an entire mature leaf was undertaken, as this was required for the estimation of total leaf damage. The method of estimation for entire leaf areas of chewed leaves was that described by Abbott *et al.* (1993), who concluded that their technique of tracing leaf outlines and damaged parts onto transparent plastic was accurate and reliable.

Leaf area and categorical damage to individual leaves were measured using a Delta-TO digital scanner (DIAS II). Damage in each category was measured using the DIAS II scanner for each leaf and then tabulated. Individual leaf damage by miners and chewers was totalled separately for each cohort of leaves and then expressed as a percentage of total leaf area for the sapling. Incidences of leaf abscission were removed from damage estimates, as factors other than arthropod damage may be involved. Differences in leaf damage between meshed and open saplings for the pre-exclusion and post-exclusion samples were analysed using the Mann-Whitney U-test. A parametric test was considered to be inappropriate because the data were percentage values. The two-tailed probability was used.

Results

Numbers of arthropods

Ordinal invertebrate means for open and meshed saplings for each sampling period are summarised in Table 1. Numbers of arthropods collected across all taxa were generally low and variance in means was high for both

pre-exclusion and post-exclusion samples. The total number of arthropods on saplings was highest in the April 1997, lower during August and October 1997, and lowest in May 1998 (Table 1).

The low numbers of arthropods collected and high numbers of zeros in the data resulted in few statistical differences. In April 1997, differences in numbers of individuals between saplings that were to be meshed and those that were to remain open were not significant. For the first post-exclusion sampling period in August 1997, a significantly larger number of spiders (Araneae) was found on meshed saplings than on open saplings ($t_{19} = 3.55$, $P < 0.005$), but no significant differences were found in numbers of other arthropods. Mean numbers of spiders had increased on both open and meshed saplings between the August and October sampling periods (Table 1), and spider abundance was again significantly higher on meshed saplings ($t_{19} = 3.73$, $P < 0.005$). No significant difference was observed between open and meshed saplings in October for other taxa. This pattern was repeated in the May sample, with spiders once again being significantly ($t_{19} = 4.71$, $P < 0.001$) more abundant on the meshed than open saplings. There were no differences in abundance for the other taxa.

The signs of differences between mean invertebrate numbers in ordinal taxa for open and meshed categories in the pre-exclusion and post-exclusion samples are shown in Table 2, together with sign total summaries. Prior to bird exclusion in April, the distribution of sign scores between taxa did not differ from that expected using a two-tailed sign test. The post-exclusion August sample showed an increase, although not significant, in the number of taxa that were most abundant on meshed saplings. This shift continued through to the October sample (Table 2), where the number of taxa that were more abundant on the meshed saplings was significantly greater ($P < 0.005$) than on the open saplings. The trend of abundance persisted in the May sample, with a greater number of taxa being more abundant on the meshed than open saplings. However, the difference was not significant.

Species richness

For the April pre-exclusion period, 42 morpho-species were collected from meshed saplings and 51 from open saplings (Table 3). The species accumulation curve for arthropods collected over this period (Fig 1a) shows that, in most paired replicates, cumulative numbers of morpho-species on open saplings were greater than, or equal to, those of meshed saplings. The diversity (H') value and species richness of open saplings was also higher than that for meshed saplings in April, prior to bird exclusion (Table 3). Evenness (J') values were almost identical for open and meshed saplings. This indicates a similar evenness of species abundance patterns between the two exclusion categories prior to experimental manipulation.

In August, 69 and 73 morpho-species were identified on open and meshed saplings respectively (Table 3). Species diversity and richness increased for both categories between the April and August, while evenness remained the same for open saplings. In contrast, meshed saplings displayed an increase in evenness of spread of

Table 1. Ordinal means (\pm se, n = 20) for invertebrates collected from open and meshed *E. calophylla* saplings during April, August and October, 1997 and May, 1998.

Order	April-97		Aug-97		Oct-97		May-98	
	Open	Meshed	Open	Meshed	Open	Meshed	Open	Meshed
Arachnida	-	0.10	-	0.05	-	-	-	-
Pseudoscorpionida	-	-	-	-	-	-	-	-
Acarina	42.60 \pm 18.50	18.85 \pm 4.15	13.95 \pm 2.09	12.50 \pm 2.30	10.85 \pm 1.50	12.50 \pm 2.36	1.80 \pm 0.65	12.10 \pm 98.70
Araneae	2.30 \pm 0.33	2.10 \pm 0.42	2.45 \pm 0.35	5.75 \pm 0.81	3.50 \pm 0.45	8.75 \pm 1.19	1.90 \pm 0.36	7.10 \pm 1.62
Diplopoda	-	-	0.10	0.25 \pm 0.47	-	0.05	-	0.10 \pm 0.07
Collembola	2.65 \pm 0.46	3.55 \pm 0.73	27.35 \pm 7.96	18.10 \pm 3.36	6.95 \pm 1.69	8.50 \pm 2.04	8.65 \pm 6.28	3.30 \pm 1.14
Insecta	-	0.05	-	-	-	-	-	-
Thysanura	-	-	0.05	-	-	-	-	-
Ephemeroptera	-	-	-	-	-	-	-	-
Blattodea-adults	-	-	-	-	0.05	0.30 \pm 0.22	0.15 \pm 0.08	0.10 \pm 0.05
Blattodea-nymphs	0.10	0.35 \pm 0.21	0.10	0.50 \pm 0.27	-	-	-	-
Mantodea	-	0.05	0.05	-	-	-	0.10 \pm 0.07	0.20 \pm 0.09
Demoptera	-	0.15	-	0.05	-	0.05	0.05 \pm 0.05	0.10 \pm 0.07
Orthoptera	0.05	-	0.15	0.10	0.40 \pm 0.12	-	-	-
Psocoptera	26.70 \pm 7.04	50.15 \pm 17.13	7.80 \pm 2.05	6.85 \pm 1.86	4.50 \pm 1.20	5.70 \pm 2.15	10.30 \pm 3.59	10.45 \pm 2.98
Hemiptera	5.90 \pm 1.25	2.95 \pm 0.65	4.25 \pm 0.96	4.90 \pm 0.80	13.40 \pm 2.80	10.00 \pm 1.18	5.65 \pm 2.27	3.20 \pm 0.86
Thysanoptera	5.85 \pm 1.49	4.10 \pm 0.79	0.45 \pm 0.11	0.60 \pm 0.34	12.20 \pm 4.35	8.20 \pm 2.41	0.80 \pm 0.21	1.30 \pm 0.40
Neuroptera-adults	-	-	0.10 \pm 0.05	-	-	-	-	-
Neuroptera-larvae	-	-	-	-	0.05	0.05	-	-
Coleoptera-adults	0.90 \pm 0.15	0.70 \pm 0.23	1.65 \pm 0.72	1.85 \pm 0.57	0.80 \pm 0.22	1.10 \pm 0.28	1.30 \pm 0.34	1.30 \pm 0.33
Coleoptera-larvae	0.30 \pm 0.39	0.25 \pm 0.11	0.45 \pm 0.19	0.25 \pm 0.11	0.40 \pm 0.12	0.35 \pm 0.20	-	-
Mecoptera	-	-	-	-	-	0.05	-	-
Diptera-adults	0.20	0.05	0.40 \pm 0.08	0.80 \pm 0.31	0.25 \pm 0.11	0.75 \pm 0.21	0.10 \pm 0.10	0.15 \pm 0.08
Diptera-larvae	0.10	-	0.45 \pm 0.77	-	-	0.40	-	-
Leidoptera-adults	-	-	-	0.10	-	0.05	0.05 \pm 0.05	-
Lepidoptera-larvae	0.60 \pm 0.16	0.80 \pm 0.29	0.95 \pm 0.37	1.35 \pm 0.41	1.85 \pm 0.55	2.55 \pm 0.68	0.50 \pm 0.21	0.50 \pm 0.22
Hymenoptera-ants	4.62 \pm 1.23	6.15 \pm 1.82	5.60 \pm 1.97	7.45 \pm 1.45	4.70 \pm 1.56	5.30 \pm 1.70	9.75 \pm 3.97	6.30 \pm 1.85
Hymenoptera-others	0.70 \pm 0.14	0.25 \pm 0.13	0.75 \pm 0.14	0.95 \pm 1.23	0.90 \pm 0.45	0.95 \pm 0.25	0.10 \pm 0.07	-
Total	93.57	90.60	66.90	62.45	60.50	66.00	41.20	46.3

Table 2. Breakdown of ordinal taxa sampled during April, August and October, 1997 and May, 1998 from open and meshed *E. calophylla* saplings; showing whether each taxon was less abundant (-), more abundant (+) or equally abundant (=) in the meshed than open saplings. Blank entries denote absence of the taxon in that sampling period.

Class	Order	Apr-97	Aug-97	Oct-97	May-98
Arachnida	Pseudoscorpionida	+	+		
	Acarina	-	-	+	+
	Araneae	-	+	+	+
Diplopoda	Polyxenida		+	+	+
Collembola		+	-	+	-
Insecta	Thysanura	+			
	Ephemeroptera		-		
	Blattodea-adults			+	-
	Blattodea-nymphs	+	+		
	Mantodea	+	-		=
	Dermaptera	+	+	+	+
	Orthoptera	-	+	+	+
	Psocoptera	+	-	+	+
	Hemiptera	-	+	-	-
	Thysanoptera	-	+	-	+
	Neuroptera-adults		-		
	Neuroptera-larvae			=	
	Coleoptera-adults	-	+	+	=
	Coleoptera-larvae	-	-	-	
	Mecoptera			+	
	Diptera-adults	-	+	+	+
	Diptera-larvae	-	-	+	
	Lepidoptera-adults		+	+	-
	Lepidoptera-larvae	+	+	+	=
	Hymenoptera-ants	+	+	+	-
Hymenoptera-others	-	+	+	-	
Number of taxa which:					
are most abundant on meshed saplings		9	14	16	8
are less abundant on meshed saplings		10	8	3	6
equally abundant between categories		0	0	1	3
significance of deviation of signs from random distribution		NS	NS	*	NS

* $p < 0.005$; NS not significant

individuals among morpho-species. The higher evenness in the meshed sapling fauna reflects an increase in abundance of several rare species and a decrease in the two most abundant morpho-species. A comparison of numbers of morpho-species accumulated over the 20 paired replicates between April and August (Fig 1a,b) reveals a partial inversion of the open and meshed sapling curves, with a number of meshed saplings supporting higher total numbers of morpho-species than their open counterparts.

The increase in numbers of morpho-species observed in meshed saplings for the August sampling period continued until October, with 106 morpho-species identified from meshed saplings, but only 76 from open saplings (Table 3). Fig 1c shows the cumulative numbers of morpho-species collected over the 20 paired replicates for October. Here, differences in total morpho-species found within each of the 20 paired saplings have increased, with all 20 meshed saplings displaying higher total numbers of morpho-species. This indicates a proportionately larger increase in numbers of morpho-species collected from meshed saplings. Differences in the Shannon-Weaver diversity indices between exclusion categories for the October data support this trend, with a higher species richness and H' value for

the meshed than open saplings, relative to April and August (Table 3). The highest species richness, species diversity and evenness values were recorded for meshed saplings in October. The elevated evenness index reflects an increase in abundance of several rare morpho-species and a substantial decrease in the most abundant morpho-species on meshed saplings. Species diversity and evenness was lower for open saplings in the October sample than for August (Table 3). Species richness, however, was slightly higher in the October sample than in August for open saplings. As morpho-species were not sorted in the May 1998 sample, diversity, richness and evenness values cannot be calculated for that period.

Arthropod size-classes

Numbers of arthropods recorded in each size-class for open and meshed saplings are presented in Fig 2. Variance in the means was generally high, and numbers of arthropods were low in all four of the larger size-classes in all sampling periods. Numbers of arthropods in size-class 2 were significantly greater on open saplings ($U = 124$, $N_1 = N_2 = 20$, $P < 0.05$) than on saplings designated for meshing during the pre-exclusion sampling period. This was asso-

Table 3. Total numbers of morphospecies identified within ordinal taxa between 20 pairs of open and meshed *E. calophylla* saplings, for April, August and October, 1997. The species richness, Shannon Wiener diversity index (H^1) and evenness (J^1) values for these sampling periods are also shown.

Class	Order	Pre-exclusion Apr-97		Post Exclusion Aug-97		Post-exclusion Oct-97		
		Open	Meshed	Open	Meshed	Open	Meshed	
Arachnida	Pseudoscorpionida	-	2	-	1	-	-	
	Araneae	17	12	21	29	18	38	
Diplopoda	Polyxenida	-	-	1	1	-	1	
Insecta	Thysanura	-	1	-	-	-	-	
	Ephemeroptera	-	-	1	1	-	-	
	Blattodea-adults	-	-	1	-	1	4	
	Mantodea	1	1	1	-	-	-	
	Dermaptera	-	1	-	1	-	1	
	Orthoptera	1	-	-	3	1	6	
	Hemiptera	12	10	14	11	26	29	
	Neuroptera	-	-	1	-	-	-	
	Coleoptera-adults	9	6	13	12	14	15	
	Mecoptera	-	-	-	-	-	1	
	Diptera-adults	-	-	5	2	1	3	
	Lepidoptera-adults (>3mm)	1	-	-	2	-	1	
	Hymenoptera-ants	10	9	11	10	15	7	
	Species richness		51	42	69	73	76	106
	Diversity (H^1)		1.18	1.15	1.27	1.37	1.16	1.51
Evenness (J^1)		0.69	0.71	0.69	0.74	0.62	0.75	

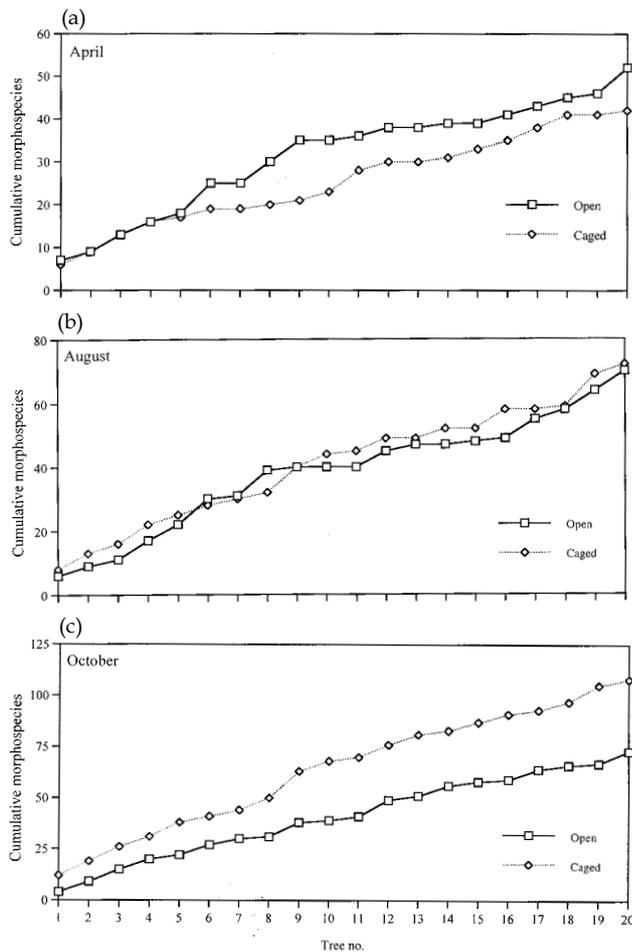


Figure 1. Accumulation of morpho-species from 20 paired *E. calophylla* saplings in two bird-exclusion categories for April, August and October, 1997.

ciated with abnormally high numbers of Thysanoptera in the open category saplings. All remaining size-classes had no significant difference between open and meshed saplings prior to enclosure (Fig 2a).

No significant differences in mean invertebrate numbers were observed between open and meshed saplings for any size-class in August, although numbers in the four largest size-classes were greater on the meshed saplings and three of the four smaller classes were greater on the open saplings (Fig 2b). In October, seven of the eight size-classes were more abundant on meshed saplings than on those to which birds had access (Fig 2c), with two of the four largest size-classes (4 and 8) being significantly more abundant ($U = 126$ and 118 respectively for $N_1 = N_2 = 20$, $P < 0.05$). In May, members of size-class 2 were significantly ($U = 110$, $N_1 = N_2 = 20$, $P < 0.05$) less abundant on the meshed than open saplings, while differences between the other sizes were not significant (Fig 2d).

Canopy size and arthropod damage to foliage

No significant difference was found in total height, crown diameter and crown depth between paired saplings prior to bird exclusion in April. An increase in mean crown diameter was recorded for all saplings after the final set of canopy measurements were taken in October. This increase was significantly greater on the open than on the meshed saplings ($U = 118$, $N_1 = N_2 = 20$, $P < 0.05$) and was not caused by restrictions of the mesh; this was designed to allow plenty of growth. No differences in total height increase or foliage height were recorded between open and meshed saplings from pre-exclusion to October.

Cumulative damage between August and October to individual leaves by leaf chewers and leaf miners for each

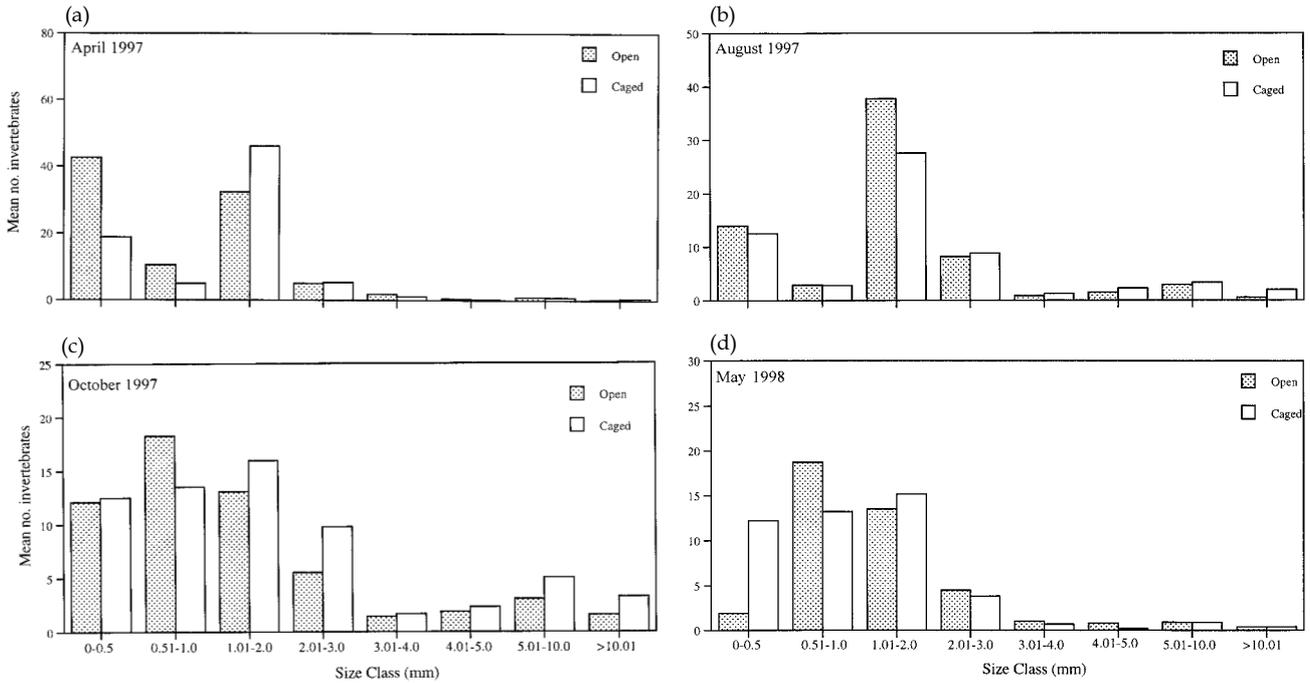


Figure 2. Mean number ($n=20$) of invertebrates in each size class collected from open and meshed *E. calophylla* saplings during April, August and October, 1997 and also May 1998.

paired replicate is shown in Fig 3. No significant difference in the leaf area damaged by leaf miners and chewers per sapling was found between exclusion categories, even though mean damage in both categories was higher on the meshed saplings. Total damage (*i.e.* chewers and miners), however, was significantly greater ($U = 5, N_1 = N_2 = 6, P < 0.05$) on the saplings from which birds had been excluded.

Discussion

The pre- and post-exclusion sampling of the canopy fauna from Marri saplings revealed changes in the abundance, richness, diversity and size of arthropods between open and meshed saplings, suggesting that predation by birds affects arthropod abundance and community structure in these woodlands. However, many of the differences between exclusion categories were not significant, owing to the generally low numbers and high variances of arthropods collected from saplings.

The removal of the fauna during each sampling contributed to the reduced abundances recorded after the initial sample. However, Recher *et al.* (1996a,b) have shown significant differences in eucalypt canopy arthropod abundances seasonally and between years, and we do not consider it likely that the removal of the fauna appreciably affected differences between open and meshed saplings. Other studies have consistently shown that birds reduce the abundance of arthropod prey (Gunnarsson 1996; Holmes *et al.* 1979; Loyn *et al.* 1983; Marquis & Whelan 1994; Moore & Young 1991; Solomon *et al.* 1976). Wiens *et al.* (1991) failed to find an effect of bird predation on arthropod abundances, but low primary productivity in the shrublands where they worked appeared to limit arthropod numbers. As the *Banksia* woodlands where we worked grow on nutrient-poor sands, and primary productivity is

probably low, it is likely that the small number of arthropods on individual saplings and the low population densities of insectivorous birds in this habitat (Bamford 1986) are a consequence of low plant productivity (Recher *et al.* 1996a). Demonstrating a significant effect of predation by birds on arthropods under these conditions probably requires a long exclusion period and a larger number of samples than we obtained before patterns can unequivocally be detected.

Despite these limitations, species richness, numbers, and size of arthropods were significantly greater on meshed Marri saplings than on open saplings during spring (October), which is the period when we expect both the

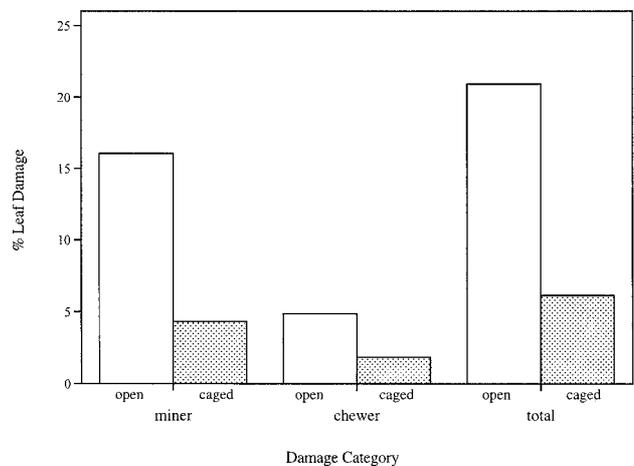


Figure 3. Percentages of leaf area damaged by leaf miners and chewers on open and meshed *E. calophylla* saplings between August and October 1997 post-exclusion sampling periods.

abundances of arthropods and bird predation to be greatest (Recher *et al.* 1996a,b). Spiders showed the greatest response to exclusion of birds; they had increased abundance and more large individuals on meshed than open Marri saplings during all post-exclusion sample periods, including May when total arthropod numbers were lowest. Gunnarsson (1983) also found reduced mortality of spiders when birds were excluded from spruce (*Picea abies*) foliage. He suggested that large spiders seem more vulnerable to predation by birds than small spiders. As predators, spiders probably respond to the removal of bird predation in two ways. First, numbers and size of spiders increase as a result of reduced predation by birds. Second, if the numbers of other arthropods increase in the absence of birds, then the prey base for spiders is increased, allowing more and larger spiders to survive. We expect spiders to show the greatest response to removing bird predation for the reasons given but, as Marquis & Whelan (1994) point out, reduced predation by wasps on meshed saplings could also enhance spider productivity. This could happen either by the unintended exclusion of wasps by the mesh or through the mesh providing better cover for spiders.

Nonetheless, removal of bird predators appears to affect arthropod community structure by allowing another group of predators, the spiders, to increase (for comparable results, see Gunnarsson 1983, 1996; Halaj 1996; Halaj *et al.* 1997). The manipulation also appeared to allow rarer and smaller species to increase in abundance, as shown by the greater evenness of distribution of morpho-species abundance patterns observed in meshed saplings. These results indicate that bird predation is a major force affecting arthropod and spider abundance, size and species richness, as well as community trophic structure. This interaction is an example of a top down, trophic cascade of the type discussed by Letourneau & Dyer (1998).

Our results also indicate that predation by birds reduces the amount of arthropod damage to eucalypt foliage. Total arthropod damage on meshed saplings was significantly higher than on saplings exposed to bird predation. Moreover, damage estimates in this study were based on an 8-week recording period and as a result, probably underestimate effects. Abbott *et al.* (1993) reported that arthropod damage to leaves of Marri occurs mainly in the first 3 months of a leaf's development. Total arthropod damage estimates of 6.2% for Marri (Abbott *et al.* 1993) are comparable to those obtained here for open saplings (6.1%). Marquis & Whelan (1994) noted that differences in arthropod numbers resulted in differences in leaf area missing at the end of the season. Meshed plants produced approximately one-third less leaf biomass and total biomass compared to the controls. These findings are similar to ours, where meshed saplings exhibited approximately three times more leaf area damage than open saplings (21% of total leaf area damaged compared to 6%).

The short duration of the experiment (1-year), the small sample sizes, and high levels of variance, meant that the results were not always significantly different. By contrast, avian predation of grassland arthropods is better demonstrated and understood due to the existence of a range of comprehensive studies (e.g. Bock *et al.* 1992; Fowler *et al.* 1991; Joern 1986, 1992). We conclude that predation by birds

affects the composition and size structure of canopy arthropod communities on eucalypts, and there is merit in initiating longer and more extensive studies in forest ecosystems such as the one studied here.

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References

- Abbott I, Van Heurck P, Burbidge T & Williams M 1993 Damage caused by arthropods and fungi to eucalypt foliage: spatial and temporal patterns in Mediterranean forest of Western Australia. *Forest Ecology and Management* 58:85-110.
- Bamford M 1986 The dynamics of small vertebrates in relation to fire in *Banksia* woodland near Perth, Western Australia. PhD Thesis, Murdoch University, Western Australia.
- Bock C E, Bock J H & Grant M C 1992 Effects of bird predation on grasshopper densities in an Arizona grassland. *Ecology* 73:1706-1717.
- Campbell R, Torgersen T & Srivastava N 1983 A suggested role for predaceous birds and ants in the population dynamics of the western spruce budworm. *Forest Science* 29:779-790.
- Fowler A C, Knight, R L, George T L & McEwen, L C 1991 Effects of avian predation on grasshopper populations in North Dakota grasslands. *Ecology* 72:1775-1178.
- Gunnarsson B 1983 Winter mortality of spruce-living spiders: effect of spider interactions and bird predation. *Oikos* 40: 226-233.
- Gunnarsson B 1996 Bird predation and vegetation structure affecting spruce-living arthropods in a temperate forest. *Journal of Animal Ecology* 65:389-397.
- Halaj J 1996 Abundance and community composition of arboreal spiders: the relative importance of habitat structure, prey availability and competition. PhD Thesis, Oregon State University, Corvallis, Oregon.
- Halaj J, Ross D & Moldenke A 1997 Negative effects of ant foraging on spiders in Douglas-fir canopies. *Oecologia* 109:313-322.
- Holmes R T 1990a Ecological and evolutionary impacts of bird predation on forest insects: an overview. *Studies in Avian Biology* 13:6-13.
- Holmes R T 1990b The structure of a temperate deciduous forest bird community: variability in time and space. In: *Biogeography and Ecology of Forest Bird Communities* (ed A Keast). SPB Academic Publications, The Hague, 121-139.
- Holmes R T, Schultz J & Nothnagle P 1979 Bird predation on forest insects: an enclosure experiment. *Science* 206:462-463.
- Joern A 1986 Experimental study of avian predation on coexisting grasshopper populations (Orthoptera: Acrididae) in a sandhills grassland. *Oikos* 46:243-249.
- Joern A 1992 Variable impact of avian predation on grasshopper assemblies in sandhills grassland. *Oikos* 64:458-463.
- Keighery B J, Keighery G J & Gibson N 1995 (System 6) Part X: Floristics of lowlands. Floristics of Reserves and Bushland Areas of the Perth Region. Wildflower Society of WA, Nedlands, Western Australia.
- Kroll J & Fleet R 1979 Impact of woodpecker predation on over-

- wintering within tree populations of the southern pine beetle (*Dendroctonus frumtalis*). In: The Role of Insectivorous Birds in Forest Ecosystems (eds J G Dickson, R N Connor, R R Fleet, J A Jackson & J C Kroll). Academic Press, New York, 269 – 281.
- Letourneau D K & Dyer L A 1998 Density patterns of *Piper* ant-plants and associated arthropods: Top-predator trophic cascades in a terrestrial system? *Biotropica* 30:162-169.
- Loynd R H 1983 Ecology, distribution and density of birds in Victorian forests. In: Birds of Eucalypt Forests and Woodlands: Ecology, Conservation, Management (eds A Keast, H F Recher, H Ford & D Saunders). Surrey Beatty & Sons, Chipping Norton, NSW, 33-46.
- Loynd R H, Runnalls R & Forward G 1983 Territorial bellminers and other birds affecting populations of insect prey. *Science* 221:1411-1413.
- Majer J D, Recher H F & Keals N 1996 Branchlet shaking: A method for sampling sapling canopy arthropods under windy conditions. *Australian Journal of Ecology* 21: 229-234.
- Majer J D, Recher H F & Postle A C 1994 Comparison of arthropod species richness in eastern & Western Australian canopies: a contribution to species number debate. *Memoirs of the Queensland Museum*. 36:121-131.
- Marquis R J & Whelan C J 1994 Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75:2007-2014.
- Moore F & Young W 1991 Evidence of food-based competition among passerine migrants during stopover. *Behavioural Ecology and Sociobiology* 28:85-90
- Morrison M, Dahlsten S, Tait R , Heald R , Milne K & Rowney D 1989 Bird foraging on incense-cedar and incense-cedar scale during winter in California. Research Paper PSW-195. USDA, Washington.
- Otvos I S 1979 The effects of insectivorous bird activities in forest ecosystems: an evaluation. In: The Role of Insectivorous Birds in Forest Ecosystems (eds J G Dickson, R N Connor, R R Fleet, J A Jackson & J C Kroll). Academic Press, New York, 341-74.
- Recher H F, Majer J D & Ford H A 1991 Temporal and spatial variation in the abundance of eucalypt canopy arthropods: the response of forest birds. *Proceedings of the International Ornithological Congress* 20:1568-75.
- Recher H F , Majer J D & Ganesh S 1996a Eucalypts, arthropods and birds: on the relation between foliar nutrients and species richness. *Forest Ecology and Management* 61:37-58
- Recher H F, Majer J D & Ganesh S 1996b Seasonality of canopy invertebrate communities in eucalypt forests of eastern and Western Australia. *Australian Journal of Ecology* 21:64-80.
- Shannon C E & Weaver W 1949 *The Mathematical Theory of Communication*. University of Illinois Press, Urbana.
- Solomon D, Glen D, Kendall D & Milsom N 1976 Predation on overwintering larvae of codling moth (*Cydia pomonella* (L.)) by birds. *Journal of Applied Ecology* 13:341-353.
- Springett B P 1978 On the ecological role of insects in Australian eucalypt forests. *Australian Journal of Ecology* 3:129-39.
- Stephen F M, Wallis G W & Smith K G 1990 Bird predation on periodical cicadas in Ozark forests: ecological release for other canopy arthropods? *Studies in Avian Biology* 13:369-74.
- Strong D R, Lawton J H & Southwood R 1983 *Insects on Plants: Community Patterns and Mechanisms*. Blackwell Scientific Publications, London.
- Torgersen T, Mason R & Campbell R 1990 Predation by birds and ants on two forest insect pests in the Pacific Northwest. *Studies in Avian Biology* 13:14-19.
- Wiens J, Cates R, Rotenberry N, Cobb B, Van Horne B & Redak R 1991 Arthropod dynamics on sage brush (*Artemisia tridentata*): effects of plant chemistry and avian predation. *Ecological Monographs* 61:299-321.