

Structure of invertebrate communities in relation to fire history of kwongan vegetation at Tutanning Nature Reserve

STUART J. LITTLE¹ and GORDON R. FRIEND²

¹ School of Environmental Biology, Curtin University of Technology, Bentley 6102, Western Australia; Present address: Natural Resources Board, Department of Planning, GPO Box 3927, Sydney 2001, New South Wales.

² Science and Information Division, Department of Conservation and Land Management, Wildlife Research Centre, Woodvale 6026, Western Australia.

ABSTRACT

Trends in abundance and composition of the ground-dwelling invertebrate communities were studied over 10 months (May 1988–February 1989) in different-aged kwongan vegetation within Tutanning Nature Reserve. Habitat structure and floristic composition were also assessed. Twenty-nine taxonomic groups of invertebrates (predominantly orders) and 125 species of Araneae (spiders) were identified. Invertebrate abundances peaked during spring (September, November) and generally showed no site preferences. Composition of the spider fauna in the oldest site (last burnt in 1932) was markedly different from that of the other sites during spring. This was related to the structural composition of the litter and the presence of emergent sheoaks (*Allocasuarina huegeliana*). The trends found in this study suggest that fire does not exert a long-term influence on the structure of the invertebrate communities in these semi-arid ecosystems.

INTRODUCTION

Native vegetation in the semi-arid wheatbelt areas of Western Australia largely occurs as small, disjunct patches of woodlands and shrublands remaining in a landscape cleared largely for agriculture (Brown and Hopkins 1983; Main 1987). The shrubland components of these remnants, termed 'kwongan' (Beard 1976), have been extensively studied in terms of their floristic composition (Brown and Hopkins 1983; Brown 1989), modes of nutrition (Lamont 1984), and

responses to fire (Bell *et al.* 1984). However, no invertebrate community surveys have previously been conducted in this vegetation type. Consequently, the richness and composition of the invertebrate community inhabiting kwongan and the effects of fire and other disturbances upon these organisms are as yet unknown.

It has been postulated that fire effects should become more prolonged as aridity increases (Hopkins 1985; Hutson 1985; Majer 1985). In their studies, Hutson and Veitch (1983) and Majer (1985) found a positive association between invertebrate recovery following fire, and rainfall. This may reflect faster plant growth and also higher rates of litter accumulation and nutrient recycling following fire as rainfall increases.

From research conducted in the more mesic forested areas of the south-west of Western Australia, where rotational burning is implemented as a management tool, invertebrate communities have shown a wide range of responses to burning. From studies of prescribed burning in jarrah (*Eucalyptus marginata*) forest, Koch and Majer (1980) found that invertebrate species richness was reduced for at least three years following burning, while Springett (1976) suggested invertebrate populations may not recover from burning within a normal five- to seven-year burning rotation. By contrast, Abbott (1984) found that the majority of soil and litter fauna recovered within three years of burning. In dry sclerophyll forest in Victoria, Neumann and Tolhurst (1991) concluded that a spring burn, and to a lesser extent an autumn burn, temporarily reduced the abundance of invertebrates involved in the decomposer cycle, particularly Collembola, larval Diptera and earthworms. Consistent with the majority of studies, however, is the finding that there is a strong association between litter density and soil and litter invertebrate abundance (e.g. Campbell and Tanton 1981; Hutson and Veitch 1983, 1985; Majer 1985; Raison, Woods and Khanna 1986; Postle 1989).

This study aimed to examine the long-term influence of fire on the structure of invertebrate communities (and spiders in particular) and their habitat in three semi-arid kwongan sites at Tutanning Nature Reserve in the Western Australian wheatbelt. The study utilized space-for-time substitution (SFT),

whereby sites with different fire histories were contemporaneously sampled to explore relationships between fire and invertebrate community structure. Limitations of the SFT approach in answering disturbance ecology questions have been discussed by Pickett (1989). Despite its limitations, this approach was adopted as a preliminary strategy to gather baseline information, since no previous research had examined this topic. The work forms part of longer-term experimental research examining the impact of fire on vertebrate and invertebrate communities at Tutanning.

STUDY SITE—TUTANNING NATURE RESERVE

Location, Climate, Soils and Vegetation

Tutanning Nature Reserve (32°31'S, 117°23'E) is situated approximately 150 km south-east of Perth (Fig. 1) and covers an area of 2140 ha. The area has a mediterranean-type climate with an annual average rainfall of 454 mm, most occurring between April and August. Temperature varies between a mean maximum of 31.7°C in January and a mean minimum of 5.6°C in August.

Vegetation communities within Tutanning are closely related to soil type and topography, though

Nyagba (1976) noted that several soil boundaries transgress vegetation boundaries. The lateritic and granitic uplands are characterized by *Dryandra* and *Petrophile* shrublands with open woodlands of powderbark wandoo (*Eucalyptus accedens*). The breakaway faces containing sandy loams support brown mallet (*E. astringens*) or *E. accedens*, while lower gravel slopes support communities of wandoo (*E. wandoo*). Stands of sheoak (*Allocasuarina huegeliana*) characterize granite outcrops and gritty sand deposits (Nyagba 1976; CALM 1988).

Although kwongan vegetation in Tutanning represents only about 3 per cent of the reserve's area, it contains more than half the species recorded there (Brown and Hopkins 1983). The three kwongan sites examined in this study were situated on the midslope position. Soils showed a duplex profile with an A horizon comprising grey or brown sand and lateritic gravels to a depth of 10–25 cm, overlying a sandy clay B horizon.

Fire History

Fire has formed an integral part of Tutanning's history. Figure 2 shows the most recent fires on the reserve and the location of the three study sites in areas last burnt in 1932, 1940, and 1965. The 1965 site was also burnt by wildfire in 1940 and was subjected to some agricultural disturbance in the late 1950s. All fires are believed to have been escapes from clearing burns on adjacent land but their intensities are unknown. The 1965 site was also prescription burnt at moderate intensity in March 1990 after the present study was completed.

METHODS

Two sampling grids were placed at each site to enable within- and between-site variation in the data to be examined. Each grid comprised 16 pitfall traps spaced at 5 m intervals, which created a 4 x 4 matrix within a 15 m x 15 m square (Fig. 3). The contents of the four pitfalls in each corner were bulked to form four replicate samples (see later).

Habitat Assessment

Vegetation structure was measured at four permanently-marked habitat points located 1 m north, south, east and west of each pitfall trap (see Fig. 3). There were thus 16 habitat points per replicate sample. Structural attributes were also assessed over the entire grid.

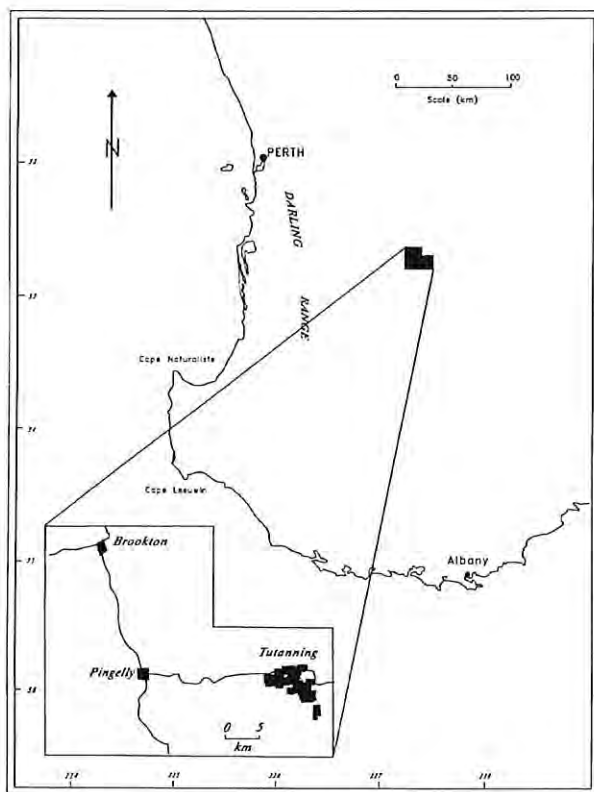


Figure 1. Map of south-west Western Australia showing the location of Tutanning Nature Reserve.

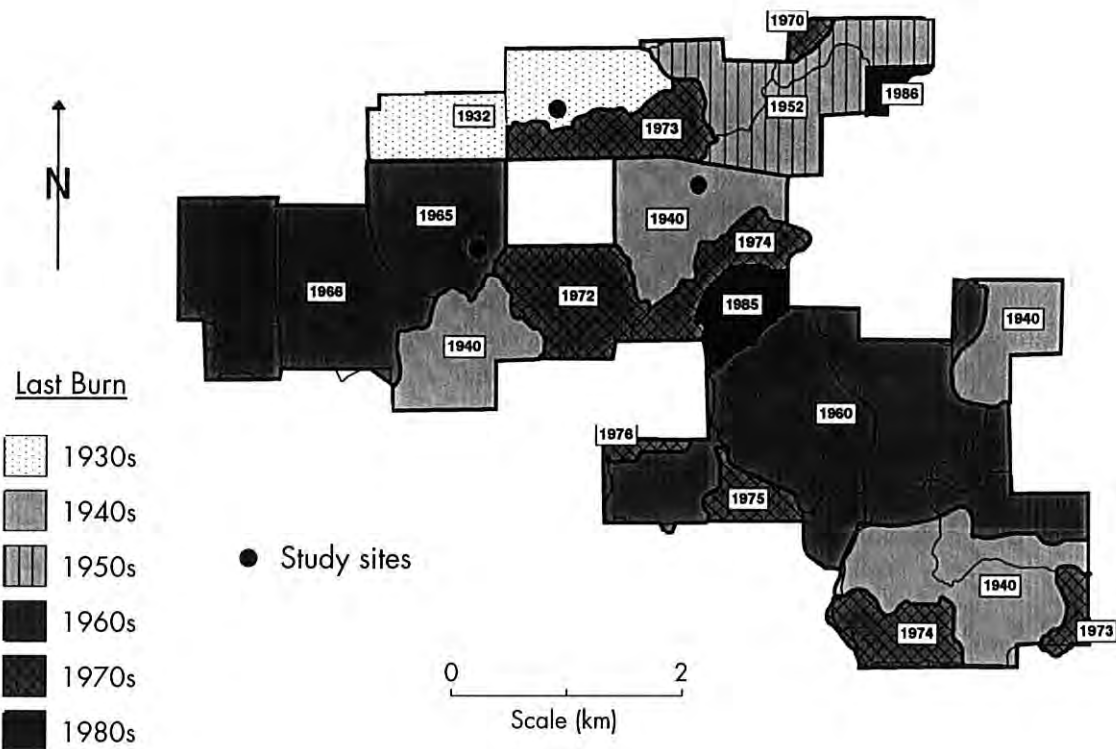


Figure 2. Tutanning Nature Reserve—fire history.

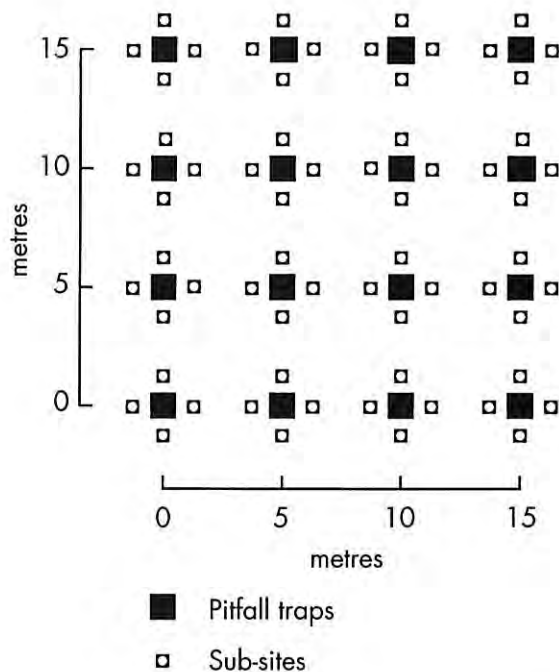


Figure 3. Layout of an invertebrate sampling grid.

(a) Habitat point measurements

The following attributes were recorded at each habitat point:

1. Leaf litter cover (percentage) in a 30 cm x 30 cm area scored as 0=absent, 1=1–25 per cent, 2=26–50 per cent, 3=51–99 per cent, and 4=100 per cent. The midpoint value of each percentage cover category was then used to calculate a percentage cover value per replicate using the following formula:

$$C = \frac{\sum fm}{16}$$

where: C = percentage cover value
 f = frequency of observation
 m = midpoint of percentage cover category

An analysis of variance and Scheffe test (Scheffe 1953; Zar 1984) were utilized to examine differences in percentage cover values between the three sites. A coefficient of variation (Zar 1984) was calculated from the mean percentage cover value of litter for each site.

2. Number of units of woody litter (dead/down branches or logs >5 mm diameter) bisected by a plane 50 cm each side of the habitat point. Woody litter diameter categories were 1=5–10 mm, 2=10–25 mm, and 3=>25 mm.

The frequency of occurrence of woody litter falling into these three categories was totalled for each

replicate (i.e. 16 habitat points) and log linear analysis of variance conducted on these data. A value of one was added to each frequency prior to statistical analysis to compensate for zero scores.

3. Number of touches of vegetation on 12 intervals of a vertically held levy rod. Height intervals (cm) used were: 1=0–12.5, 2=12.6–25, 3=26–50, 4=51–75, 5=76–100, 6=101–125, 7=126–150, 8=151–175, 9=176–200, 10=201–250, 11=251–300, 12=>300.

These data were used to calculate the horizontal and vertical distribution of foliage. The horizontal distribution of foliage was calculated by dividing the number of habitat points within each replicate which had a recorded contact by the number of habitat points within each replicate (16). This was then converted to a percentage and analysis of variance used to identify any site differences.

Site differences in the vertical distribution of foliage were examined by using log linear analysis of variance on the frequency of observations in each of the levy rod intervals. A value of one was added to the frequency of each of the classes to compensate for zero values. The vertical distribution of foliage was also assessed for each site by dividing the total number of plant contacts per levy rod interval by the number of rods which touched any vegetation. This was used to create a vertical profile of plant cover density.

4. Majority of touching vegetation in intervals 1–12 alive (1) or dead (0).

The percentage of live standing vegetation per site was calculated by tallying the number of 'alive' recordings per site, and dividing this by the number of habitat points which had a recorded contact. These data were transformed to natural logarithms and analysis of variance used on the transformed data to assess site differences.

5. Maximum height (cm) of living understorey vegetation (<3 m) within 20 cm of the levy rod. These data were subjected to an analysis of variance to examine differences between sites.

(b) Grid measurements

The following site characteristics were measured or estimated over each entire grid:

1. Percentage of total live foliage in each of five layers *viz.* 0–0.5 m, 0.6–1.0 m, 1.1–2.0 m, 2.1–5.0 m, and >5 m.
2. Percentage canopy cover (>2 m) derived from four readings (N,E,S,W) of a canopy densiometer taken over the centre of each grid.
3. Projected foliage cover (percentage) of understorey vegetation (<2 m).
4. Percentage of soil surface which is sand <2 mm, gravel 2–4 mm, gravel 5–10 mm, and gravel >10 mm.

Measurements of these site characteristics were then averaged for each site and standard errors calculated.

Floristics

Plant species falling within a radius of 5.64 m (100 m²) of the centre of each grid were recorded (presence/absence) by A. Hopkins and J. Harvey in early November 1988. Site differences in plant species richness were examined by using log linear analysis of variance.

Hierarchical Classification Analysis (HCA) of the presence/absence data used the average-linkage method and squared Euclidean distance measure (Gauch 1982). Similarity of the plant species composition of the six grids was examined using Sorensen's (1948) 'quotient of similarity' $QS=2c/a+b$ where a= the number of species in sample A, b= the number of species in sample B, and c= the number of species common to samples A and B. HCA was also performed on Sorensen's similarity index to examine whether these groupings differed from those identified by HCA on the presence/absence data.

Invertebrate Sampling

Pitfall traps were used to sample the invertebrate fauna. The limitation of this sampling technique is outlined by Southwood (1978) and Adis (1979). Although limited in its efficiency for comparing different community types and estimating absolute invertebrate populations, Southwood (1978) notes that this method can be used to assess the relative abundance of invertebrate populations in similar habitat types. Pitfall trapping was also selected because of its ease of operation.

Each pitfall trap consisted of a plastic cup (90 mm diameter, 110 mm deep), placed inside a sleeve of PVC piping, enabling pitfall traps to be set and removed with minimum disturbance to the surrounding soil and litter. This design of trap is similar to that described by Majer (1978a).

When in use, each pitfall was half-filled with Galt's solution which consisted of 5 per cent sodium chloride, 1 per cent potassium nitrate, 1 per cent chloral hydrate, a trace of glycerine, and the remaining 93 per cent water. Traps were operated for ten consecutive days for each of the months of May (autumn), July (winter), September and November (spring) in 1988, and January and February (summer) 1989. At the end of each ten-day sampling period the contents of the four pitfall traps in each corner of a grid were bulked to form four replicate samples. Each sample was labelled according to the sample time, site, and position on the grid. Samples were fine-sieved in the field and transferred from Galt's solution to 70 per cent ethanol. Sand-filled cups were placed in the PVC sleeves to close the pits.

Invertebrates were sorted to class level using a stereo microscope. Arachnids and insects were subsequently identified to order level, the latter with the aid of keys described in CSIRO (1970). The abundance of each taxonomic unit was then recorded for each sample. Hymenoptera Formicidae (ants), Coleoptera adults

(beetles), and Araneae (spiders) were placed in separate vials, the latter taxon being identified to species level. Collembola were not included in taxonomic sorting.

Statistical Analysis of Invertebrate Data

Computer analysis of the invertebrate abundance data employed the SAS and Systat programs. Log linear analysis of variance (AOV) was used on the abundance values to examine site preferences, time of sampling (months), and grid (within-site) differences in the invertebrate data. All abundances were raised by a value of one to compensate for zero abundances.

Scheffe's pairwise comparison tests were performed on those groups showing significant differences between months. These tests grouped together months with similar means. Similarly, Scheffe's tests were performed on those taxa showing significant differences between sites, identifying any site which had unusual abundance characteristics.

Statistical Analysis of Spider Data

Spiders were identified using the keys of Main (1980) and Mascord (1980) and with the assistance of Dr Louis Koch. A species reference collection was created for future research purposes. Community parameters calculated from the spider abundance data included: total number of individuals, species richness, diversity, and the evenness of species distribution calculated as: $J' = H' / \log_2 S$ where H' = the information content of a sample, and S = the number of species (Pielou 1975).

Similarity of species composition and abundance was examined using Hierarchical Classification Analysis (HCA), utilizing the average-linkage method to cluster groups and squared Euclidean distance as the distance measure (Gauch 1982). This analysis procedure used the totals for each of the eighteen month/site combinations, and then clustered these combinations so that similar communities were grouped together.

RESULTS

Habitat Assessment

(a) Habitat point measurements

Scheffe's pairwise comparisons revealed that the 1932 site had a significantly higher mean percentage litter cover value than the other sites ($p < 0.05$). Table 1 shows the mean percentage cover value, standard error and coefficient of variation for the three sites.

No significant site differences were found for woody litter abundance. However, there was a significant interaction effect between the three woody litter categories and sites ($F = 3.24$, $p < 0.05$), with the 1932 site scoring a much higher frequency of woody litter in the 5-10 mm diameter category (Fig. 4).

Sites did not differ significantly in their canopy

TABLE 1

Mean percentage litter cover values, standard errors and coefficient of variation (V) for the three sites ($n = 8$).

SITE	MEAN	STANDARD ERROR	V(%)
1932	48.8	4.3	24.9
1940	29.7	1.2	11.8
1965	32.0	2.4	21.6

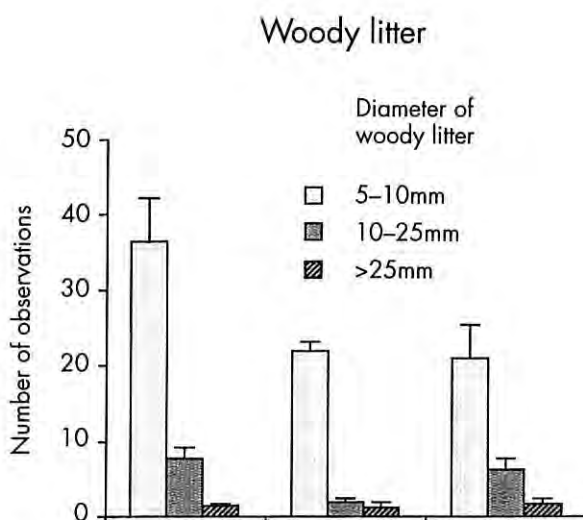


Figure 4. Site differences in the mean frequency of the three woody litter classes ($n = 8$). Standard errors shown as bars above the means.

cover, percentage live standing vegetation and frequency of vegetation 'touches'. The interaction effect between sites and levy rod interval was also not significant. Plant cover density profiles (Fig. 5) indicated that all three sites had very dense vegetation up to 0.4 m. The 1932 site showed the presence of emergents forming a sparse upper canopy at 1.4 m and above, whereas the 1940 and 1965 sites showed negligible vegetation cover above 1.4 m. However, analysis of variance did not find this difference to be significant.

Maximum vegetation heights were not significantly different between sites. However, differences between grids within sites were significant ($F = 3.16$, $p < 0.05$).

Plant cover density profiles

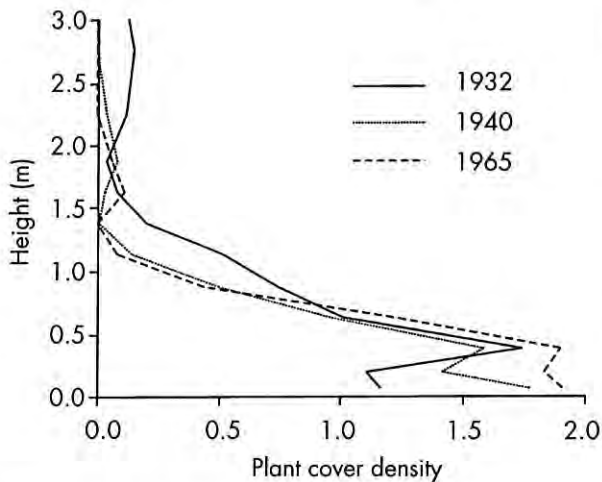


Figure 5. Vertical profiles of plant cover density.

(b) Grid measurements

The proportion (percentage) of total foliage in each of five layers (0–0.5 m, 0.6–1.0 m, 1.1–2.0 m, 2.1–5.0 m, and >5 m) was consistent with the results of the levy rod data. The percentage canopy cover (>2 m) and projected foliage cover of understorey vegetation (<2 m) also revealed trends that were consistent with the vertical structure measurements for each habitat point; these results are not discussed further.

Coarse soil fabric composition was similar for each of the three sites with over 70 per cent of coarse soil fabric comprising sand <2 mm.

Plant Floristics

Analysis of variance revealed that there was no significant difference in plant species richness between the sites.

Hierarchical Classification Analysis on the presence/absence floristic data (Fig. 6) indicated that the 1940 site separated first, and showed the least within-site similarity in plant species composition. The 1965 site showed the highest within-site similarity. Grouping of the grids on the basis of Sorensen's similarity index confirmed the trend revealed by the groupings from the presence/absence data.

Invertebrates

A total of 29 broad taxonomic invertebrate groups (class and order) was sampled: Annelida (earthworms), Scorpionida (scorpions), Pseudoscorpionida (pseudoscorpions), Opiliones (harvestmen), Araneae (spiders), Acarina (mites), Isopoda (woodlice), Diplopoda (millipedes), Chilopoda (centipedes), Thysanura (bristle-tails), Blattodea (roaches),

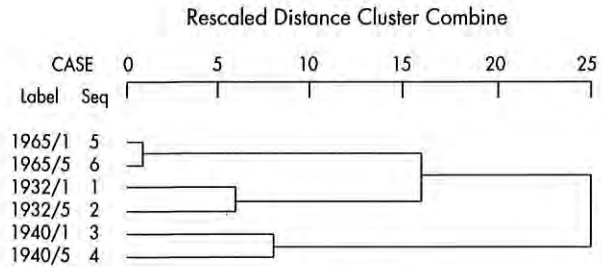


Figure 6. Dendrogram of grid groupings using Hierarchical Classification Analysis on floristic presence/absence data. The two grids are identified as 1 (replicates 1-4) and 5 (replicates 5-8).

Mantodea (mantids), Isoptera (termites), Dermaptera (earwigs), Orthoptera (grasshoppers and locusts), Phasmatodea (stick-insects), Psocoptera (book-lice), Hemiptera (bugs), Thysanoptera (thrips), Neuroptera adults (lacewings), Neuroptera larvae (antlions), Coleoptera adults (beetles), Coleoptera larvae, Diptera adults (flies), Diptera larvae, Lepidoptera adults (moths), Lepidoptera larvae, Hymenoptera Formicidae (ants), and Hymenoptera others (wasps and bees).

Formicidae accounted for over 60 per cent of the total number of invertebrates captured and this tended to mask trends in the other groups in the analyses. Thus, the data for total invertebrate abundance were analysed twice, once including Formicidae and once excluding this taxon.

With the Formicidae included, strong seasonal effects were shown for total invertebrates ($F=103.8$, $p<0.001$), with abundances peaking in summer (Fig. 7). Site differences were not apparent ($p>0.05$), but there was a significant interaction effect between months and sites ($F=4.1$, $p<0.001$) indicating variable seasonal trends between sites. Grids within sites differed significantly ($p<0.05$). Total invertebrate abundances showed similar site and seasonal trends when Formicidae were excluded, but showed a spring rather than a summer peak (Fig. 8). Furthermore, within-site differences (between grids) were no longer significant ($p>0.05$).

Only eight invertebrate taxa (Acarina, Araneae, Isoptera, Hemiptera, Coleoptera adults, Diptera adults, Hymenoptera Formicidae, and Hymenoptera (excluding Formicidae)) were sufficiently abundant to indicate within- and between-site differences, and to warrant the use of further statistical analysis. All eight taxa showed highly significant seasonal effects ($p<0.001$) and interaction (months/sites) effects ($p<0.001$).

However, only the Araneae, Diptera adults, and Formicidae showed site differences ($p<0.05$). Within-site differences were only significant for Formicidae ($p<0.05$).

For the Acarina, seasonality effects were apparent ($F=118.9$, $p<0.001$) with greatest abundance occurring in January and least in May and July (Fig. 9). No site preference was shown by this taxon, though the

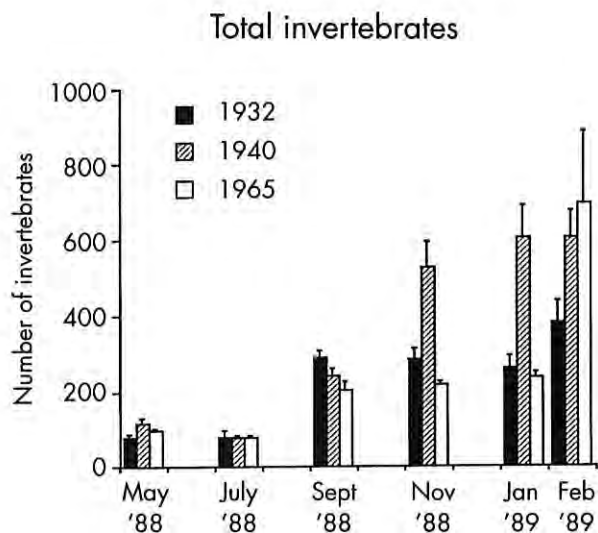


Figure 7. Ten-day means per replicate ($n=8$) for Total Invertebrates in the three study sites. Within-site standard errors shown as bars above the means.

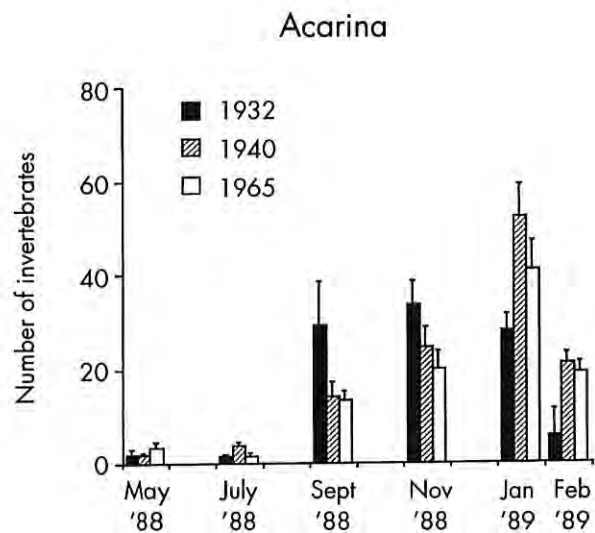


Figure 9. Ten-day means per replicate ($n=8$) for Acarina in the three study sites. Within-site standard errors shown as bars above the means.

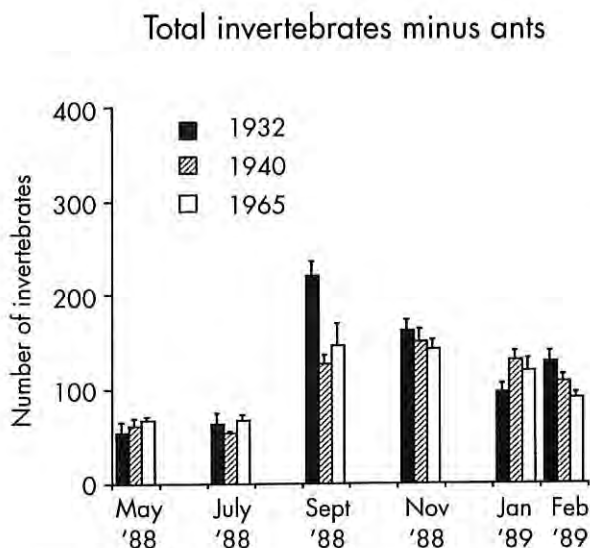


Figure 8. Ten-day means per replicate ($n=8$) for Total Invertebrates (excluding Formicidae) in the three study sites. Within-site standard errors shown as bars above the means.

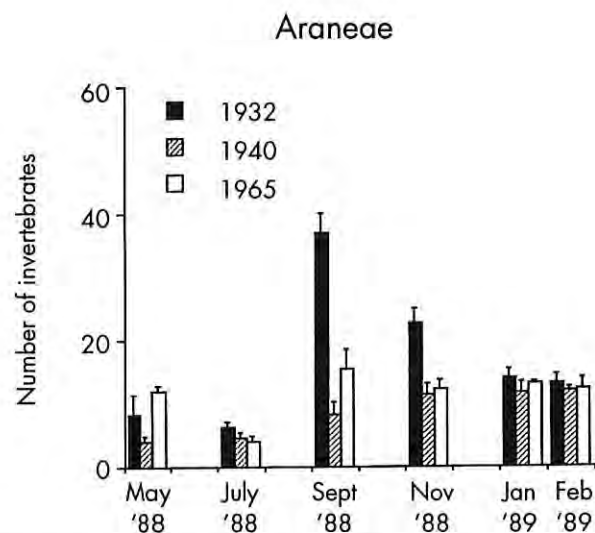


Figure 10. Ten-day means per replicate ($n=8$) for Araneae in the three study sites. Within-site standard errors shown as bars above the means.

interaction effect proved significant ($F=2.9$, $p<0.01$). Acarina abundance in the 1932 site increased sharply in September and peaked in November, whereas abundance in the 1940 and 1965 sites rose more gradually to peak in January.

Site and seasonality differences were apparent for Araneae ($F=13.0$, $p<0.05$; $F=26.1$, $p<0.001$, respectively; Fig. 10). Scheffé tests revealed that the 1940 site had a significantly lower abundance of spiders than the other two sites ($p<0.05$). The 1932 site had the highest abundance, but this fell just outside the

0.05 level of significance ($0.05<p<0.07$). Abundances in all sites were lowest in winter but rose during spring. Peak abundances varied between sites, giving a significant months/sites interaction effect ($F=5.6$, $p<0.001$), with the 1932 site clearly having the greatest abundance in spring. More detailed analyses of the spider data are given below.

Numbers of Isoptera were borderline for statistical analysis, but strong seasonal effects were apparent ($F=32.0$, $p<0.001$). This taxon was absent from the pitfall samples during May and July but numbers rose in

November and remained consistently high throughout summer (Fig. 11). Site differences were not apparent, although the interaction between months and sites proved to be highly significant ($F=5.0$, $p<0.001$) with the 1932 and 1940 sites peaking in February, and the 1965 site peaking in November.

Strong seasonal trends were also apparent for Hemiptera ($F=32.0$, $p<0.001$), with numbers peaking in September (Fig. 12). Although all three sites were consistent in their September peak, abundances remained higher in the 1940 and 1965 sites during the November and January samples. These different responses revealed a highly significant interaction effect between months and sites ($F=5.0$, $p<0.001$), despite there being no significant site differences.

Coleoptera adults showed highly significant seasonal trends ($F=44.2$, $p<0.001$). Numbers were highest in September and lowest in January (Fig. 13). Site differences were not apparent for this taxon. There was, however, a significant interaction between months and sites ($F=6.1$, $p<0.001$), there being a considerable difference in numbers between the 1940 and 1965 sites in the July sample.

Diptera adults showed seasonal and site effects ($F=38.7$, $p<0.001$; $F=12.8$, $p<0.05$; respectively). Abundance was greatest during spring and lowest during autumn and winter (Fig. 14). Scheffe tests revealed that numbers were significantly lower in the 1940 site. A significant interaction effect between months and sites was also apparent ($F=5.1$, $p<0.001$), the 1932 site peaking in abundance in September, and the 1940 and 1965 sites peaking in November.

Formicidae abundance showed very strong seasonality ($F=147.4$, $p<0.001$). Numbers captured were greatest during February and lowest during July (Fig. 15). The 1965 site was consistently lower in ant abundance than the other two sites for all but the February sample, when numbers peaked above the other two sites. This was reflected in the significant interaction effect between sites and months ($F=3.2$, $p<0.01$). Site preferences were also shown by this taxon ($F=10.2$, $p<0.05$), the 1940 site having a significantly higher abundance than the other two sites. Within-site differences were also apparent ($F=4.3$, $p<0.01$), indicating that localized effects within each site were influencing captures.

Seasonal effects were also apparent for Hymenoptera, excluding the Formicidae ($F=26.2$, $p<0.001$) with the lowest numbers being recorded in the May, July, and September samples (Fig. 16). No significant site differences were found, although there was a significant interaction between months and sites ($F=4.6$, $p<0.001$) indicating that numbers fluctuated markedly between sites at different sample times.

A summary of the seasonal and site trends revealed by analysis of variance on the transformed log data is shown in Tables 2 and 3. Table 4 provides a list of the principal invertebrate groups trapped, their main food source, the season they peaked in abundance, and their site preferences.

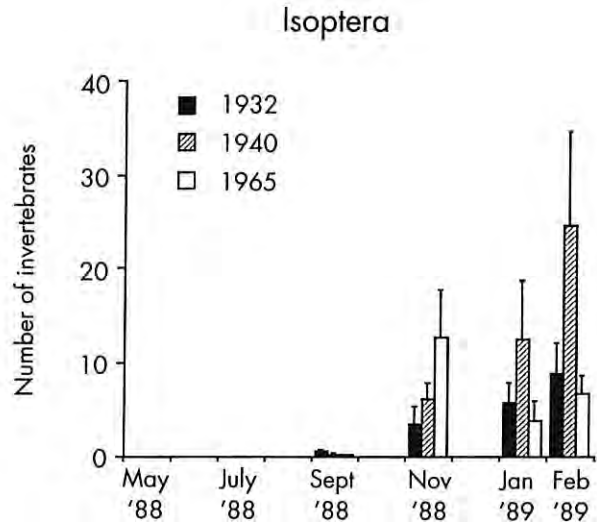


Figure 11. Ten-day means per replicate ($n=8$) for Isoptera in the three study sites. Within-site standard errors shown as bars above the means.

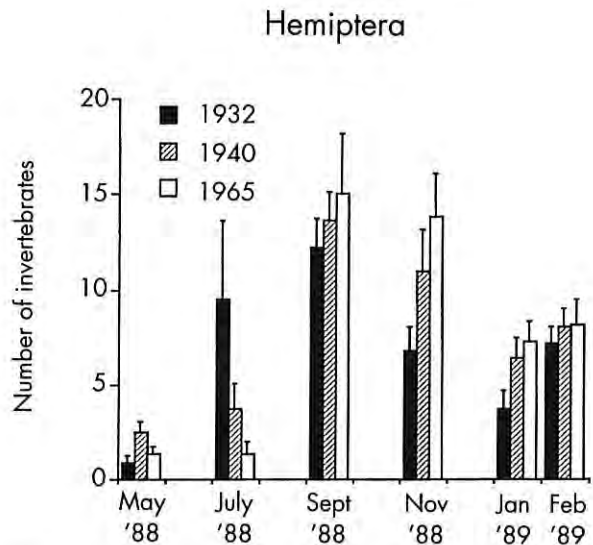


Figure 12. Ten-day means per replicate ($n=8$) for Hemiptera in the three study sites. Within-site standard errors shown as bars above the means.

Coleoptera – adults

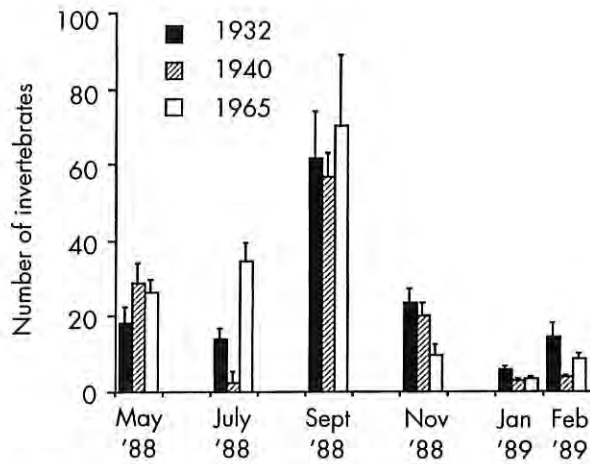


Figure 13. Ten-day means per replicate ($n=8$) for Coleoptera (adults) in the three study sites. Within-site standard errors shown as bars above the means.

Formicidae

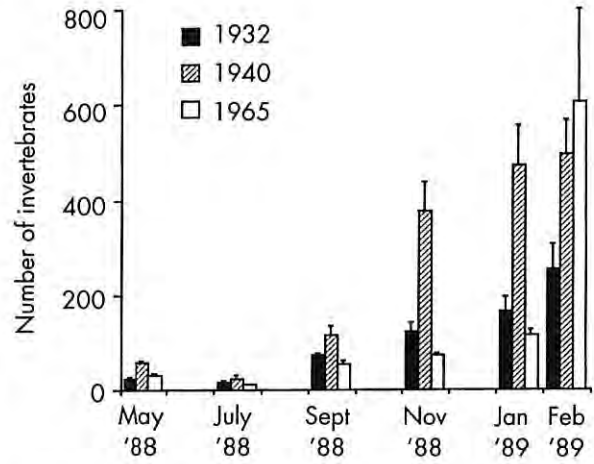


Figure 15. Ten-day means per replicate ($n=8$) for Formicidae in the three study sites. Within-site standard errors shown as bars above the means.

Diptera – adults

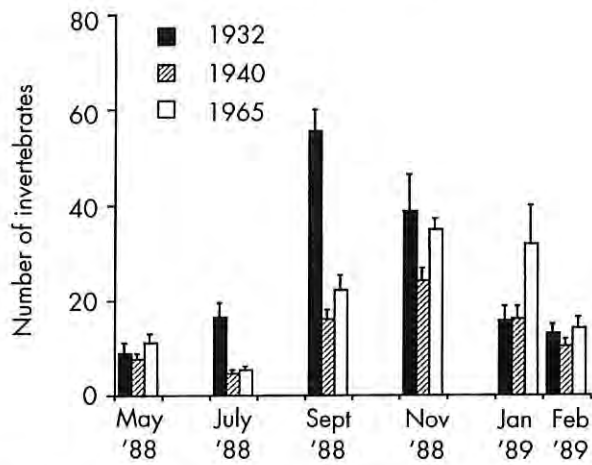


Figure 14. Ten-day means per replicate ($n=8$) for Diptera (adults) in the three study sites. Within-site standard errors shown as bars above the means.

Hymenoptera (excluding Formicidae)

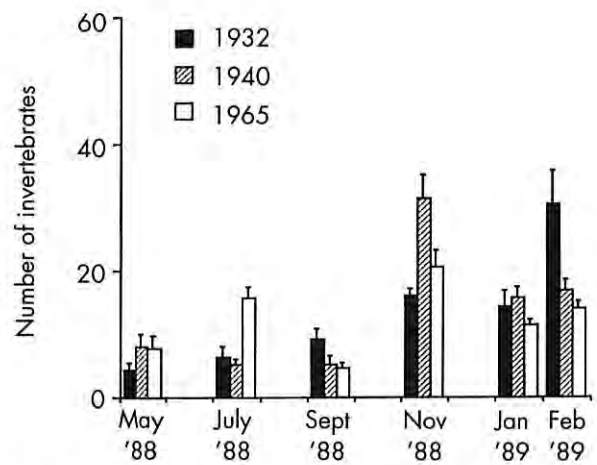


Figure 16. Ten-day means per replicate ($n=8$) for Hymenoptera (excluding Formicidae) in the three study sites. Within-site standard errors shown as bars above the means.

TABLE 2

Means and standard errors of invertebrate abundances per replicate according to month. The data are compared using log linear analysis of variance; ***P<0.001; NA, not analysed.

TAXON	MONTH												
	May '88		Jul '88		Sep '88		Nov '88		Jan '89		Feb '89		
	\bar{X}	S.E.	\bar{X}	S.E.	\bar{X}	S.E.	\bar{X}	S.E.	\bar{X}	S.E.	\bar{X}	S.E.	
Annelida	0.00	(0.00)	0.42	(0.18)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	NA
Arachnida													
Scorpionida	0.04	(0.04)	0.00	(0.00)	0.04	(0.04)	0.38	(0.13)	1.08	(0.29)	0.50	(0.18)	NA
Pseudoscorpionida	0.00	(0.00)	0.00	(0.00)	0.04	(0.04)	0.04	(0.04)	0.00	(0.00)	0.00	(0.00)	NA
Opiliones	0.08	(0.06)	1.88	(0.45)	0.42	(0.15)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	NA
Acarina	2.46	(0.52)	2.29	(0.46)	19.08	(3.52)	26.21	(2.66)	40.46	(3.78)	23.67	(2.32)	***
Araneae	8.13	(1.27)	5.00	(0.47)	20.21	(2.96)	15.54	(1.46)	12.96	(0.79)	12.46	(0.80)	***
Crustacea Isopoda	0.42	(0.15)	0.17	(0.10)	0.33	(0.12)	1.04	(0.31)	1.50	(0.39)	3.29	(0.62)	NA
Diplopoda	1.33	(0.33)	0.67	(0.18)	1.75	(0.47)	0.00	(0.00)	0.42	(0.12)	0.42	(0.13)	NA
Chilopoda	0.17	(0.10)	0.04	(0.04)	0.29	(0.14)	0.21	(0.10)	0.17	(0.08)	0.17	(0.08)	NA
Insecta													
Thysanura	0.00	(0.00)	0.00	(0.00)	0.25	(0.09)	0.88	(0.18)	1.46	(0.36)	0.58	(0.13)	NA
Blattodea	0.04	(0.04)	0.13	(0.09)	0.00	(0.00)	0.42	(0.17)	1.08	(0.24)	0.92	(0.22)	NA
Mantodea	0.00	(0.00)	0.00	(0.00)	0.04	(0.04)	0.00	(0.00)	0.04	(0.04)	0.13	(0.07)	NA
Isoptera	0.00	(0.00)	0.00	(0.00)	0.29	(0.11)	7.46	(1.95)	7.38	(2.32)	13.42	(3.79)	***
Dermaptera	0.46	(0.17)	0.50	(0.12)	0.79	(0.23)	0.38	(0.15)	0.33	(0.14)	0.71	(0.18)	NA
Orthoptera	1.42	(0.21)	1.21	(0.28)	2.42	(0.48)	2.17	(0.37)	1.83	(0.25)	2.13	(0.30)	NA
Phasmatodea	0.13	(0.07)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.04	(0.04)	0.04	(0.04)	NA
Psocoptera	0.08	(0.08)	0.00	(0.00)	0.17	(0.10)	0.08	(0.06)	0.38	(0.20)	0.04	(0.04)	NA
Hemiptera	1.58	(0.28)	4.88	(1.56)	13.58	(1.25)	10.46	(1.27)	5.79	(0.64)	7.75	(0.61)	***
Thysanoptera	0.04	(0.04)	0.08	(0.06)	1.13	(0.26)	9.63	(1.64)	0.50	(0.15)	0.42	(0.12)	NA
Neuroptera adults	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.04	(0.04)	0.17	(0.10)	0.00	(0.00)	NA
Neuroptera larvae	0.04	(0.04)	0.00	(0.00)	0.08	(0.06)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	NA
Coleoptera adults	24.42	(2.63)	23.50	(2.77)	62.88	(7.47)	17.75	(2.31)	3.83	(0.54)	8.92	(1.59)	***
Coleoptera larvae	2.13	(0.44)	1.75	(0.45)	1.75	(0.45)	0.17	(0.08)	0.25	(0.12)	0.25	(0.11)	NA
Diptera adults	9.21	(1.04)	8.71	(1.53)	31.29	(4.08)	32.50	(3.04)	21.17	(3.30)	12.54	(1.03)	***
Diptera larvae	0.83	(0.25)	0.25	(0.12)	0.29	(0.13)	2.92	(2.92)	0.00	(0.00)	0.42	(0.18)	NA
Lepidoptera adults	0.04	(0.04)	0.25	(0.11)	0.83	(0.29)	1.17	(0.25)	0.63	(0.24)	0.29	(0.13)	NA
Lepidoptera larvae	0.54	(0.15)	0.54	(0.19)	0.38	(0.16)	0.21	(0.08)	0.08	(0.08)	0.17	(0.10)	NA
Hymenoptera ants	35.92	(4.16)	16.83	(2.51)	80.08	(8.18)	188.88	(35.00)	250.96	(43.20)	450.88	(74.58)	***
Hymenoptera others	6.79	(1.00)	9.08	(1.29)	6.38	(0.88)	22.71	(2.00)	13.88	(1.13)	20.50	(2.32)	***
Total invertebrates	96.29	(7.22)	78.42	(5.79)	244.79	(13.46)	341.21	(36.87)	366.38	(46.43)	560.58	(73.92)	***
Total invertebrates (excluding ants)	60.38	(4.82)	61.58	(4.54)	164.71	(12.66)	152.33	(6.51)	115.42	(6.89)	109.71	(5.72)	***

TABLE 3

Means and standard errors of invertebrate abundances per replicate according to site. The data are compared using log linear analysis of variance; * $P < 0.05$; NS, not significant; NA, not analysed; # denotes significant differences between grids nested within sites, $P < 0.05$.

TAXON	SITE					
	1932		1940		1965	
	\bar{X}	S.E.	\bar{X}	S.E.	\bar{X}	S.E.
Annelida	0.04	(0.03)	0.02	(0.02)	0.15	(0.09) NA
Arachnida						
Scorpionida	0.38	(0.11)	0.25	(0.12)	0.40	(0.13) NA
Pseudoscorpionida	0.00	(0.00)	0.01	(0.01)	0.00	(0.00) NA
Opiliones	0.44	(0.14)	0.60	(0.25)	0.15	(0.05) NA
Acarina	20.85	(2.79)	19.69	(2.84)	19.03	(1.53) NS
Araneae	16.88	(1.74)	8.69	(0.72)	11.58	(0.83) *
Crustacea Isopoda	1.33	(0.26)	1.81	(0.37)	0.23	(0.07) NA
Diplopoda	1.06	(0.24)	1.04	(0.22)	0.19	(0.06) NA
Chilopoda	0.27	(0.09)	0.10	(0.04)	0.15	(0.05) NA
Insecta						
Thysanura	0.38	(0.10)	0.42	(0.11)	0.79	(0.20) NA
Blattodea	0.65	(0.15)	0.33	(0.10)	0.31	(0.11) NA
Mantodea	0.02	(0.02)	0.04	(0.03)	0.04	(0.03) NA
Isoptera	3.10	(0.84)	7.25	(2.29)	3.92	(1.13) NS
Dermaptera	0.69	(0.12)	0.29	(0.07)	0.60	(0.15) NA
Orthoptera	1.71	(0.22)	2.58	(0.28)	1.29	(0.15) NA
Phasmatodea	0.04	(0.03)	0.04	(0.03)	0.02	(0.02) NA
Psocoptera	0.06	(0.05)	0.25	(0.11)	0.06	(0.05) NA
Hemiptera	6.69	(0.92)	7.52	(0.78)	7.81	(1.04) NS
Thysanoptera	2.15	(0.73)	0.96	(0.26)	2.79	(0.90) NA
Neuroptera adults	0.00	(0.00)	0.10	(0.50)	0.00	(0.00) NA
Neuroptera larvae	0.02	(0.02)	0.02	(0.02)	0.02	(0.02) NA
Coleoptera adults	22.85	(3.51)	22.50	(3.00)	22.29	(4.59) NS
Coleoptera larvae	1.75	(0.32)	1.00	(0.18)	0.52	(0.16) NA
Diptera adults	24.67	(2.96)	13.10	(1.20)	19.94	(2.16) *
Diptera larvae	0.60	(0.16)	1.58	(1.46)	0.17	(0.06) NA
Lepidoptera adults	0.33	(0.09)	0.96	(0.22)	0.31	(0.08) NA
Lepidoptera larvae	0.25	(0.08)	0.38	(0.12)	0.33	(0.09) NA
Hymenoptera ants	108.40	(15.68)	255.75	(35.11)	147.63	(43.04) *#
Hymenoptera others	13.46	(1.63)	13.79	(1.56)	12.42	(1.00) NS
Total invertebrates	229.08	(20.65)	361.10	(38.87)	253.65	(43.32) NS#
Total invertebrates (excluding ants)	120.69	(9.72)	98.22	(8.66)	109.42	(5.31) NS

TABLE 4

Principal groups of invertebrates showing feeding habits, main peak in occurrence and site preferences. ¹O = Order, F. = Family; ²N.P. = No Preference.

CLASS	TAXON ¹	FEEDING HABITS	MAIN PEAK IN OCCURRENCE	SITE CHARACTERISTICS ²
Arachnida	O.Acarina	Various	Late spring, summer	N.P.
Arachnida	O.Araneae	Predators	Spring	Low in 1940 site high in 1932 site
Insecta	O.Isoptera	Wood and grass feeders	Late Spring, summer	N.P.
Insecta	O.Hemiptera	Sap suckers	Spring	N.P.
Insecta	O.Coleoptera (adults)	Various	Spring	N.P.
Insecta	O.Diptera (adults)	Various	Spring	Low in 1940 site
Insecta	O.Hymenoptera F.Formicidae	Predators, nectar and seed feeders	Summer	High in 1940 site
Insecta	O.Hymenoptera (excluding Formicidae)	Nectar feeders	Late spring, summer	NP

Spiders

The dendrogram created from Hierarchical Classification Analysis (HCA) on spider presence/absence data using the average-linkage method is shown in Figure 17. The 1932 September sample was included in the original analysis but is not shown on the dendrogram as it was markedly different from the other month/site combinations and caused compaction of the groups. The classification was truncated at the seven-group level because dichotomies beyond this level were fragmentary and contributed little to further understanding.

HCA grouped spider communities in relation to time of sampling rather than in relation to sites. The three kwongan sites had similar spider species composition during autumn and winter, but revealed

different community structure in spring and summer. These differences were particularly marked for the 1932 site during September (not shown) and November.

Table 5 provides a summary of the parameters of the spider fauna measured during the study. The number of individuals and species richness showed general peaks in spring with minimal values occurring in winter for all sites. Diversity was generally higher in late spring and summer. Overall, total numbers of spiders, species richness, and diversity were greatest in the 1932 site for the September to January samples.

Table 6 shows the total number of individual spiders according to family for each site and sampling period. No statistical analyses were conducted on these data. However, the more abundant families (notably the Clubionidae, Gnaphosidae, Salticidae, and Theridiidae) do show site and seasonal differences.

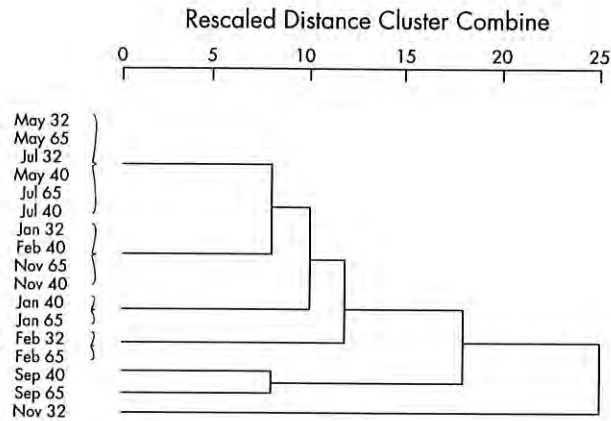


Figure 17. Dendrogram of sample groupings using Hierarchical Classification Analysis based on spider presence/absence data.

TABLE 5

Spider fauna parameters for the three sites for each sample period.

PARAMETER	MONTH					
	May '88	July '88	Sep '88	Nov '88	Jan '89	Feb '89
NUMBER OF INDIVIDUALS						
1932	67	50	294	182	112	105
1940	91	37	67	92	94	96
1965	37	33	124	99	105	98
SPECIES RICHNESS (S)						
1932	12	12	37	32	31	31
1940	17	14	15	23	26	25
1965	22	14	27	26	25	22
DIVERSITY (H)						
1932	2.092	2.027	2.718	2.832	2.977	2.853
1940	2.586	2.059	2.044	2.586	2.582	2.874
1965	2.249	2.391	2.653	2.762	2.560	2.369
EVENNESS (J')						
1932	0.842	0.816	0.753	0.817	0.867	0.831
1940	0.913	0.780	0.755	0.824	0.792	0.893
1965	0.728	0.906	0.805	0.848	0.795	0.767

TABLE 6

Total number of spider individuals trapped according to family, site and sample period.

FAMILY	MONTH					
	May '88	Jul '88	Sep '88	Nov '88	Jan '89	Feb '89
ARANEIDAE						
1932	2	0	28	7	3	3
1940	3	2	18	2	3	9
1965	6	0	15	10	6	4
CLUBIONIDAE						
1932	22	23	95	25	21	24
1940	3	4	18	19	18	5
1965	28	12	41	18	27	9
CTENIZIDAE						
1932	8	9	3	1	0	0
1940	10	12	0	0	0	4
1965	9	6	0	0	2	0
GNAPHOSIDAE						
1932	9	4	114	119	57	59
1940	3	16	26	59	47	57
1965	8	9	61	62	59	73
SALTICIDAE						
1932	0	1	30	18	18	11
1940	2	0	4	3	13	10
1965	0	1	3	7	8	8
THERICIDAE						
1932	22	13	10	0	0	0
1940	7	1	1	0	1	0
1965	42	4	1	1	1	1
THOMISIDAE						
1932	1	0	2	1	5	2
1940	1	1	0	1	1	0
1965	2	0	0	0	0	0
ZODARIIDAE						
1932	0	0	2	8	4	5
1940	0	0	0	5	7	9
1965	0	0	0	0	2	1

DISCUSSION

The major finding of this study was that invertebrate populations were similar for all three sites, implying that site history is not affecting invertebrate fauna composition in the longer term. Abundance differences were found for spiders, flies, and ants, however, and these appear to be closely related to differences in floristic composition and litter cover between sites.

Neither plant species richness nor floristic composition appear to be related to time since fire. Although all three sites were similar in terms of their plant species richness, the 1940 site showed a different plant floristic composition. This supports the findings of Brown and Hopkins (1983) who found that only a very small percentage of floristic variability in kwongan could be attributed to time since fire. However, Brown and Hopkins (1983) also suggested that floristic differences were possibly linked to differences in soil type. In this study soil types were consistent for all three sites and no differences were found in coarse soil fabric composition. Differences in soil chemical properties, however, were not assessed. Hence, the different floristic composition of the 1940 site appears to be related to environmental differences which were beyond the scope of this study.

The presence of a high litter cover and an abundance of woody litter at the 1932 site may be a result of long-term fire exclusion from this area. In his study of *Banksia* woodland, Bamford (1986) found that the litter layer became more structurally complex the greater the time after fire. The litter layer of the 1932 site, however, also appears to be influenced by the presence of emergent sheoaks (*Allocasuarina huegeliana*). This accounts for the high abundance of woody litter (5-10 mm diameter) recorded at this site. The 1932 site is only about 4 ha and is enclosed by sheoak woodland whereas the 1940 and 1965 sites are larger (each about 10 ha) and bordered by wandoo (*Eucalyptus wandoo*) on one side with sheoak on the other. The size and location of the 1932 site in relation to the surrounding woodland areas, and the prolonged absence of fire at this site, appear to be favouring the encroachment of sheoaks into the kwongan, thus affecting the structural composition of the litter layer.

Influence of Fire on Ants, Flies, and Spiders

The abundance of ants did not appear to be consistently influenced by fire history. Majer (1978b) made similar observations based on a study of different land-use types at Dwellingup, WA. The higher abundance of ants in the 1940 site may be related to this site's different floristic composition, or again, to environmental factors which were beyond the scope of this study. Higher captures in the 1940 site may also be related to the presence of one or two numerically dominant species, though an analysis of ants at a species

level was beyond the scope of this study.

By contrast, the abundances of spiders and flies were significantly lower at the 1940 site. The low abundance of spiders appears to be related to litter differences and this is addressed below. It is unusual, however, that the pitfall sampling method (designed to effectively sample only the epigeic invertebrate fauna) should capture enough flies to identify a statistically significant difference between sites. The lower abundance of flies in the 1940 site may be related to the greater within-site variability in floristic composition. However, more detailed vegetation and invertebrate data, using a variety of sampling techniques, would be required to substantiate this explanation.

Spider abundance, species richness and diversity all identified the 1932 site as being markedly different from the other two sites, particularly during spring (September, November). These characteristics of the spider fauna may be related to the high cover and variability of litter and the ecotonal nature of this site which allows spiders representative of both kwongan and sheoak to exist. The latter effect may arise through the presence of emergent sheoaks within the kwongan, which enable the spiders to cast webs and forage over a greater area than in the other two sites. The sheoaks also shade the ground, reducing desiccation and hence facilitating foraging and migration. They may also be influencing the structural diversity of the litter layer (by dropping branches and twigs), thereby providing this site with a greater array of microhabitats.

Scope and Limitations of the Study

Limitations in the pitfall sampling technique have been outlined by several authors (Southwood 1978; Adis 1979; Majer 1981). Pitfall traps sample epigeic invertebrates only and show a bias towards the more mobile taxa (Majer 1981). In this study, the dominance of ants in pitfall captures highlights this bias. Another criticism of the pitfall trapping method is that activity, as measured by the traps, may not necessarily reflect abundance (Southwood 1978; Majer 1981). In the case of ants, surface activity peaked in summer as revealed by the large number of ants captured during this time. However, during winter and autumn when captures were low, large numbers may still have been present at the nests. The proximity of pitfall traps to ant nests was also not assessed and this may have contributed to the significant difference in ant abundance between grids nested within sites, as well as possibly influencing site preferences. Given these limitations in the pitfall trap sampling method, site and seasonal differences in abundances of ants and total invertebrates (including Formicidae) need to be considered cautiously.

A further limitation of this study is that the season of burn and fire intensity are unknown for each of the sites. Weather at the time of the burn greatly influences fire intensity. Furthermore, as Hobbs and Atkins (1988) note, most woodland and shrub communities vary greatly in their array of standing vegetation and

litter composition. Weather and variability in fuel quantity and distribution combine to cause a high degree of spatial variation in fire intensity, but no data on these factors were available for this study.

To date, studies of invertebrate populations in the drier areas of Australia have been minimal, with the exception of Greenslade (1979, 1981), Edmonds and Specht (1981), and Majer (1985). There have also been no reported invertebrate community studies conducted in kwongan vegetation. A critical examination of the results of this study in the light of other research is therefore limited. Given these comparison limitations, this paper should be viewed as identifying areas where a considerable amount of research is still required.

This study utilized space-for-time substitution (SFT) to examine successional aspects of invertebrate community structure in semi-arid vegetation. Though limited in its ability to address disturbance ecology questions (Pickett 1989), SFT is of considerable value when carried out in conjunction with longer-term experimental studies. It is anticipated that this study will serve as a baseline for longer-term work at Tutanning examining the effects of prescribed burning on invertebrate (and vertebrate) communities.

CONCLUSIONS

Invertebrate populations peaked during spring, and were lowest during late autumn and early winter. The soil and litter invertebrate populations were very similar for all three sites and showed no evidence of long-term disturbance effects.

Ant abundance was highest in the 1940 site and this was possibly related to a different floristic composition at this site. This difference in floristic composition appeared to be related to environmental factors beyond the scope of this study.

The 1932 site showed a higher abundance and different community structure of spiders during spring. This was attributed to leaf litter cover and woody litter abundance providing an array of microhabitats, the presence of emergent sheoaks providing a wider foraging area, and the proximity of the kwongan to neighbouring sheoak woodland.

Leaf litter cover and woody litter abundance was greatest in the 1932 site. This site also showed the greatest variability in leaf litter cover. These litter characteristics appear related to both time since fire and the presence of emergent sheoaks.

ACKNOWLEDGEMENTS

The authors wish to thank Jonathan Majer, David Mitchell, Angus Hopkins, Judith Harvey, Matthew Williams, Siva Ganeshanandam, Louis Koch, Anthony Postle and Andrew Gunell for their assistance and advice during this study. Jim Rolfe's computer graphics skills produced Figures 1, 2, 6 and 17. Ian Abbott, Graham Hall and Jonathan Majer commented on a draft of the manuscript.

REFERENCES

- Abbott, I. (1984). Changes in the abundance and activity of certain soil and litter fauna in the jarrah forest of Western Australia after a moderate intensity fire. *Australian Journal of Soil Research* **22**, 463–469.
- Adis, J. (1979). Problems of interpreting arthropod sampling with pitfall traps. *Zoologischer Anzeiger Jena* **202**, 177–184.
- Bamford, M.J. (1986). The dynamics of small vertebrates in relation to fire in banksia woodland near Perth, Western Australia. Ph.D. Thesis. Murdoch University, W.A.
- Beard, J.S. (1976). An indigenous term for the Western Australian sandplain and its vegetation. *Journal of the Royal Society of Western Australia* **59**, 55–57.
- Bell, D.T., Hopkins, A.J.M. and Pate, J.S. (1984). Fire in the kwongan. In Pate, J.S., and Beard, J.S. (Eds.) *Kwongan: Plant Life of the Sandplain*. University of Western Australia Press, Perth. pp.178–204.
- Brown, J.M. (1989). Regional variation in kwongan in the central wheatbelt of south-western Australia. *Australian Journal of Ecology* **14**, 345–355.
- Brown, J.M. and Hopkins, A.J.M. (1983). The kwongan (sclerophyllous shrublands) of Tutanning Nature Reserve, Western Australia. *Australian Journal of Ecology* **8**, 63–73.
- CALM (1988). *Tutanning Nature Reserve: Interim guidelines for fire protection*. Department of Conservation and Land Management, Perth. Unpublished.
- Campbell, A.J. and Tanton, M.T. (1981). Effects of fire on the invertebrate fauna of soil and litter of a eucalypt forest. In Gill, A.M., Groves, R.H. and Noble, I.R. (Eds.) *Fire and the Australian Biota*. Australian Academy of Science, Canberra. pp. 215–241.
- CSIRO (1970). *The Insects of Australia*. Melbourne University Press, Melbourne.
- Edmonds, S.J. and Specht, M.M. (1981). Dark Island heathland, South Australia: faunal rhythms. In Specht, R.L. (Ed.) *Ecosystems of the World 9B—Heathlands and Related Shrublands—Analytical Studies*. Elsevier, Amsterdam. pp. 15–27.
- Gauch, H.G. (1982). *Multivariate Analysis in Community Ecology*. Cambridge University Press, Sydney.
- Greenslade, P. (1979). Microarthropods as indicators of range condition. 2nd Biennial Conference, Australian Rangeland Society, Adelaide.

- Greenslade, P. (1981). Survival of Collembola in arid environments: observations in South Australia and the Sudan. *Journal of Arid Environments* **4**, 219–228.
- Hobbs, R.J. and Atkins, L. (1988). Spatial variability of experimental fires in south-west Western Australia. *Australian Journal of Ecology* **13**, 295–299.
- Hopkins, A.J.M. (1985) Fire in the woodlands and associated formations of the semi-arid region of south-western Australia. In Ford, J. (Ed.) *Fire Ecology and Management of Western Australian Ecosystems*. WAIT Environmental Studies Group Report No.14. Western Australian Institute of Technology, Perth. pp. 83–90.
- Hutson, B.R. (1985). Rates of litterfall and organic matter turnover at three South Australian indigenous forest sites. *Australian Journal of Ecology* **10**, 351–359.
- Hutson, B.G. and Veitch, L.G. (1983). Mean annual population density of Collembola and Acari in the soil and litter of three indigenous South Australian forests. *Australian Journal of Ecology* **8**, 113–126.
- Hutson, B.R. and Veitch, L.G. (1985). Relationships between litterfall rate, litter mass and decomposition rate in *Eucalyptus* forests in southeastern Australia. *Australian Journal of Ecology* **10**, 443–450.
- Koch, L.E. and Majer, J.D. (1980). A phenological investigation of various invertebrates in forest and woodland areas in the south-west of Western Australia. *Journal of the Royal Society of Western Australia* **63**, 21–28.
- Lamont, B.B. (1984). Special modes of nutrition. In Pate J.S. and Beard J.S. (Eds.) *Kwongan: Plant Life of the Sandplain*. University of Western Australia Press, Perth. pp. 236–245.
- Main, A.R. (1987). Management of remnants of native vegetation—a review of the problems and the development of an approach with reference to the wheatbelt of Western Australia. In Saunders, D.A., Arnold, G.W., Burbidge, A.A. and Hopkins A.J.M. (Eds.) *Nature Conservation: The Role of Remnants of Native Vegetation*. Surrey Beatty and Sons, Sydney. pp.1–13.
- Main, B.Y. (1980). *Spiders of Australia*. The Jacaranda Press, Milton, Queensland.
- Majer, J.D. (1978a). An improved pitfall trap for sampling ants and other epigeic invertebrates. *Journal of the Australian Entomological Society* **17**, 261–262.
- Majer, J.D. (1978b). Preliminary survey of the eigaic invertebrate fauna with particular reference to ants, in areas of different land-use types at Dwellingup, Western Australia. *Forest Ecology and Management* **1**, 321–334.
- Majer, J.D. (1981). The role of invertebrates in minesite rehabilitation. Forests Department of Western Australia Bulletin No. 93.
- Majer, J.D. (1985). Fire effects on invertebrate fauna of forest and woodland. In Ford, J. (Ed.) *Fire Ecology and Management in Western Australian Ecosystems*. WAIT Environmental Studies Group Report No. 14. Western Australian Institute of Technology, Perth. pp. 103–106.
- Mascord, R. (1980). *Spiders of Australia*. A.H. & A.W. Reed Pty. Ltd., Sydney.
- Neumann F.G. and Tolhurst, K. (1991). Effects of fuel reduction burning on epigeal arthropods and earthworms in dry sclerophyll eucalypt forest of west-central Victoria. *Australian Journal of Ecology* **16**, 315–330.
- Nyagba, L. (1976). Soils and landforms in a semi-arid lateritic terrain south West Australia (The Tutanning Reserve). M.Sc. Thesis. University of Western Australia, Perth.
- Pickett, S.T.A. (1989). Space-for-time substitution as an alternative to long-term studies. In Likens, G.E. (Ed.) *Long-term Studies In Ecology: Approaches and Alternatives*. Springer-Verlag, New York. pp 110–135.
- Pielou, E.C. (1975). *Ecological Diversity*. Wiley & Sons, New York.
- Postle, A.C. (1989). Variations in soil and litter invertebrate populations within the northern Jarrah forest. Ph.D. Thesis. University of Western Australia, Perth.
- Raison, R.J., Woods, P.V. and Khanna, P.K. (1986). Decomposition and accumulation of litter after fire in sub-alpine eucalypt forests. *Australian Journal of Ecology* **11**, 9–19.
- Scheffe, H. (1953). A method of judging all contrasts in the analysis of variance. *Biometrika* **40**, 87–104.
- Sorensen, T.A. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of vegetation on Danish commons. *Kongelige Danske Videnskabernes Selskab Biologiske Skrifter* **5**, 1–34.
- Southwood, T.R.E. (1978) *Ecological Methods*. 2nd Edn. Chapman and Hall, London.
- Springett, J.A. (1976). The effect of prescribed burning on the soil fauna and on litter decomposition in Western Australia. *Australian Journal of Ecology* **1**, 77–82.
- Zar, J.H. (1984). *Biostatistical Analysis*. 2nd Edn. Prentice-Hall International, New Jersey.