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# Spiders, Spinifex, Rainfall and Fire: Long-term changes in a community of desert spiders

Peter R. Langlands<sup>a1</sup>

email: don\_quixote@mail.com

Karl E. C. Brennan<sup>a</sup>

email: k.brennan@curtin.edu.au

David J. Pearson<sup>b</sup>

email: davidp@calm.wa.gov.au

<sup>a</sup> Department of Environmental Biology, Curtin University of Technology, GPO Box U 1987, Perth, WA 6845, Australia

<sup>b</sup> Department of Conservation and Land Management, PO Box 51, Wanneroo WA 6946, Australia

Corresponding author

Peter R. Langlands

63 Helena Street, Guildford, Perth, WA, 6055, Australia

email: don quixote@mail.com

Phones + 61 8 9279 1808

Fax + 61 8 9274 5220

Present address

<sup>1</sup> 63 Helena Street, Guildford, Perth, WA, 6055, Australia

#### **Abstract**

Critical to conserving biodiversity in arid regions is understanding the spatial and temporal patterning of biota. For mammals and reptiles, rainfall and fire are important forces determining these patterns. Few studies have considered these factors on invertebrates and even fewer over an extended time frame. Spiders were pitfall trapped over 14 years (1989 - 2003) as part of an experimental fire study in the Great Victoria Desert, Western Australia. Spider species composition showed marked changes between seasons. Rainfall appears the dominant driving force in this system with less pronounced fire effects. Greater rain during February, March and April a year before March samples were collected was correlated with increased spider abundance. Given the highly seasonal structure of spider assemblages, favourable weather during mating and juvenile development may increase recruitment the following season. Spider abundance was also positively correlated with total rain six and twelve months before sampling. Bottom-up effects of rain may cause pulses of productivity and increased spider abundance. Spider species richness increased with rain three months before sampling. This result may be explained by more juveniles moulting to adults or alternatively an increase in adult survival.

Keywords: Fire; Rainfall; Invertebrates; Araneae; Arid conservation; Bottom-up effects

#### INTRODUCTION

Over 70 % of Australia's landmass is arid or semi-arid (Williams and Calaby, 1985). In these regions European settlement and the introduction of exotic species have had detrimental effects on the biota. One third of the mammal species within the Critical Weight Range are now extinct (Burbidge and McKenzie, 1989). Also, many birds, reptiles and plants are threatened (James et al., 1995). To conserve biodiversity in arid Australia knowledge of the spatial and temporal patterning of native biota is needed (James et al., 1995). With the exception of vertebrates, knowledge of most taxa in these regions is poor. Invertebrates dominate species diversity (Wilson, 1987), yet quantitative data on their distribution and abundance and the factors influencing it are

largely unknown. Greater knowledge of invertebrates in arid Australia is needed to understand these ecosystems. Spiders may also provide an additional monitoring tool for conservation (Churchill, 1997; Clausen, 1986). Indeed, interest in assessing the biodiversity of spiders in semi-arid and arid regions has increased in recent years (e.g. Harvey et al., 2000; Main et al., 2000).

There are many potential environmental factors that may affect spider diversity and abundance. Rainfall and fire are believed to be major determinants of temporal and spatial patterns of various native biotas in arid Australia (Stafford Smith and Morton, 1990). Fire is a natural perturbation, but its impact is largely dependent upon future rain (which may be very unpredictable) and the subsequent timing of fires (Saxon, 1984). Nothing is known of the impact of both rainfall and fire on arid spider assemblages. It is of particular interest given increasing emphasis on re-establishing anthropogenic fire regimes for nature conservation (Burrows and Abbott, 2003; Griffin and Friedel, 1985; Saxon, 1984).

In arid Australia typically low rainfall is interrupted by occasional and unpredictable heavy rains from cyclones (Williams and Calaby, 1985). Rain can be intense, 210 mm or 80 % of the median annual rainfall may fall in 24 hours. Several such events may occur in a single year and may recharge water tables which sustain the unusually high standing biomass of perennial plants (Stafford Smith and Morton, 1990). Due to aridity decomposition rates are slow. High perennial biomass and slow decomposition means that fires play a major role in nutrient cycling (Griffin and Friedel, 1985; Stafford Smith and Morton, 1990).

Aborigines in central Australia used fire for hunting, cooking, signalling, clearing land and providing warmth (Gould, 1971; Jones, 1969; Kimber, 1983). Frequent and extensive use of fire created a mosaic of areas with different post-fire ages (Burrows and Christensen, 1991; Latz and Griffin, 1978). The removal of Aboriginal people in recent times has caused a significant alteration to the fire regime. Today, fire is less frequent with occasional large wildfires burning thousands of square kilometres (Allan and Southgate, 2002; Latz and Griffin, 1978). Clearly, understanding the effects of fire on flora and fauna are important for successful management aimed at conserving biodiversity.

The response of invertebrates to fire is poorly documented compared to vertebrates, particularly mammals and reptiles (Friend, 1995). A review of the consistency of responses by invertebrates following fire in Australia (increases, decreases or no change in abundance) found wide variation among studies (Friend, 1995). One group displaying consistent responses was spiders (Araneae).

Spiders are ideal bio-indicators as they are diverse and abundant predators. Therefore changes in spider faunas are likely to reflect ecological impacts at lower levels in the food chain (Churchill, 1997; Clausen, 1986). Both hunting and web building spiders are sensitive to changes in habitat structure (Duffy, 1962; Riechert and Gillespie, 1986). Likewise, litter depth and structure affects species richness and composition of spiders (Uetz, 1991). Spiders are also an important food source for vertebrates, and are a favoured prey of many insectivorous marsupials (Fisher and Dickman, 1993).

Many studies have examined the response of spiders to fire (Andersen and Muller, 2000; Abbott et al., 2003; Brennan et al., 2003; Huhta, 1971; Little, 1993; Merrett, 1976; Moretti, 2002; York, 1999). However, few studies have followed the effects of fire with regular sampling for more than five years and most studies lack pre-fire data. No studies are from arid environments. Sampling over extended periods is important for invertebrate communities. The influence of location, season and yearly variation can often outweigh that of fire (Friend, 1995). Indeed, studies have shown that spider abundance is related to rain before sampling (Huhta, 1971; Polis et al., 1998; Spiller and Schoener, 1995). Similarly, the detection of fire effects was contingent on rain before sampling for beetles (Blanche et al., 2001). Rainfall was assumed to have a positive relationship with spider abundance following that found on desert islands (Polis et al., 1998).

In 1987 the Western Australian Department of Conservation and Land Management (CALM) initiated a study to investigate the effects of experimental fires on the flora and fauna of the Great Victoria Desert. A multi-taxa approach was used with mammal, reptile and invertebrate communities pitfall trapped, and vegetation assessed. Presented here are the results for spiders collected during the study over the period 1989 to 2003. This study focussed on four questions: 1) Does spider

abundance and species richness decrease with fire?; 2) Does increased rain in the months before sampling increase spider abundance and species richness?; 3) Does spider species composition change due to fire and can this be related to post-fire changes in ground cover?; and 4) How does rainfall prior to sampling influence spider species composition?

#### **METHODS**

# Study area

The study area was located in Queen Victoria Spring Nature Reserve (QVSNR), approximately 215 km ENE of Kalgoorlie and 25 km NNE of Queen Victoria Spring (30° 14' S, 123° 41' E)(Fig. 1). The reserve is lies on the south-western edge of the Great Victoria Desert (GVD), which covers over 420,000 km² (Shephard, 1995) across southern Australia (inset Fig. 1). The reserve covers over 2,726 km² and is managed by CALM.

Rainfall is highly variable and unreliable in both summer and winter. During autumn and winter, cold fronts crossing the south-west of Western Australia may bring sporadic showers (Pearson, unpublished). Summer rainfall results from thunderstorms from the north-west or occasionally from cyclonic rains. Tropical cyclones crossing the north-west coast can cause heavy rain and localised flooding (Pearson, unpublished). Summer days are hot and can reach temperatures in excess of 45 °C. Winter days are mild but nights are cold, with records as low as -7 °C (Pearson unpublished).

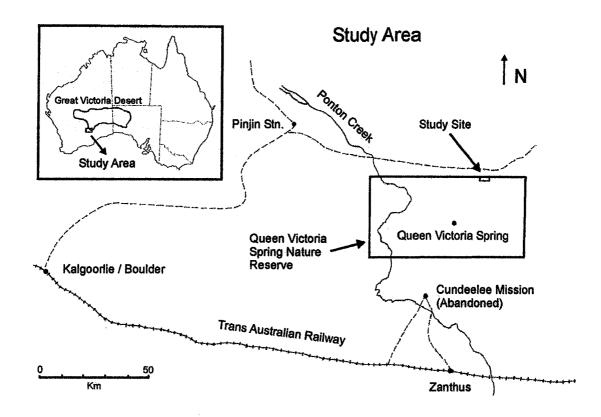


Fig. 1. Location of study area. Inset: Extent of Great Victoria Desert

# Study site

Unlike many countries, deserts in Australia are mostly well vegetated. The vegetation of QVSNR reflects its location close to the boundaries of three biogeographic regions. The reserve is situated between the Murchison and the Great Victoria Desert regions and immediately to the south is the Coolgardie region (IBRA, see Thackway and Cresswell, 1995). The rich and varied flora consists of 552 species of vascular plants (Pearson, unpublished). All plots in the study area had similar vegetation, consisting predominately of marble gum *Eucalyptus gongylocarpa* Blakely, mallee *E. youngiana* F. Muell. and spinifex *Triodia desertorum* (C.E. Hubb.) Lazarides. This vegetation type is typical of the GVD and is consistent with Beard's (1974) category of "tree steppe". Prior to experimental burning the study site had not been burnt for over 30 years. Five plots were sampled for invertebrates. Each plot was 25 hectares (500 x 500 m). The layout of plots and location of vertebrate and invertebrate pitfall trapping grids is shown in Fig. 2.

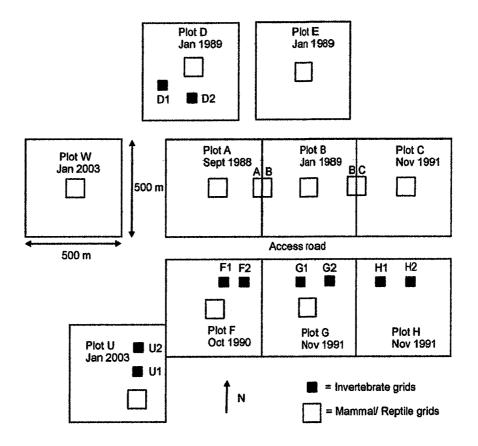


Fig. 2. Layout of plots  $(500 \times 500 \text{ m})$  and location of vertebrate and invertebrate pitfall trapping grids. Time of plot fires indicated. Not to scale.

# **Burning treatments**

Four invertebrate plots were established in 1989 (plots D, F, G and H) with plot U established in 1992 (Table 1). The three treatments were; severe intensity summer wildfire, 'patchy' spring fire and long unburnt controls (> 30 years since fire). Funding constraints and flooding of the access road for 18 months after a cyclone limited sampling. The months most sampled were March (8 samples), December (3) and October (3) with one sample in January and September (Table 1). All plots were burnt by a wildfire in January 2003 and monitoring has ceased.

Table 1

Plots sampled for invertebrates, with dates of pitfall sampling and burning. The number of times burnt is indicated (0 being long unburnt samples). All dates were sampled for spiders except those marked with a dash.

Sampling	Plot D	Plot F	Plot G	Plot H	Plot U
Dates	Burnt	Burnt	Burnt	Burnt	(Control)
	Jan 1989	Oct 1990	Nov 1991	Nov 1991	Not Burnt
9-14 Dec 1989	1	0	0	0	<b>I</b>
13-17 Mar 1990	1	0	0	0	-
24-28 Oct 1990	1	-	0	0	-
5-10 Jan 1991	1	1	0	0	-
21-26 Mar 1991	1	1	0	0	-
14-19 Sept 1991	1	1	0	0	-
12-16 Dec 1991	1	1	1	1	-
24-29 Mar 1992	1	1	1	1	-
22-27 Oct 1992	1	1	1	1	0
12-17 Dec 1992	1	1	1	1	0
10-15 Mar 1993	1	1	1	1	• 0
26-31 Mar 1994	1	1	1	1	0
29/30 Mar-2 Apr	1	1	1	1	0
24-29 Oct 1998	1	1	1	1	0
22-26/27 Mar 2000	1	1	1	1	0
20-23 Mar 2003	2	2	2	2	1

Plot D was burnt on 21 January 1989 in a summer fire. During the fire, winds were on average 10 kmhr<sup>-1</sup> but with gusts to 25 kmhr<sup>-1</sup>. The ambient temperature was 36°C. The average rate of spread of the fire was 750 mhr<sup>-1</sup>. No pre-fire samples were available for this plot as the fire deviated from the planned plot, jumping an external firebreak. Plot F was burnt on 25 October 1990 in a spring fire. During the fire, wind speed was variable (10-20 kmhr<sup>-1</sup>) and the ambient temperature was 26°C. The average rate of spread was 520 mhr<sup>-1</sup>.

Plots G and H were originally set up as long unburnt controls. Both were burnt by a wildfire that entered the reserve from the north-west in November 1991, jumping over firebreaks around the study area. In the strictest sense, plots G and H are pseudoreplicates, because they were burnt by the same wildfire (Hurlburt, 1984). However, Van Mantgem et al. (2001) argue that pseudo-replicates are appropriate in studies of the specific effects of a particular fire. Although they caution that using pseudo-replicates remains inappropriate for generalised effects of fire (Van Mantgem et al.,

2001). Here plots G and H are treated as true replicates, as the questions asked were restricted to the specific effects of these fires. After G and H were burnt, new controls were established, and plot U was sampled from October 1992 until the completion of the study.

#### Rainfall

Rainfall was monitored by a remote weather station located at the study site from 1989 to 1992. Total monthly rainfall records for 1988 to 2002 were obtained from the Bureau of Meteorology Perth, for the closest recording station (Edjudina 110 km NNW). Rainfall at QVSNR and Edjudina was significantly correlated (r = 0.848, p < 0.01, n = 33). Therefore, rain data from Edjudina was used for analyses as it covered the entire study period.

#### **Invertebrate sampling**

Each plot contained two invertebrate grids with 16 pitfall traps in a 4 x 4 layout, with 5 m between each trap. Each grid was approximately 100 m from the plot edge and 50 m apart. The two grids within each plot are pseudo-replicates (Hurlbert, 1984) and are treated as such. Pitfall traps were plastic cups (8.5 cm surface diameter, 5.8 cm base diameter, 11 cm deep with white interior). These were placed inside a sleeve of PVC piping left permanently in the ground, thus allowing easy re-sampling and the reduction of soil disturbance caused by digging-in traps (see Greenslade, 1973). Traps were half filled with Galt solution (Main, 1976). Galt solution can lead to deterioration of specimens and its future use is not recommended. Traps were usually set for 5 days, but occasionally for 3 or 4 days (Table 1). Individual pitfall traps were bulked for storage. Four pitfall traps from each corner were sieved and combined into one vial. This created four vials per grid, and a total of eight vials for each plot at each sampling date.

#### Spider identification

Invertebrates collected were sorted to Order and stored in 80 % ethanol. Adult spiders were identified to family using Raven et al. (2002). Species level identifications were based on differences in genitalia (male palp or female epigyny). As most species of spiders in Australia are undescribed (Yeates et al., 2004), specimens were assigned morphospecies codes where no name could be found (Oliver and Beattie, 1993, 1996a, 1996b). Females were matched to males were possible using colour pattern and body size (females larger). Taxonomists from the Western Australian Museum (WAM), Queensland Museum and University of Western Australia verified a reference collection of species and morphospecies. All specimens are lodged with the WAM (registration numbers T48343-T49300, T52350-T53178). The abundance of juvenile spiders was recorded, but they were not identified.

#### Vegetation assessment

Ground cover was assessed using point transects with a wheelpoint apparatus (Griffin, 1989). During sampling, contact with plants or other habitat factors by the wheel spokes was recorded at each metre interval. Categories were bare ground, leaf litter, spinifex and other plant species. Four to five transects, each approximately 50 m, were performed per plot running north-south parallel to vertebrate pit lines. At each plot the value of each ground cover category was summed and expressed as a percentage of total points recorded.

# Data analysis

As matching male and female morphospecies together can be difficult (Brennan et al., in press; Jocque and Baehr, 1992), spider data were analysed twice; once with males and once with males and females. The sexes used are indicated and for brevity both analyses are not presented where similar results were obtained.

It was necessary to standardize spider abundance as the number of days of pitfall trapping varied between samples. Abundance was standardized to three days (the shortest sampling period during the study). Species richness is used here to indicate the number of spider species and was standardized by individual-based rarefaction (Colwell and Coddington, 1994; Gotelli and Colwell, 2001). The program Primer 5 (Primer-E, 2001) was used for rarefaction and multivariate analyses.

# Analyses of fire effects

Plots with pre-fire data (F, G and H) were used to examine differences before and after burning. The mean species richness and abundance for pre-fire samples for each site were calculated. The difference between the pre-fire means and post-fire samples are shown against time since fire. The use of differences rather than actual values is thought superior to other techniques, as it helps to standardize response variables allowing easier comparison between plots (Van Mantgem et al., 2001).

A data matrix of spider species abundance by samples was constructed. A similarity matrix between samples was then calculated on fourth-root transformed data using the Bray-Curtis similarity co-efficient (Bray and Curtis, 1957). Non-metric multidimensional scaling (NMDS) with 100 iterations was used to create two-dimensional representations of similarity matrices. Accuracy of ordinations was assessed using group-average cluster analysis (Clarke, 1993). A two-way analysis of similarity (ANOSIM) was performed using 1000 permutations to test for significant differences between a priori factors of SAMPLING MONTH and YEAR. The factor SAMPLING MONTH had levels January, March, September, October and December. Levels for YEAR were the individual years between 1989 and 1994 plus 1998, 2000 and 2003. Interaction effects cannot be established directly by two-way ANOSIMs, however, repeating paired one-way ANOSIMs between each group can indirectly establish interaction effects (Clarke, 1993). Significance of pair-wise ANOSIMs between factor levels was set at  $\alpha \le 0.01$ , to reduce possible family-wise error due to multiple comparisons (Quinn and Keough, 2002).

Similarity percentages (SIMPER) were performed for groups (factor levels) found to be significantly ( $\alpha \le 0.01$ ) different from each other. This allowed identification of

species important in characterising and discriminating between groups. Cumulative contributions were cut arbitrarily at 40 %. The dissimilarity to standard deviation ratio of the SIMPER analysis can be used to indicate species that are consistently good discriminators between groups (Clarke, 1993). The three species with the highest dissimilarity to standard deviation ratios were identified as good discriminators for each pair-wise comparison.

The BIO-ENV function was used to explore the relationship between spider species composition and ground cover. Eight March samples were used from plots that had matching vegetation data. Prior to analysis, the ground cover categories (bare ground, leaf litter, spinifex and other plants) were checked for autocorrelation using the Spearman correlation coefficient. The ground cover categories spinifex and bare ground showed strong negative autocorrelation (r > -0.8) and were therefore used separately (Clarke and Ainsworth, 1993). The habitat matrix was constructed using Euclidean distance. Correlation between the habitat and spider matrices was assessed using a Mantel's test with the Spearman correlation coefficient.

# Analyses of rainfall effects

Rainfall prior to March samples was tested for correlation with species richness and abundance. Total rainfall for three (Dec-Feb), six (Sept-Feb) and twelve (Mar-Feb) months prior to sampling were chosen for analysis arbitrarily. As spiders are highly seasonal (Humphreys, 1988), rain during March and a month either side (February to April) from the year prior to sampling was also used. These rainfall periods were tested for correlation (n = 7) with spider species richness and abundance. Only plots sampled for the whole length of the study were used (plots D, F, G and H). Analyses were performed with SPSS (SPSS Inc, 2001) using the Spearman correlation coefficient. Species composition for March samples and rain falling three, six and twelve months prior to sampling were assessed for correlation. The BIO-ENV procedure was used as described above.

#### RESULTS

A total of 3,529 spiders were collected, of which 62.5 % (2,213) were adults and the remaining 37.5 % (1,323) juveniles. The adult spiders represented 29 families, 67 genera and 186 species and morphospecies. The majority of adult spiders were males (1,921; 87 %; 133 species).

#### Influence of fire on spider abundance and species richness

Spider abundance and species richness changed after burning, however assigning causality is difficult. Plots F, G and H show a similar pattern in the abundance of males following fire (Fig. 3a). Abundance decreases one to two years after fire followed by an increase in abundance between years two to four. However, a similar pattern also occurs seven to ten years post-fire. This result suggests sampling year is important for spider abundance. It is important to note that plot F was burnt one year earlier than plots G and H. Hence, the decreases seven and eight years post-fire are from the same sampling date (March 1998). Species richness (males) following fire shows no clear pattern with different responses between plots (Fig. 3b). Changes in abundance and species richness of males and females are similar to that of males.

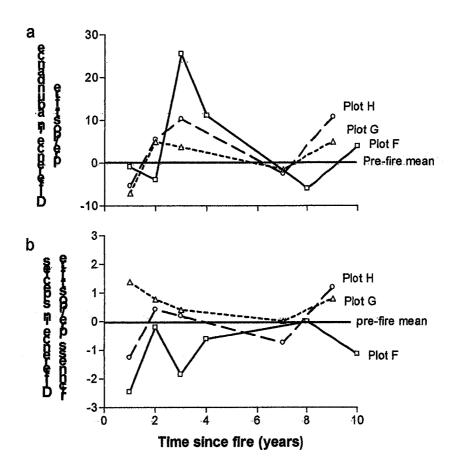


Fig. 3. Difference between the pre-fire mean (spider abundance or species richness) and post-fire samples with time since fire (years). Data are for March samples following a single fire at plots with pre-fire samples (F, G and H) for: (a) the difference in abundance (males) standardized for three days and (b) the difference in species richness (males) rarefied to 10 individuals.

#### Influence of rainfall on spider abundance and species richness

Yearly spider abundance in March samples was highly variable with some years catching twice the number of spiders. Sampling years with high spider abundance coincided with years of increased rain prior to sampling. Rain between February and April a year prior to sampling showed the strongest correlation with abundance of males and females (r = 0.912, p = 0.002) and males (r = 0.808, p = 0.014) (Fig. 4a). The abundance of males and females was also correlated with rainfall six (r = 0.692, p = 0.042) and twelve (r = 0.743, p = 0.028) months before sampling (Fig. 4b). Despite a similar pattern for male abundance, rain six and twelve months before sampling was

not significant. There was no relationship between rain three months before sampling and abundance of males and females or males. Spider abundance and rainfall show less congruence during the first few sampling years (1990-1992).

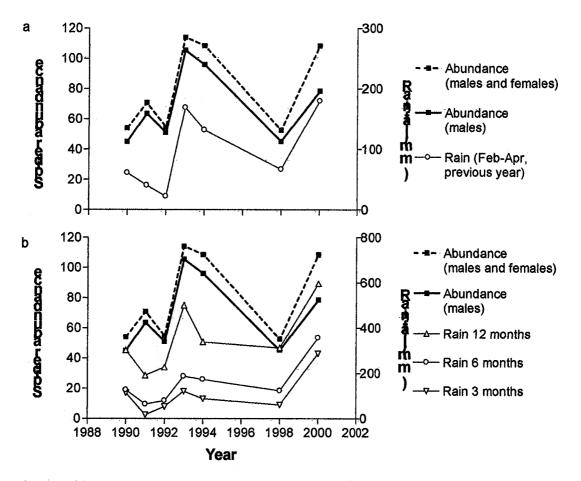


Fig. 4. Spider abundance (males and females, males) for March samples following a single fire compared with rainfall (mm) for (a) rainfall during February to April the previous year and (b) three, six and twelve months prior to sampling. Abundance for plots D, F, G and H combined for each sampling date and standardized to three trapping days.

Greater rainfall in the three months before sampling coincided with an increased number of male spider species (r = 0.678, p = 0.047) (Fig. 5). Species richness for males was not significantly correlated with rainfall six or twelve months before sampling. Although the pattern of spider species richness for males and females is very similar (Fig. 5), there was no significant correlation with any period of rainfall.

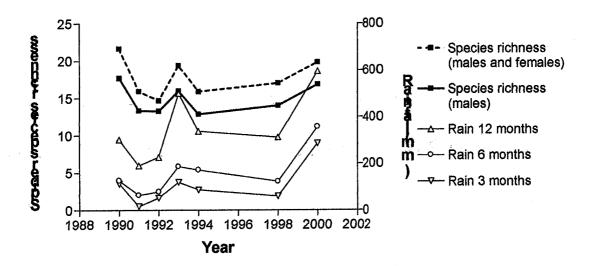


Fig. 5. Spider species richness (males and females, males) with rainfall (mm) three, six and twelve months prior to March samples (except 2003). Plots D, F, G and H combined for each sampling date and rarefied to 53 individuals for males and 61 individuals for males and females.

# Influence of fire on spider species composition

Ordination of all samples (by NMDS) shows a strong influence of seasonality on species composition (Fig. 6). March, October and December samples each form tight, distinct clusters. January and September, with only one sample each, are similar to December and October samples. Sampling month has a stronger influence on species composition than burning. Unburnt samples are more similar to burnt samples from the same sampling time, than unburnt samples from other sampling times (Fig. 6). Ordination of males and females gave a similar result.

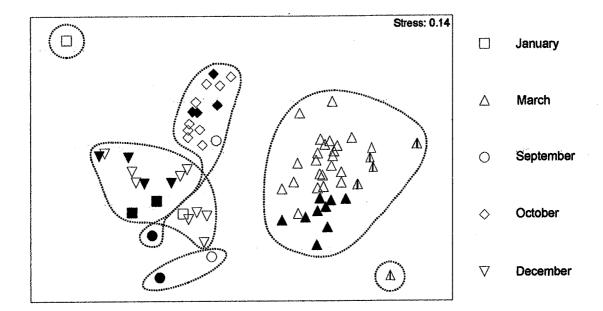


Fig. 6. Ordination of similarity in species composition of male spiders. Different shaped symbols represent different months of sampling. Pre-fire samples are depicted by shaded symbols and post-fire by unshaded symbols. March samples after the January 2003 wildfire are depicted by triangles with a vertical line. Dashed lines represent groups with > 20 % similarity from cluster analysis.

Analysis of similarity (ANOSIM) showed species composition for male spiders differed significantly with sampling month (R-statistic 0.829, p < 0.01) and year (R-statistic 0.355, p < 0.01). There was no interaction effect between sampling month and year. All pair-wise comparisons for sampling months March, October and December were significant (Table 2). SIMPER analysis of pair-wise comparisons between sampling month showed that many species were collected in only one sampling time (Table 3). For example when March and October were compared, Zodariidae *Habronestes* sp. 09 was found only in March. Conversely, Zodariidae *Minasteron* sp. 03 and Nemesiidae *Kwonkan* sp. 06 were collected in high abundances in October but were low or absent in March (Table 3).

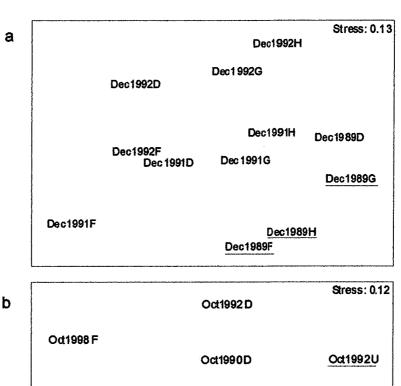
Table 2 R-statistics for pair-wise comparisons between sampling months, from a two-way ANOSIM of SAMPLING MONTH versus YEAR (all samples). \*\* denotes a significant difference at  $p \le 0.01$ . Groups too small for pair-wise analyses are represented by a dash.

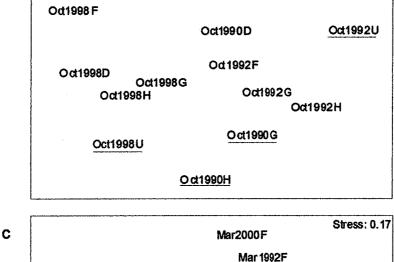
Season	January	March	September	October	December
January					
March	0.672				
September	0.406	1.000			
October	-	0.991**	-		
December	0.323	0.986**	0.688	0.764**	

Within sampling months, spider species composition differs slightly between long unburnt and burnt samples. There is some separation between unburnt and burnt samples in March, October and December (Fig. 7). More rigorous testing of this data was precluded owing to the few replicates available.

Table 3: Individual species contributions to differences in taxonomic composition between pair-wise comparisons of sampling month, from SIMPER analysis of all samples. Data were standardized and fourth root transformed. Mean abundance for each season is labelled a or b. Only significant ( $p \le 0.01$ ) pair-wise combinations are shown. For each pair-wise comparison the three best discriminating species (highest dissimilarity to standard deviation ratio) are in **bold** font.

Pairwise							
				Mean	Dissimilarity/	Contribution	contribution
comparison	Species	Ø	Ω	dissimilarity	as	(%)	(%)
7	Zodariidae Habronestes sp. 09 (macedonensis group)	8.62	0.00	7.55	1.93	7.84	7.84
Mar (a) vs Dec (b) N	Miturgidae genus 1 sp. 12	0.00	2.23	6.57	1.77	6.82	14.66
Average Z	Zodariidae Habronestes sp. 08 (macedonensis group)	2.86	0.00	6.42	1.39	6.67	21.32
dissimilarity	Zodariidae <i>Minasteron</i> sp. 03	0.03	3.92	6.00	1.05	6.23	27.56
=96.31% Z	Zodariidae <i>Cavasteron</i> sp. 05	0.19	2.46	5.55	1.46	5.76	33.31
7	Zodariidae Habronestes sp. 13 (pictus group)	3.14	00.00	4.37	0.94	4.54	37.85
<i>6.</i> -	Nemesiidae <i>Anam</i> e sp. 04	0.00	0.92	3.83	96.0	3.97	41.83
N	Zodariidae Habronestes sp. 09 (macedonensis group)	8.62	0.00	5.54	2.14	5.94	5.94
Mar (a) vs Oct (b) Z	Zodariidae Habronestes sp. 08 (macedonensis group)	2.86	0.00	4.60	1.60	4.93	10.86
Average 2	Zodariidae <i>Minasteron</i> sp. 03	0.03	10.46	4.39	1.62	4.71	15.57
dissimilarity	Nemesiidae <i>Kwonkan</i> sp. 06	0.00	2.00	4.39	2.03	4.70	20.27
=93.26%	Lycosidae Hogna sp. 12 (pexa group)	0.00	5.54	4.06	1.50	4.36	24.63
	Miturgidae genus 1 sp. 05	0.84	10.31	3.82	1.52	4.09	28.72
.7	Zodariidae Habronestes sp. 13 (pictus group)	3.14	0.00	3.18	1.03	3.41	32.14
.7	Zodariidae Cavasteron sp. 05	0.19	3.54	2.74	1.17	2.94	35.07
**	Satticidae Grayenulla sp. 05	0.14	1.85	2.67	1.33	2.86	37.93
fee	Nemesiidae <i>Anam</i> e sp. 02	0.00	1.38	2.62	1.37	2.80	40.74
	Miturgidae genus 1 sp. 05	0.00	10.31	5.79	5.39	7.05	7.05
Dec (a) vs Oct (b)	Nemesiidae <i>Kwonkan</i> sp. 06	0.00	2.00	4.51	2.07	5.48	12.53
Average	Lycosidae <i>Hogna</i> sp. 12 (pexa group)	0.00	5.54	4.18	1.52	5.08	17.61
dissimilarity	Miturgidae genus 1 sp. 12	2.23	0.85	3.74	1.59	4.55	22.16
=82.22%	Zodariidae <i>Minasteron</i> sp. 03	3.92	10.46	3.45	1.10	4.20	26.36
17	Zodariidae Cavasferon sp. 05	2.46	3.54	3.06	1.16	3.72	30.08
-	Nemesiidae <i>Aname</i> sp. 04	0.92	0.00	2.87	1.01	3.50	33.58
<u>*-</u>	Nemesiidae <i>Anam</i> e sp. 02	0.00	1.38	2.69	1.39	3.27	36.85
•	Salticidae <i>Grayenulla</i> sp. 05	0.15	1.85	2.68	1.31	3.26	40.11





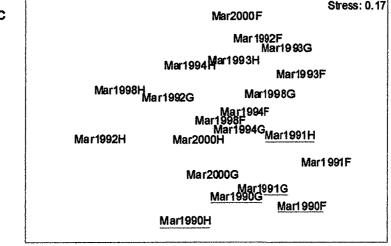


Fig. 7. Non-metric multi-dimensional scaling of similarity in spider species composition (males) for (a) December samples (b) October samples and (c) March samples (plots F, G and H only without 2003). Unburnt samples are underlined.

# Influence of fire on vegetation and its relation to changes in spider species composition

Summer fires cause substantial changes to the landscape with most vegetation removed. All spinifex is burnt and 80 % of the ground is bare ten months after the summer fire in plot D (Fig. 8a). Spinifex is typically 20 to 40 % of aerial cover in unburnt vegetation in this area (D. Pearson, unpublished data). Even 11 years after fire, the slow regeneration of spinifex means that it contributes only 10 % of aerial cover. Leaf litter increases rapidly in the first two years after fire through the falling of dead leaves and woody debris. The cover of other plants (fire ephemerals and re-sprouting shrubs) increases rapidly in the four years immediately post-fire (Fig. 8a).

Spring fires are less severe with frequent patches left unburnt, but the composition of ground cover is still considerably altered by the appearance of fire ephemerals (Fig. 8b). In plot G, spinifex cover decreases from 36 % pre-fire to only 1 % ten months post-fire. Spinifex recovers faster when compared to summer fires with 19 % cover within nine years. The return of spinifex corresponds to decreases in spider abundance seven years after fire. Bare ground increases by 10 % after the spring fire and returns to pre-fire levels within nine years. Leaf litter cover shows little change over the sampling period, with a slight increase after fire (Fig. 8b). Other plants increase rapidly from 9 % cover before fire to 29 % ten months after fire and remain 23 % of ground cover thereafter.

Although ground cover changes markedly after fire, it shows poor correlation with spider species composition. The category bare ground shows best correlation with spider species composition for March samples (r = 0.548). The next best correlation was the combination of bare ground and other plant species (r = 0.531). Although spinifex was inter-correlated with bare ground (r > -0.8), its correlation with spider species composition was less (r = 0.339).

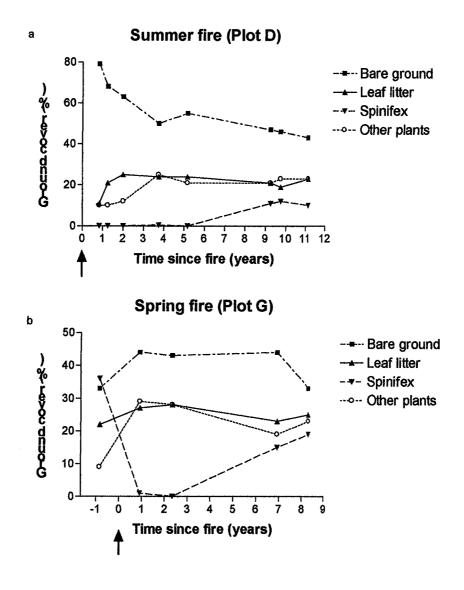


Fig. 8. Change in the proportion of ground cover after (a) a summer fire (Plot D) and (b) a spring fire (Plot G). Arrows indicate fires.

# Influence of rainfall on spider species composition

Spider species composition for March samples shows no correlation with rain prior to sampling. These data are not considered further.

#### **DISCUSSION**

# Influence of fire on spider abundance and species richness

In this study spider abundance decreased immediately after fire, but the interpretation of results was confounded by yearly variation. Decreases in species richness and abundance immediately after fire have been reported for spiders in several studies in more mesic environments (Abbott et al., 2003; Andersen and Muller, 2000; Brennan et al., 2003). However, rarely have studies been able to consider long-term changes. Interestingly, a similar decrease in spider abundance occurred seven to eight years after fire. This may indicate that sampling year is an important factor determining spider abundance. Variation in environmental conditions between years may explain these changes. An alternative mechanism to explain this is the decline of post-fire opportunistic plants, which may provide more nutritious foliage for a variety of spider prey (Whelan, 1995). After seven to eight years spinifex cover and shrubs again dominate the plant communities and the foliage may be less palatable for some invertebrate herbivores.

The impact of fire on spider species richness differed greatly between plots with no apparent pattern. This may indicate that the various experimental fires had limited impacts on species richness of spiders. Alternatively, a larger study may be required to untangle the impact of fire from that of other environmental factors. For invertebrates, changes between seasons and yearly variation can outweigh those of fire (Friend, 1995). Also, the intense summer fire treatment lacked pre-fire data, making interpretation tenuous. It is likely that higher intensity summer fires have greater impacts on the spider fauna, due to the total removal of understorey vegetation and greater heat during the fire.

#### Influence of rainfall on abundance and species richness

More rain during February to April a year prior to March samples coincided with increases in spider abundance. The strong seasonality of spiders may partly explain this trend. Species composition of spiders appears highly dependent on sampling month.

This suggests that a large proportion of spider species caught in March are reproducing at this time, with males being more active. Being soft bodied, spiders are sensitive to water loss. The most vulnerable stages of their life cycle are egg development, dispersal of young and mating activities (Main, 1981). Favourable weather (increased rain but not flooding) may reduce the potential risk of desiccation for males when searching for mates. Female fecundity, juvenile survival and recruitment may also be increased with greater rainfall during February to April.

Increased rainfall for periods six and twelve months before sampling was also positively correlated with spider abundance. Rainfall in arid Australia is likely to cause pulses of productivity, stimulating plant growth, animal activity and reproduction (James et al., 1995). A bottom-up effect from rainfall may be responsible for increased spider abundance. In other environments bottom-up effects of rain on spiders are known (Dondale and Binns, 1977; Polis et al., 1998; Spiller and Schoener, 1995). Increased plant growth may cause increased numbers of herbivorous insects and this is likely to provide spiders with additional food resources. Spider populations are often limited by food (Wise, 1993). Therefore rain may allow increased fitness and survival of spiders. The absence of a significant correlation between abundance and rainfall three months before sampling may indicate insufficient time for spider populations to respond. The reduced congruence between abundance and rainfall for the first few years of sampling may be due to the impact of the experimental fires, since plots D, F, G and H were burnt in the first three years of invertebrate sampling.

Based on limited data, it was thought previously that communities of predatory arthropods in deserts fluctuate little in response to precipitation (Polis and Yamashita, 1991). In the Namib Desert biomass of carnivorous arthropods increased only 34 % after rains compared to herbivores (110 %) and omnivores (1534 %) (Seely and Louw, 1980). However, in the present study and that of Polis et al. (1998) spider abundance was found to increase by over 100 % in favourable years. This suggests that predatory arthropods are capable of significant responses to precipitation. Polis and Yamashita (1991) also suggest that life history influences the response of invertebrates to abiotic factors. Short-lived opportunistic species are more likely to respond than long-lived species (eg. Mygalomorphs). Therefore not all species in this spider community may be

responding in the same way. Future studies should elucidate what role life history traits play.

Higher predators and parasites can also influence spiders by exerting top-down effects. Lizards, scorpions and parasitoid wasps influence spider density on islands in the Gulf of California and the Caribbean (Polis et al., 1998; Spiller and Schoener, 1995). Lizards are very diverse in Australian deserts with more than 40 species found in spinifex areas in the Great Victoria Desert (Pianka, 1986). It is likely that spider abundance is influenced by pressure from lizards and other predators such as scorpions. However, predation pressure may be mediated by rainfall (Dawes-Gromadski, 2002; Polis et al., 1998). These possible indirect influences of rainfall are potentially important but will be difficult to elucidate in future studies.

At a finer temporal scale, rain falling immediately before or during sampling may also influence spider activity and hence capture rates. Under favourable conditions of rainfall, temperature and humidity, spider activity and thus observed abundance may increase as pitfall traps are biased to activity levels (Huhta, 1971; Luff, 1975). Short-term response to rain has been reported for beetles in an Australian tropical savanna (Blanche et al., 2001). Beetle species richness was related to total rainfall during the week of sampling and three weeks prior to sampling. However, the Australian tropics have a pronounced wet-dry season that may accentuate the importance of rain following protracted dry periods. In North America Uetz (1975) did not find any correlation between spider richness and weekly rainfall, temperature or relative humidity. In the present study problems with the remote weather station precluded testing these hypotheses. However, the recording of daily weather conditions during sampling and for periods before sampling is merited in future studies.

In studies of rainfall and rodent population dynamics in arid Australia cumulative monthly rainfall (CMR) or cumulative monthly rainfall residual (CMRR) have been used for correlation (Masters, 1993; Moro and Morris, 2000; Southgate and Masters, 1996). The CMRR is calculated as the cumulative difference between the actual and long-term mean monthly rainfall for a site (Sutherland et al., 1991). Dickman et al. (1999b) pointed out that CMRR is appropriate only for months with normally distributed rainfall (Sutherland et al., 1991). With non-normal rainfall distributions

CMRR is biased and insensitive to subsequent drought periods (Dickman et al., 1999b). Further, in arid Australia unpredictable large rainfall events are common and monthly rainfall is not normally distributed (Williams and Calaby, 1985). Dickman et al. (1999b) corrected for this problem by incorporating an exponential decay function into CMRR values. This decay rate was based on empirical study of seed decline, a major food resource of target species. The CMRR could not be used here as the food requirements of desert spiders and possible decay rates are unknown. It is unlikely that food source (predominantly insects) decay rates could be established for spiders. Cannibalism and intraguild predation are common among spiders (Wise, 1993), which would also limit decay rate predictions.

#### Influence of fire and rainfall on spider species composition

The observed difference in species composition between sampling months is greater than that between burnt and long unburnt samples. There was little separation between unburnt and burnt samples when individual sampling months were examined. However, a lack of possible permutations excluded testing for significant differences using ANOSIMs. An ANOSIM2 (two-way layout without replication, Clarke and Warwick, 1994) indicates a significant difference in groups before-and-after fire for each plot. This procedure, unfortunately, does not reveal which groups are significantly different. Therefore the significant difference could be between before-and-after fire samples or within before-fire samples or after-fire samples.

Sampling date has a large influence on observed spider assemblages. Seasonal stratification is considerable in spider communities (Chew, 1961; Humphreys, 1988; Norris, 1999). The strong effect of sampling month noted here suggests desert spiders have set developmental, activity or mating times. Analysis of similarity percentages (SIMPER) shows some species are only collected in specific sampling months. This is due to some species only appearing as adults (and hence identifiable to morphospecies) in specific months, or alternatively they are not active during other months. An example of a desert spider with fixed life cycle timing is *Agelenopsis aperta* (Agelenidae) from the Chihauhuan Desert of New Mexico (Riechert, 1974). The proportion of different age classes changed during the year. Particular months had greater proportions of adults

(June and July), sub adults (March and April) and juveniles (August and September). This life cycle was linked with seasonal changes in rainfall, temperature and humidity.

Fixed seasonal reproductive periods are surprisingly common in dasyurids and many reptiles in arid Australia (Dickman et al., 1999a; Dickman et al., 2001; Masters, 1993). While the season of mating may vary (winter and spring in dasyurids), many juveniles of both dasyurids and reptiles are dispersing or establishing home ranges during March (Dickman et al., 2001; Pearson, unpublished). Spiders active during this period potentially provide an important food resource for these vertebrates. In contrast rodents (primarily herbivores and granivores) are able to breed year round, with population eruptions following rainfall and flushes of resources (Dickman et al., 1999b; Newsome and Corbett, 1975; Predavac, 1994).

Rainfall prior to sampling showed no correlation with spider species composition. This suggests the period of sexual maturity or activity of spiders is unaltered by rainfall months before sampling. This further supports the result found for fire and species composition, the time of maturity or activity is set for many spider species.

# Influence of fire on vegetation and its relation to changes in spider species composition

Fire caused significant changes to understorey vegetation and ground cover. Spinifex and other plants took longer to return to pre-fire biomass after a summer fire than in plots burnt by patchy spring fires. Summer fires were hotter and removed almost all understorey vegetation leaving just ash and burnt stumps of shrubs. Spinifex accounted for only 10 % of ground cover eleven years after a summer fire but was 19 % of cover only nine years after a spring fire. The spinifex species at this site, *Triodia desertorum*, regenerates almost entirely by seed (Pearson, unpublished). Therefore regeneration of spinifex cover is much slower than that of re-sprouting species present in the landscape.

Bare ground was best correlated with spider species composition in March samples with matching vegetation data, but the correlation was relatively poor. Increased bare ground after fire may favour ground-hunting species. Two months after the wildfire in

January 2003, a large number of Lycosidae juveniles were found in burnt areas (Langlands, pers. obs.). This however, may be due to easier detection when understorey vegetation has been removed by fire. Previous Australian studies have found Lycosidae to be more abundant after fire (Brennan, 2002) or only found in frequently burnt sites (York, 1999). Conversely, a North American study found that four of the five Lycosidae genera were more abundant in unburnt sites (Hanula and Wade, 2003). It seems quite likely that families might respond differently between different environments in different hemispheres.

The habitat variable ground cover may be too coarse to correlate well with spider species assemblages. Spiders respond to the structural complexity of litter and vegetation (Riechert and Gillespie, 1986; Uetz, 1991). Percentage ground cover does give some indication of habitat structure. However, more detailed measurement of vertical structure or micro-habitat variables are appropriate for some groups of spiders and should be incorporated into the design of future studies.

#### CONCLUSIONS

Most studies examining the response of invertebrates to fire are conducted over short time spans (< 5 years). If sampling in this study had ceased only a few years after fire, its conclusion would have been that fire caused a short-term decrease in abundance and no clear effect on species richness. However, with longer-term sampling it was possible to elucidate the important influence of rainfall. Rain in the year prior to March samples increased observed spider abundance and species richness. This highlights the importance of long-term studies in explaining complex ecological processes, especially in highly variable arid regions. If the re-introduction of anthropogenic fire regimes is to be valid for biodiversity conservation, then it is necessary to understand the mediating influence of rainfall.

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