Records of the Western Australian Museum Supplement No. 61: 269–279 (2000).

Biogeography of scorpion communities in the southern Carnarvon Basin, Western Australia

G.T. Smith[1†] and N.L. McKenzie[2]

[1] CSIRO Division of Wildlife and Ecology, LMB4, PO Midland, Western Australia 6056, Australia

[2] Department of Conservation and Land Management, PO Box 51, Wanneroo,
Western Australia 6065, Australia

Abstract – Ten scorpion species of four genera were recorded from 61 quadrats positioned through the 75 000 km^2 study area, and sampled continuously over a 12 month period (114 000 trap nights). An average of 3.1 species were recorded per quadrat. Analysis of the data matrix revealed that species abundance patterns related to various climatic and soil attributes, particularly soil texture, while assemblage composition conformed with annual average precipitation.

INTRODUCTION

Scorpions are an important component of the macro- and mesofauna of arid ecosystems; their density is exceeded only by ants, termites and isopods, and their biomass only by ants and termites (Polis and Yamashita, 1991). There are no comparable data for Australian scorpion communities, although the predominantly arid zone *Urodacus yaschenkoi* (Birula) and the semi-arid to arid zone *U. armatus* Pocock have densities and biomass (Marples and Shorthouse, 1982; Smith, 1995, 1998) similar to scorpions elsewhere in the world (Polis and Yamashita, 1991). These data suggest that scorpions play an important ecological role in Australia's arid areas. In particular, their ecological role in guilds of small ground dwelling carnivores is liable to be extensive because of their density and biomass, so their influence on the composition of the communities cannot be ignored. In food-web terms, they connect to many other species (Polis and Strong, 1996).

While the low metabolic rates (Withers and Smith, 1993) and high production efficiencies of scorpions (Polis, 1993), restrict their role in energy and nutrient cycling, their role in the structuring of invertebrate communities can be important (Polis *et al.*, 1989; Polis, 1993). Given these physiological attributes, rainfall and soil-type might not be as important in determining scorpion patterns of occurrence across landscapes as they are for most other taxa. Even so, Lamoral (1987), Locket (1993), Smith (1998) and others have shown that certain soil attributes do influence scorpion distributions at small spatial scales.

Although arid regions are the most speciose, the diversity of scorpions at any site is low, ranging from 1 to 13, with an average of 7 (Polis and Yamashita, 1991). Comparable Australian data are limited. At the scale of two degree blocks, the highest diversity in Australia is 10, in the block around Alice Springs (data from Koch, 1977). At smaller scales, eight sites in the Tanami Desert had a mean diversity of 2.3 (range 1–3, total species = 4) (S.R. Morton and G.T. Smith, unpublished data), whereas for eight sites near Alice Springs, the mean was 5.5 (range 4–7, total species = 10) (C. Schlesinger and G.T. Smith, unpublished data). In the semi-arid wheatbelt of Western Australia, 17 sites gave a mean of 4.0 (range 3–6, total species = 12) (Smith, 1995). Within the area of the Carnarvon Basin, Koch (1977) recorded the presence of eight species, but he had no site specific data on species richness.

The low diversity, wide distributions and generalist habitat requirements of Australian scorpions make detailed zoogeographic analysis of limited use in delimiting areas of conservation importance, a primary aim of the present survey. Koch (1981) was only able to group the species into three broad latitudinal bands, representing the southern temperate, semi-arid and -arid centre and northern tropical zones.

We present the first site specific data on the diversity and abundance of scorpions in the Carnarvon Basin, and examine the relationship between assemblage composition and abiotic environmental parameters. Biogeographical conclusions from the study are currently limited because of taxonomic restraints. Even preliminary examination of the collections showed the need for a revision of all scorpion genera, an undertaking too large for this study.

---

† Deceased 30 June 1999

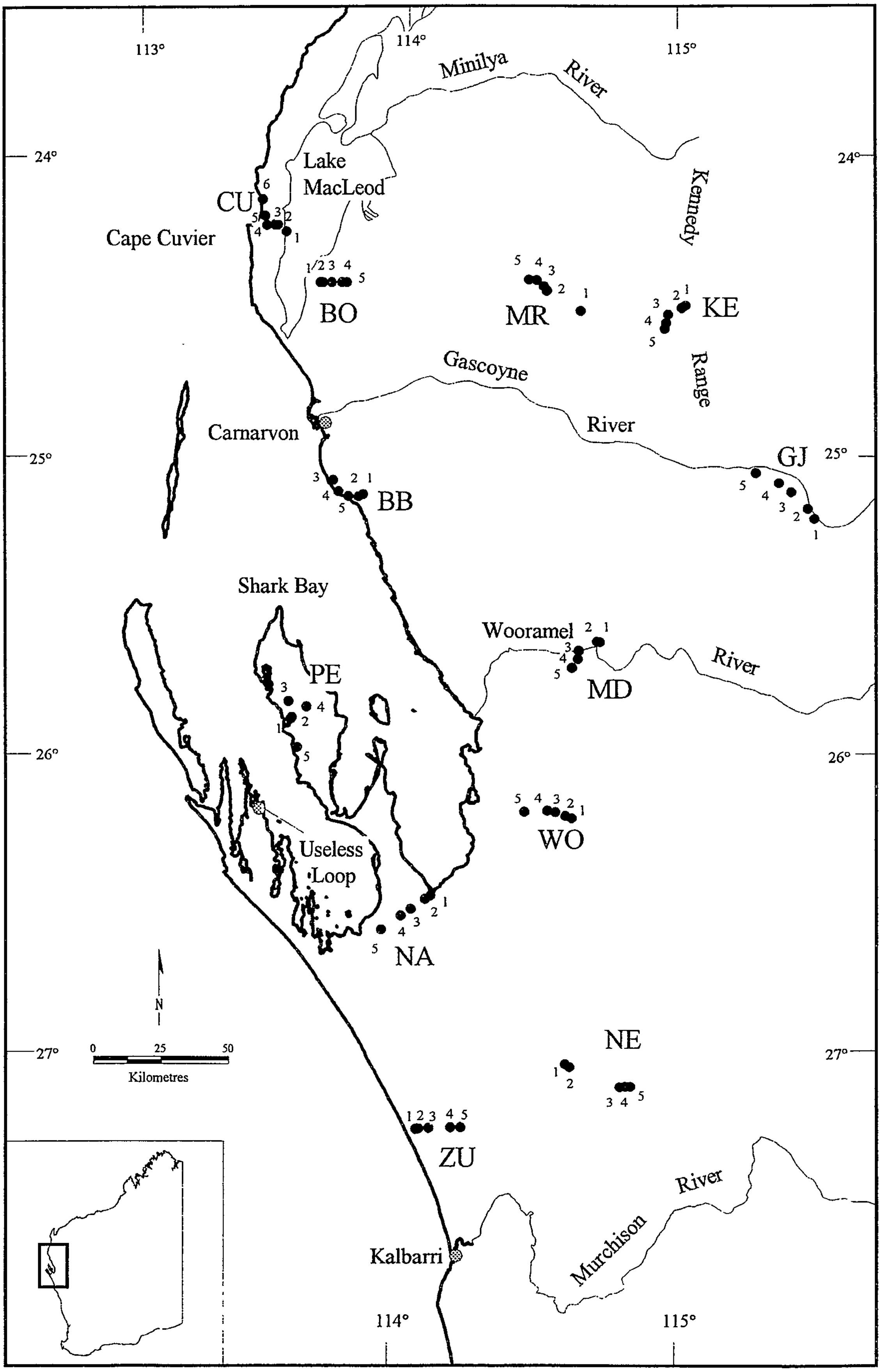

Figure 1 The Carnarvon Basin study area, showing survey areas. Survey Area and quadrat locations are indicated: Bush Bay (BB), Boolathana (BO), Cape Cuvier (CU), Edel Land (EL), Gascoyne Junction (GJ), Kennedy Range (KE), Meedo (MD), Mardathuna (MR), Nanga (NA), Nerren Nerren (NE), Peron Peninsula (PE), Woodleigh (WO) and Zuytdorp (ZU).

METHODS

Study Area

The Carnarvon Basin study area covers 75 000 km^2 on Australia's western coast. It is centred on Shark Bay, and extends northwards from 28°S (the Murchison River) to 23°30'S (the Minilya River), and eastwards to beyond Gascoyne Junction (25°S 115°E, Figure 1). Details of the physical environment are given by Wyrwoll, Courtney and Sandercock (2000) and Wyrwoll, Stoneman, Elliott and Sandercock (2000). The area south of Shark Bay has a semi-arid climate influenced by temperate weather systems (mainly winter rainfall). North of Shark Bay, the climate is influenced by both tropical and temperate systems; semi-arid at the coast, but arid with locally unreliable summer and winter rainfall further inland. In phytogeographical terms, the study area comprises the northern half of the Irwin District of the South-western Province, as well as the southern half of the Carnarvon District of the Eremean Province (Beard, 1980).

The region is a lowland with a complex landscape mosaic characterised by gentle gradients, and is dominated by extensive alluvial plains with some erosional uplands, such as the Kennedy Range, in the east. Two large, ephemeral rivers (Gascoyne and Wooramel) lined with groves of River Gum (*Eucalyptus victrix*) cross the plain from east to west. Low open woodlands of bowgada (*Acacia linophylla*) and snakewood (*A. xiphophylla*) over *Atriplex, Senna* and *Eremophila* shrubs and tussock grasses cover the plains, with *Acacia grasbyi* in areas where calcretes are exposed. Scattered low red sand ridges on the plains support shrubs over mainly hummock-grasses. In the northern areas the plains grade into red sand dune fields that support hummock-grass and mulga (*A. aneura*) communities. In the south, the plains support woodlands of *Eucalyptus loxophleba* and *Callitris glaucophylla*, with mallee (*Eucalyptus* spp.), *Banksia, Allocasuarina* and *Actinostrobus* scrubs and heaths on greyish and yellow sand dunes. A strip of limestone that follows the coast southwards from Shark Bay, is partially mantled by pale yellow to grey sands supporting low proteaceous heaths with emergent thickets of *Banksia* and mallee. White coastal sand dunes support *Spinifex longifolius* communities. Samphire and saltbush communities occur on low-lying saline areas, such as the fringes of Lake MacLeod and the coastal flats of Shark Bay. Detailed descriptions of the vegetation in the study area are provided by Beard (1975, 1976), Payne *et al.* (1987) and Keighery *et al.* (2000).

Sampling Procedure

Twelve survey areas were established in the Carnarvon Basin Study Area (Figure 1). Five quadrats were established in each area, except Cape Cuvier (6 quadrats). In each quadrat, five 20 litre pitfall traps containing a mixture of ethylene glycol and formalin were set up and operated for 12 months from August 1994. Hereafter these are referred to as invertebrate traps. Captured material was collected in October 1994, January 1995, May 1995 and August 1995. Additional scorpions were collected in October 1994 and May 1995 from the vertebrate pitfall traps set on the quadrats in conjunction with the invertebrate traps (see McKenzie *et al.*, 2000). Quadrat location and descriptions are provided in Appendix A, and details of the climatic and soil attributes are given in Wyrwoll, Courtney and Sandercock (2000) and Wyrwoll, Stoneman, Elliott and Sandercock (2000).

Taxonomy

Initially, scorpions were sorted and classified using the keys in Koch (1977). Many of our specimens could not be identified in terms of the characters used by Koch, so a morphospecies (hereafter referred to as species) approach was adopted where required, to provide a more realistic taxonomy for the ecological analyses.

Data Analysis

The numbers of each species collected in the invertebrate and vertebrate traps were combined to give an abundance value for each species as well as a species richness value for each of the 61 quadrats. Quadrat data were combined to provide the same type of data for the 12 survey areas. We selected a sub-set of quadrat physical attributes for our analyses, taking into account auto-correlations and the natural history of the scorpions.

Three analytical procedures were used. Spearman Rank Correlation was used to seek correlations between the physical attributes of the quadrats and the abundance of each species. The significance level was set at 1% to minimise Type-1 errors. The species abundance data were analysed in relation to the soil texture data using a Kruskal-Wallis K-sample test. Soil texture data for each quadrat are provided in Appendix 1 of Wyrwoll, Stoneman, Elliott and Sandercock (2000). They were estimated from samples taken near the surface (0–10 cm depth) and at a depth of 20 cm. The numerical analysis package PATN (Belbin, 1995) was used to analyse the species presence-absence data from the 12 survey areas. The species were classified according to their co-occurrence at the same survey area, using the association measure Two-step (Belbin, 1980) and an UPGMA sorting strategy (Sneath and Sokal, 1973). The quadrats were classified according to the similarity in their species composition using the association measure of Czekanowski (1932) and an UPGMA sorting strategy. The group structure apparent in the resulting dendrogram of survey areas was analysed against the quadrat physical attributes, one by one, using the GSTA module of PATN. Kruskal-Wallis K sample test was used to assess the significance of the relationship, and 'Semi-Strong Hybrid Multi-Dimensional Scaling' (Belbin, 1991) was used to reduce the dimensionality in the data.

RESULTS

A total of 1466 scorpions was collected from the invertebrate traps and 184 from the vertebrate traps. The specimens were assigned among 10 morphospecies/species. Ten species-level taxa, belonging to four genera and three families, were captured.

Family Bothriuridae

Cercophonius granulosus Kraepelin

The genus has been revised by Acosta (1990) and his key was used for the determination.

Family Buthidae

Lychas C.L. Koch

Initially, specimens were assigned to seven morphospecies, in terms of their overall size, hand morphology, shape of sub-aculear prong, total pecten teeth count and colour pattern. Then:

- three morphs with affinities to *L. alexandrinus* Hirst, and which had overlapping variation in the characters listed above, were grouped under *Lychas* sp. 1,
- another three morphs with affinities to *L. marmoreus* (C.L. Koch) were grouped under *Lychas* sp. 3 for similar reasons and
- the final morph was clearly a new species because it showed little variation, and was labelled *Lychas* sp. 2.

Total pecten teeth counts of these three morphospecies have unimodal frequency distributions, with minor overlap between them (27% between sp. 1 and sp. 2, 1% sp. 2/sp. 3, 0% sp. 1/sp. 3). The mean, standard deviation and range for the total pecten teeth counts for males and females of the three morphospecies are given in Table 1. The mean differences between the morphospecies for both males and females (Table 1) are significantly different (Kruskal-Wallis: H=118.39, p=0.000; H=150.12, p=0.000, respectively). Although these data provide some support for the validity of the morphs, it should be noted that similar differences in pecten teeth counts have been recorded in the buthid *Centruroides vittatus* over a comparable geographic range (Brown, 1996).

Isometroides vescus (Karsch) and *Isometroides* sp. 1

The latter has close affinities with *I. angusticaudus* (N.A. Locket, personal communication).

Family Urodacidae

Urodacus armatus Pocock

Examination of the large series of specimens assigned to this species, revealed patterns of variation in size, colour and morphology throughout its range. Three broad groupings were noted in the total pecten teeth counts of Western Australian specimens, with minor overlap between their ranges (G.T. Smith, unpublished data). Male specimens from this survey fall into two of these groups (Table 2) but, pending taxonomic revision, all specimens have been grouped under *U. armatus*.

Urodacus hartmeyeri Kraepelin

Specimens from Cape Cuvier were paler, had a shorter tail, smaller terminal spine on the dorsolateral keel of the fourth tail segment and a lower total pecten teeth count than specimens from other survey areas (Table 2).

Urodacus hoplurus Pocock

No apparent differences from the description given in Koch (1977).

Urodacus mckenziei Volschenk, Smith and Harvey

A sister species to *U. megamastigus* L.E. Koch, considerably smaller and differing in a number of morphological and meristic features (Volschenk *et al.*, 2000).

Species Analysis

The most frequently captured species was *Urodacus hartmeyeri* with 717 captures. Six species were captured from 75 to 264 times, while *Isometroides* sp. 1 (n=16), *Urodacus hoplurus* (n=15) and *Cercophonius granulosus* (n=4) were relatively uncommon (Table 3).

There was considerable variation in the number of scorpions captured between seasons in the

Table 1 Mean, standard deviation and (range) of the total pecten counts for males and females of the three morphospecies of *Lychas*.

	Lychas sp. 1	*Lychas* sp. 2	*Lychas* sp. 3
Female	44.1±2.58 (39–50)	37.8±1.53 (34–40)	27.8±1.92 (24–34)
Male	44.3±2.61 (37–49)	38.7±1.77 (35–42)	30.3±1.53 (27–34)

Table 2 Geographical variation in pecten teeth counts for male *Urodacus* (see Figure 1). Mean ± standard deviation (sample size); — = none captured.

Survey area	***U. armatus***	***U. mckenziei***	***U. hartmeyeri***
North coast			
CU	--	--	44.3±2.34 (40)
Central coast and inland			
PE	38.0 (1)	39.7±2.60 (23)	50.0±3.43 (10)
BB	39.0±2.90 (6)	--	49.0±2.38 (7)
BO	38.2±2.68 (11)	--	52.6±2.76 (10)
GJ	37.1±1.97 (40)	--	52.1±2.60 (10)
KE	39.1±2.66 (15)	--	52.1±2.98 (9)
MR	39.0±2.64 (10)	--	52.1±2.60 (10)
Southern			
MD	38.2±2.31 (15)	45.3±1.64 (10)	55.5±4.58 (10)
NA	44.0±0.0 (2)	43.3± 1.91 (8)	55.6±2.95 (10)
WO	46.5±1.58 (10)	--	56.1±4.59 (8)
NE	47.0±4.43 (7)	38.5±1.73 (4)	55.3±2.21 (10)
ZU	--	38.3±2.42 (58)	--

invertebrate pitfall-traps. Eighty-eight percent (n=975) of *Urodacus* spp. were captured in the January to May period, mostly (898) adult males. Captures of adult females, and of immature males and females, showed the same pattern. In contrast, captures of *Lychas* spp. and *Isometroides* spp. (n=675) were more even, with 38% of captures in the October to January period and 43% in the January to May period (Table 3).

The relationship between abiotic factors and the abundance of individual scorpion species at the 61 quadrats was examined using Spearman Rank Correlation. The factors used are listed in Table 4. Overall there were 18 significant correlations, although one of these would be expected by chance alone at the 1% level. At the 1% level or lower, three species showed no significant correlations with the abiotic factors assessed (*C. granulosus*, *Isometroides* sp. 1 and *U. armatus*).

All species were found in a wide variety of vegetation formations and Spearman Rank Correlation analyses revealed no discernible patterns with vegetation attributes. The significant correlations suggest the following interpretations:

- *Lychas* sp. 1 is more abundant on silty soil and in warm, dry areas with the wide temperature ranges found away from the coast,
- the positive relationship between *Lychas* sp. 2 abundance and the shear strength of the soil indicates that it prefers heavier soils,
- *Lychas* sp. 3 has a positive association with sandy soils,
- *I. vescus* is more abundant in areas with a subdued temperature range, i.e. coastal areas, and prefers alkaline soils high in calcium,
- in contrast, *U. hartmeyeri* has a negative relationship with alkaline soils, phosphorus and exchangeable cations and

Table 3 Total number of specimens captured during each sampling period. Wet pits: 1 = August to October, 2 = October to January, 3 = January to May, 4 = May to August. Dry pits: 5 = May, 6 = October.

Species	**Sampling Period**					
	1	**2**	**3**	**4**	**5**	**6**
Cercophonius granulosus	0	0	0	2	0	2
Lychas sp. 1	30	66	52	23	23	9
L. sp. 2	34	82	53	13	61	21
L. sp. 3	5	26	37	7	0	0
Isometroides vescus	7	47	30	2	10	1
I. sp. 1	4	0	4	1	5	2
Urodacus armatus	4	2	97	11	3	23
U. hartmeyeri	1	55	644	9	5	3
U. hoplurus	0	3	11	1	0	0
U. mckenziei	0	1	101	1	0	0
Total	**85**	**282**	**1029**	**70**	**120**	**64**
Total *Urodacus*	5	61	853	22	8	26
Total *Lychas/Isometroides*	80	221	176	48	112	38

Table 4 Spearman Rank Correlation coefficients between physical attributes and species' abundance. [$p < 0.01$ **, $p < 0.001$ ***, $p < 0.0001$ ****].

Attribute	Species						
	Lychas sp. 1	*Lychas* sp. 2	*Lychas* sp. 3	*Isometroides vescus*	*Urodacus hartmeyeri*	*Urodacus hoplurus*	*Urodacus mckenziei*
Annual Average Temperature							-0.43***
Annual Temperature Range	0.37**			-0.61****			
Average Coldest Quarter Temperature				0.42**			-0.37**
Annual Average Precipitation	-0.39**					-0.34**	
Average Coldest Quarter Precipitation	-0.36**						0.38**
Soil pH(H_2O)				0.38**	-0.36**		
% Sand			0.34**				
% Silt	0.45***						
Soil Phosphorus: P(HCO_3)					-0.34**		
Soil Potassium: K(HCO_3)							-0.33**
Soil Calcium: Ca(HCO_3)				0.46***			
Cation Exchange Capacity					-0.44***		
Soil Textural Shear Strength		0.38**					

- *Urodacus hoplurus* is more abundant in drier areas, while *U. mckenziei* is more abundant in temperate areas.

The effect of soil texture on the relative abundance of each the 10 scorpion species across the 61 quadrats was examined. Soil textures were measured at two levels in the soil profile. Only four of the 20 Kruskal-Wallis tests were significant: *Lychas* sp. 1 relative abundance showed relationships with soil texture at both 0–10 cm and at 20 cm depths (H=6.47, p=0.040; H=14.61, p=0.006 respectively). *Isometroides* sp. 1 and *U. hoplurus* abundance was related to soil texture at 20 cm depth (H=11.43, p=0.023; H=12.70, p=0.013 respectively).

The distributions of the species within the study area are documented in Appendix 1. The only species found in all survey areas were *Lychas* sp. 3 and *Urodacus hartmeyeri*. *Lychas* sp. 1, *L.* sp. 2, *Isometroides vescus* and *U. armatus* were found in 10 or 11 survey sites, while *U. hoplurus*, *U. mckenziei* and *C. granulosus* were found in six, five and one (ZU3) respectively. Species occurred at an average of 0.2 to 3.3 (± 1.23 s.d.) quadrats per survey area, depending on the species. There was a significant positive correlation between the number of quadrats per survey area that a species was found on, and the number of survey areas in which it was recorded (r = 0.932, p 0.001) (Appendix 1).

For the six most widespread species in the study area, geographical trends in abundance were overt when the survey areas were split into classes (refer to Figure 1):

- survey areas influenced by temperate weather patterns (ZU, NE, NA, PE) versus those by northern patterns (the rest), and
- survey areas influenced by coastal (CU, BO, BB, PE, NA, ZU) versus the inland sites (the rest).

Lychas sp. 1 and *Urodacus armatus* were most abundant in northern inland areas, whereas *Isometroides vescus* favoured areas near the northern coast, *Lychas* sp. 2 the north and *Lychas* sp. 3 coastal areas in the north. *U. hartmeyeri* showed no such trends.

Community analysis

Quadrat species richness ranged from 0 to 6, with a mean of 3.1. Survey area richness varied from 5 to 8 (mean 6.8).

The data matrix of species presence and absence

Table 5 Data matrix of scorpion species re-ordered according to their co-occurrences at the same survey areas. The survey areas have been re-ordered according to similarities in their species composition.. Survey area codes and precipitation figures are printed vertically.

Species	Survey Areas											
	BB	BO	GJ	MR	WO	MD	CU	NA	NE	PE	KE	ZU
Lychas sp. 1	*	*	*	*	*	*	*	*	*	*	*	
Lychas sp. 2	*	*	*	*	*	*	*	*	*	*	*	
Lychas sp. 3	*	*	*	*	*	*	*	*	*	*	*	*
Urodacus hartmeyeri	*	*	*	*	*	*	*	*	*	*	*	*
Urodacus armatus	*	*	*	*	*	*		*	*	*	*	*
Isometroides vescus	*	*	*	*	*		*	*	*	*		*
Urodacus mckenziei						*		*	*	*		*
Isometroides sp. 1	*	*				*						
Urodacus hoplurus	*	*	*	*	*	*						
Cercophonius granulosus												*
Annual Average Precipitation (mm)	226	238	205	228	209	207	251	247	251	256	232	324

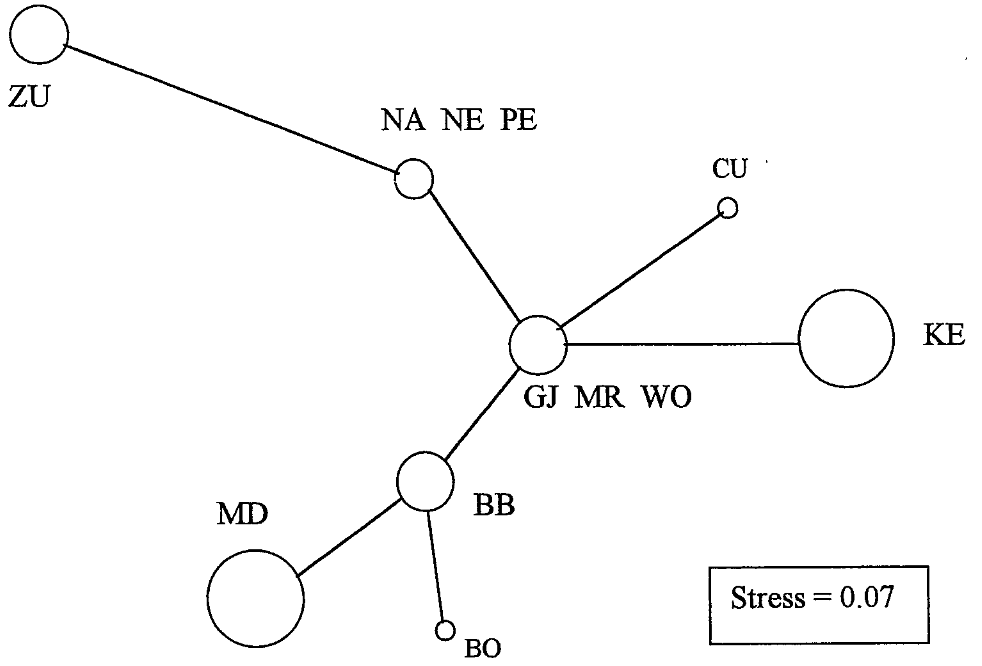

Figure 2 Three dimensional ordination of the survey areas according to similarities in their scorpion species composition (presence-absence data) (stress = 0.07). The third dimension is indicated by the circle diameters. A Minimum Spanning Tree has been superimposed as links between the circles. The point labels are the survey area codes from Figure 1.

at the 12 survey areas, re-ordered according to the classification analyses, is presented in Table 5. The partitions depend on the four species with restricted distributions in the study area: *C. granulosus, Isometroides* sp. 1, *U. hoplurus* and *U. mckenziei.* The three partitions defined from the classification of survey areas in terms of similarities in their species composition showed a significant relationship with Annual Average Rainfall (Kruskal-Wallis H=8.1, p.=0.018) (Table 5). The result of the 'Semi-Strong Hybrid Multi-Dimensional Scaling' analysis was consistent with this relationship (Figure 2) in that the temperate areas to the south were arrayed on the opposite side of the cluster to the arid areas, inland.

DISCUSSION

A large sample of scorpions was collected during our survey across a relatively small geographic area. Examination of the specimens demonstrated inadequacies in our taxonomic knowledge of Australian scorpions. A new *Urodacus* species, *U. mckenziei,* has been described from the collection (Volschenk *et al.,* 2000). Two other *Urodacus* species need further study in view of the geographical variation we noted and the possibility that the variation may be more related to local environmental conditions than to genetic variation (Yamashita and Polis, 1995). Among the buthids, there are at least two undescribed species. With this degree of taxonomic uncertainty, the full biogeographical implications of the collection will need to await future taxonomic revisions.

As the number of quadrats sampled was low (61 for an area of more than 75 000 km^2), our survey would not be expected to provide an exhaustive listing of the area's entire scorpion fauna. Nevertheless, pitfall trapping has been shown to give good data on species richness, provided that there is an adequate number of traps and that they are operated in all seasons (Smith, 1995). The traps in the present study were operated continuously for one year (114 000 trap-nights) so, within the constraints imposed by the taxonomy, our data probably provide a reasonably accurate picture of the communities sampled.

However, in surveys of this type there is a low probability that any single trap will capture a sedentary species with narrow habitat requirements. For example, *Cercophonius granulosus* was found in only one quadrat and, although it is known to occur in the Useless Loop townsite (Figure 1), it was not captured by pitfall traps set nearby. By analogy with the related *C. michaelensi,* it probably has specific habitat requirements which are patchily distributed (Smith, 1995). It is unlikely that the present study provides an accurate picture of its environmental envelope or community relationships.

The collection was dominated by the other buthids and by *Urodacus,* especially *U. hartmeyeri* which occurs at high densities in parts of the study area. Some 350 male *U. hartmeyeri* were collected from 388 pitfall trap-nights near Useless Loop in March 1993 (D. Riseby, personal communication) and a site on Pingroves Pastoral Lease, east of Kalbarri, had a minimum density of 2500/ha (G.T. Smith, unpublished data).

Adult males made up 98% of the *Urodacus* specimens from our Carnarvon Basin quadrats. This pattern of capture in pitfall traps is typical for members of the genus that have been studied in Western Australia because, except for the adult males during the late summer/early autumn breeding season, *Urodacus* scorpions are sedentary, rarely moving away from their burrows (Smith, 1995 and G.T. Smith, personal observations). During the breeding season the males spend a considerable amount of time on the surface looking for females, and may move over tens of metres in a night. It is reasonable to assume that the number of adult males provides a reliable index of population density for the *Urodacus* species. In contrast, the buthid species are essentially vagrants, which explains the more even pattern of captures (and sample sex-ratios) we observed during the warmer months (Smith, 1995). Again, their general surface mobility suggests that their long-term capture rates should provide a reasonable index of their populations. Thus, the use of capture abundance data, rather than presence/absence data in our analyses appears justified and, while our understanding of the ecology of the species is uneven, the present study should provide an accurate picture of environmental envelopes and community relationships for most of the species.

At broad geographical scales, the distribution and abundance of scorpions is influenced by temperature and rainfall, with soil and vegetation having minor importance (Koch, 1977; Polis, 1990). At smaller scales however, edaphic and vegetation characteristics do influence many species (Polis, 1990 and references therein; Locket, 1993; Smith, 1995, 1998).

The quadrat-size and environmental descriptors chosen in the present study suited vertebrate and plant analyses, but overlooked some of the small-scale patchiness and micro-habitat features thought to be important for invertebrates. This may explain why we found relatively few significant correlations between the scorpion abundance patterns and the environmental attributes (18/130). In fact, three of the 10 species showed no significant correlations at all.

Four species showed significant correlations with rainfall or temperature attributes, but the implications of these correlations are clouded by the scarcity of data on the distributions and ecologies of these scorpions. The negative relationship between *U. hoplurus* and annual rainfall may reflect the location of the study area, which straddles the western boundary of its arid zone distribution (Koch, 1977). *Urodacus mckenziei* appears to have adapted to a more temperate climate than its arid-zone sister species, *U. megamastigus* (Koch, 1977). The greater abundance of *Lychas* sp. 1 at the warmer and drier inland quadrats probably reflects its arid zone origins (Koch, 1977, under *L. alexandrinus*). *Isometroides vescus* has a predominantly arid zone distribution, so its greater abundance in coastal areas of our study area appears anomalous (Koch, 1977).

Soil attributes are known to influence the distributions of a number of scorpion species at various scales – soil hardness, texture and rock cover (Lamoral, 1987; Polis, 1990; Locket, 1993; Smith, 1966, 1995, 1998). However, patterns in Carnarvon Basin scorpion occurrence did not conform tightly with soil attributes, even for the burrowing species that should have been most influenced. For instance, *Urodacus armatus, U. hartmeyeri* and *U. mckenziei* showed few significant relationship with soil attributes, and the analysis of the data on *U. hoplurus* revealed only one significant soil correlation – it was more abundant at quadrats with fine-textured sub-surface soils (high clay content). This association is probably related to the need for higher soil consistence, to prevent collapse of its large burrows (up to 60 cm deep and 4–5 cm in diameter). The preference of *Lychas* sp. 1 for these heavier soils is probably related to its use of other species' burrows, especially ants and spiders. Burrows in heavier soils retain their structural integrity longer after being abandoned, thus providing a ready source of shelter. A similar argument can be made for the preference of *Isometroides vescus* for soils with a higher clay at depth. In this case, the species uses the burrow of its principal prey, trapdoor spiders. To interpret the observed correlations with soil chemical attributes (Table 4) we need more data on the natural history of Carnarvon Basin scorpions.

All species were found in a wide variety of vegetation formations and, while variation was visible in the abundances, sample sizes were too small for analysis. The species are habitat generalists at the scale of resolution determined by our 16 ha quadrats, a pattern similar to that found in the central wheatbelt of Western Australia (Smith, 1995). More detailed studies that use much smaller quadrats and measure an appropriately scaled set of microhabitat attributes are required to elucidate the factors that influence their small-scale distribution and abundance.

Six species had wide distributions across the study area. Four of these are species with wide arid- or semi-arid distributions, one is at the northern edge of its otherwise mesic range, and *Lychas* sp. 2 is only known from our study area. Of the four species with restricted distributions in the study area, three are undescribed and need further investigation because they may have been collected from other regions previously, and the fourth, *C. granulosus*, has a patchy coastal distribution that extends as far north as Cape Range (Koch, 1977; Acosta, 1990).

The area is more speciose than previously portrayed (Koch, 1977; Smith, 1995), in terms of both its overall species richness (10) and the richness of the survey areas (ranging from 5 to 8). In these terms it is about average on a world scale (Polis and Yamashita, 1991), comparable to Alice Springs, but considerably richer than either the Tanami Desert or the Western Australian wheatbelt (see Introduction).

The communities in the survey areas show a great deal of similarity in their species composition, being dominated by the abundant and widespread species such as *U. hartmeyeri*, which was the most common species in nine of the 12 survey areas. All but one of the widespread species have predominantly arid zone distributions. The communities fall into two groups, one influenced by temperate climatic patterns and the other by wet-to-arid patterns, a differentiation based mainly on the distribution of the three undescribed species with restricted distributions. This pattern should emerge even more strongly as taxonomic resolution improves, because the same climatic gradient is overt in the geographical variation found in the pectin teeth counts of each of the three *Urodacus* taxa measured (Table 2).

In combination, the lack of strong co-occurrence patterns and the eclectic array of significant correlations that emerged when the species were analysed individually, suggest that these scorpions are not neighbours in ecological space. It implies that scorpion species are liable to be scattered through the larger guild of small ground-foraging carnivores (Polis and Strong, 1996; Spiller and Schoener, 1998) such as spiders, centipedes and small lizards.

ACKNOWLEDGEMENTS

We thank Alison Sampey and Paul West for sorting the material from the pitfall traps and who, along with Julianne Waldock, Mark Harvey, Nich Hall and Jim Rolfe, assisted with the collection of the samples. We also thank two anonymous referees for their constructive comments on the manuscript.

Funding was provided by the Commonwealth through the National Reserves System Co-operative Program of the Australian Nature Conservation Agency (now Environment Australia), together with funds provided by the Western Australian Department of Conservation and Land Management and the Western Australian Museum.

REFERENCES

Acosta, L.E. (1990). El genero *Cercophonius* Peters, 1861 (Scorpiones, Bothriuridae). *Boletin de la sociedad de Biologia de Concepcion* **61**: 7–27.

Beard, J.S. (1975). *Vegetation Survey of Western Australia. Pilbara. Explanatory Notes to Sheet 5, 1 : 1 000 000 Series.* University of Western Australia Press, Nedlands.

Beard, J.S. (1976). *Vegetation Survey of Western Australia. Murchison. Explanatory Notes to Sheet 6, 1 : 1 000 000 Series.* University of Western Australia Press, Nedlands.

Beard, J.S. (1980). A new phytogeographic map of Western Australia. *Western Australian Herbarium Research Notes* No. 3: 37–58.

Belbin, L. (1980). TWOSTEP: a program incorporating asymmetric comparisons that uses two steps to produce a dissimilarity matrix. CSIRO Division of Land Use Research Technical Memorandum 80/9. CSIRO, Canberra.

Belbin, L. (1991). Semi-Strong Hybrid Scaling: a new ordination algorithm. *Journal of Vegetation Science* **2**: 491–496.

Belbin, L. (1995). *PATN Technical Reference*. CSIRO Division of Wildlife and Ecology, Canberra.

Brown, C.A. (1996). Interpopulation and intersexual variation in pectine tooth counts in *Centruroides vittatus* (Scorpionida, Buthidae). *Journal of Arachnology* **24**: 262–264.

Czekanowski, J. (1932). Coefficient of racial likeness, und durchschnittliche differenz. *Anthropologischer Anzeiger* **9**: 227–249.

Keighery, G.J., Gibson, N., Lyons, M.N. and Burbidge, A.H. (2000). Flora and vegetation of the southern Carnarvon Basin, Western Australia. *Records of the Western Australian Museum* Supplement No. 61: 77–154.

Koch, L.E. (1977). The taxonomy, geographic distribution and evolutionary radiation of Australo-Papuan scorpions. *Records of the Western Australian Museum* **5**: 83–367.

Koch, L.E. (1981). The scorpions of Australia: aspects of their ecology and zoogeography. *In* Keast, A. (ed.), *Ecological Biogeography of Australia*: 873–884. W. Junk, The Hague.

Lamoral, B. (1978). Soil hardness, an important and limiting factor in burrowing scorpions of the genus *Opisthophthalmus* C.L. Koch, 1837 (Scorpionidae, Scorpionida). *Symposium of the Zoological Society of London* **42**: 171–181.

Locket, A. (1993). Scorpion distribution in a dune and swale mallee environment. *Memoirs of the Queensland Museum* **33**: 593–598.

Marples, T.G. and Shorthouse, D.J. (1982). An energy and water budget for a population of the arid zone scorpion *Urodacus yaschenkoi* (Birula 1903). *Australian Journal of Ecology* **7**: 117–127.

McKenzie, N.L., Rolfe, J.K., Aplin, K., Cowan, M. and Smith, L.A. (2000). Herpetofauna of the southern Carnarvon Basin, Western Australia. *Records of the Western Australian Museum* Supplement No. 61: 335–360.

Payne, A.L., Curry, P.J. and Spencer, G.F. (1987). An inventory and condition survey of the rangelands in the Carnarvon Basin, Western Australia. Technical Bulletin No. 78. Department of Agriculture, South Perth.

Polis, G.A. (1990). Ecology. *In* Polis, G.A. (ed.) *The Biology of Scorpions*: 247–293. Stanford University Press, Stanford.

Polis, G.A. (1993). Scorpions as model vehicles to advance theories of population and community ecology: the role of scorpions in desert communities. *Memoirs of the Queensland Museum* **33**: 401–410.

Polis, G.A., Myers, C.A. and Holt, R.D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20**: 297–330.

Polis, G.A. and Strong, D.R. (1996). Food web complexity and community dynamics. *American Naturalist* **147**: 813–846.

Polis, G.A. and Yamashita, T. (1991). The ecology and importance of predaceous arthropods in desert communities. *In* Polis, G.A. (ed.) *The Ecology of Desert Communities*: 180–222. University of Arizona Press, Tucson.

Smith, G.T. (1966). Observations on the life history of the scorpion *Urodacus abruptus* Pocock (Scorpionidae) and an analysis of its home sites. *Australian Journal of Zoology* **14**: 383–398.

Smith, G.T. (1995). Species richness, habitat and conservation of scorpions in the Western Australian wheatbelt. *Records of the Western Australian Museum* Supplement No. **52**: 55–66.

Smith, G.T. (1998). Density of the burrowing scorpion *Urodacus armatus* (Scorpiones; Scorpionidae) in relation to vegetation types: implications for population decline following agricultural clearing. *Pacific Conservation Biology* **4**: 209–214.

Sneath, P.H.A. and Sokal, R.R. (1973). *Numerical Taxonomy. The Principals and Practice of Numerical Classification*. W.H. Freeman, San Francisco.

Spiller, D.A. and Schoener, T.W. (1998). Lizards reduce spider species richness by excluding rare species. *Ecology* **79**: 503–516.

Volschenk, E.S. Smith, G.T. and Harvey, M.S. (2000). A new species of *Urodacus* from Western Australia, with descriptive notes on *Urodacus megamastigus* (Scorpiones: Urodacidae). *Records of the Western Australian Museum* **20**: 57–68.

Withers, P.C. and Smith, G.T. (1993). Effect of temperature on the metabolic rate and evaporative water loss of the scorpion *Urodacus armatus*. *Journal of Thermal Biology* **18**: 13–18.

Wyrwoll, K.-H., Courtney, J. and Sandercock, P. (2000). The climatic environment of the Carnarvon Basin, Western Australia. *Records of the Western Australian Museum* Supplement No. 61: 13–27.

Wyrwoll, K.-H., Stoneman, T., Elliott, G. and Sandercock, P. (2000). The geo-ecological setting of the Carnarvon Basin, Western Australia: geology, geomorphology and soils of selected sites. *Records of the Western Australian Museum* Supplement No. 61: 29–75.

Yamashita, T. and Polis, G.A. (1995). Geographical analysis of scorpion populations on habitat islands. *Heredity* **75**: 495–505.

Manuscript received 6 August 1998; accepted 26 June 1999.

Appendix 1 Number of specimens captured between August 1994 and August 1995. Locations for the quadrats in each survey area (Figure 1) are listed in Appendix A (this volume).

Quadrat	Species									
	Cercophonius granulosus	*Lychas* sp. 1	*Lychas* sp. 2	*Lychas* sp. 3	*Isometroides vescus*	*Isometroides* sp. 1	*Urodacus armatus*	*Urodacus hartmeyeri*	*Urodacus hoplurus*	*Urodacus mckenziei*
BB1	0	4	0	0	0	0	5	0	1	0
BB2	0	0	0	4	3	0	0	87	0	0
BB3	0	5	0	7	3	11	4	0	0	0
BB4	0	1	0	8	1	0	0	0	0	0
BB5	0	0	1	15	1	0	0	0	0	0
BO1	0	21	6	0	17	1	0	0	0	0
BO2	0	0	0	0	1	3	0	0	0	0
BO3	0	2	14	2	17	0	0	5	1	0
BO4	0	0	19	1	3	0	0	18	0	0
BO5	0	0	11	2	3	0	14	39	0	0
CU1	0	0	0	0	1	0	0	0	0	0
CU2	0	0	13	1	4	0	0	0	0	0
CU3	0	0	3	2	0	0	0	0	0	0
CU4	0	0	14	0	11	0	0	4	0	0
CU5	0	0	2	1	9	0	0	52	0	0
CU6	0	2	0	1	2	0	0	7	0	0
GJ1	0	11	1	2	0	0	39	0	0	0
GJ2	0	1	4	1	0	0	0	17	0	0
GJ3	0	0	40	0	1	0	0	3	0	0
GJ4	0	3	0	0	0	0	5	1	2	0
GJ5	0	2	1	0	0	0	0	0	0	0
KE1	0	0	0	0	0	0	0	1	0	0
KE2	0	0	2	0	0	0	0	3	0	0
KE3	0	8	0	1	0	0	1	6	0	0
KE4	0	9	0	0	0	0	0	0	0	0
KE5	0	15	0	0	0	0	6	12	0	0
MD1	0	0	1	0	0	1	10	3	1	10
MD2	0	0	4	0	0	0	11	1	0	0
MD3	0	0	0	3	0	0	0	0	0	0
MD4	0	1	21	0	0	0	0	10	0	0
MD5	0	2	3	0	0	0	0	48	2	0
MR1	0	29	1	0	0	0	0	1	3	0
MR2	0	11	0	0	1	0	4	3	0	0
MR3	0	0	0	0	0	0	6	65	0	0
MR4	0	4	1	1	0	0	0	34	0	0
MR5	0	1	0	0	0	0	0	8	0	0
NA1	0	1	0	1	0	0	2	0	0	0
NA2	0	3	0	2	0	0	1	21	0	4
NA3	0	0	0	5	1	0	0	6	0	4
NA4	0	6	1	8	0	0	0	9	0	0
NA5	0	0	0	4	0	0	0	3	0	0
NE1	0	8	0	7	0	0	0	18	0	0
NE2	0	0	0	4	1	0	7	3	0	4
NE3	0	3	5	0	0	0	1	14	0	0
NE4	0	1	1	1	0	0	0	1	0	0
NE5	0	2	0	0	0	0	0	9	0	0
PE1	0	0	0	0	0	0	0	0	0	0
PE2	0	0	13	0	2	0	0	2	0	23
PE3	0	0	8	0	0	0	0	0	0	0
PE4	0	8	1	0	0	0	2	90	0	0
PE5	0	0	11	2	3	0	0	0	0	0
WO1	0	5	0	0	0	0	0	34	0	0
WO2	0	5	7	2	1	0	0	30	0	0
WO3	0	12	54	0	0	0	0	40	0	0
WO4	0	9	1	0	3	0	0	0	0	0
WO5	0	8	0	0	0	0	12	9	6	0
ZU1	0	0	0	0	0	0	0	0	0	0
ZU2	0	0	0	1	0	0	0	0	0	0
ZU3	4	0	0	0	2	0	0	0	0	5
ZU4	0	0	0	0	0	0	6	2	0	42
ZU5	0	0	0	2	6	0	1	2	0	11