

Weak negative responses of spider diversity to short-term 'kraaling'

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ABSTRACT

The influence of short-duration, concentrated kraaling (enclosure) has been documented for plants, wildlife, and macro-invertebrates. However, limited information is available on its impact on ground-dwelling spiders. The purpose of this study was to assess the effect of short-duration kraaling, time since cattle removal, and microhabitat variables on spider assemblages in Matabeleland North Province, Zimbabwe. We used a matched-pair and space for time design (inside vs outside previously kraaled inclusions) across 11 sites, using four cattle herds (H_1 , H_6 , H_7 and H_{Nguni}). Spiders were sampled in the early and late rainy season with pitfall traps left open for 14-day sampling periods and emptied twice in each period. We captured 634 spiders, comprising 63 species in 44 genera and 18 families. The most abundant family was Lycosidae (37%; 16 spp.), followed by Gnaphosidae (15%; 10 spp.) and Salticidae (14.5%; 7 spp.). Generalised linear mixed models showed that generic richness was greater in sites with more bare ground. However, this effect was reversed in previously kraaled sites, and was particularly evident for spider abundance that responded negatively relative to unkraaled sites. Furthermore, with a U-shaped recovery, generic richness increased with time since kraaling. Model-based multivariate models showed that short-duration kraaling had a significant impact on spider assemblage structure, but this impact was relatively small compared with the effect of seasonality. Most of the species that made significant contributions to this multivariate response were less abundant in kraaled sites. Spider diversity, therefore, had a weak negative response to short-term kraaling. However, these impacts should also be assessed at broader scales, including areas where cattle go to graze during the day.

Keywords: Araneae, cattle, ground dwelling spiders, holistic planned grazing, rangeland, savanna, vegetation, Zimbabwe.

Introduction

Cattle enclosures, referred to as bomas (Stelfox 1986), livestock corrals (Augustine *et al.* 2009) or kraals (Huruba *et al.* 2018), have been part of daily management within livestock practices in most African rangelands for decades (Augustine 2003), and are used as overnight protection enclosures from theft and livestock predators. In addition, kraals provide confinements that enable milk extraction and the concentrated manure production for crop cultivation (Abagale and Ayuegabe 2015). Kraals are usually constructed of material ranging from thorn scrub branches (Augustine *et al.* 2009) and fences (Stelfox 1986). They are commonly circular or rectangular, the former being preferred to avoid bunching of livestock in corners (Borg 1996).

During the day, cattle normally graze within a few kilometres from the kraal. When inside the kraals at night, cattle dung and urine redistribute nutrients consumed during the day, forming heterogeneous nutrient-rich patches (Augustine 2003). Enclosures can be short-term, usually lasting for 7 days or less (Huruba *et al.* 2018), or long-term, where kraal owners utilise the same location for decades within the vicinity of water resources such as boreholes or shallow pans (Kizza and Areola 2010). The former is a recently developed practice that has since been incorporated as part of the innovative management approach called holistic planned grazing (Savory and Parsons 1980;

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Savory 1983). The latter comprises the traditional kraaling culture in most semi-arid regions in southern Africa.

The influence of abandoned kraal sites has been well documented (Kizza and Areola 2010; Chikorowondo *et al.* 2017, 2018). Abandoned kraal sites enhance the soil nutrient status, including nitrogen, phosphorus and potassium (Huruba *et al.* 2017, 2018; Muvengwi *et al.* 2018), and are important as nutrient sources utilised in crop production (Kangalawe *et al.* 2008). The nutrient-rich patches enhanced by kraaling have implications for vegetation diversity (Sibanda *et al.* 2016; Huruba *et al.* 2018), as well as their utilisation by wildlife (Huruba *et al.* 2018), as a result of grass resprouting and an increase in palatable grass species (Sibanda *et al.* 2016; Huruba *et al.* 2018).

Apart from work on diversity and abundance (Muvengwi *et al.* 2018) and functional diversity of macro-invertebrates (Chikorowondo *et al.* 2018), limited knowledge exists on the influence of previously kraaled enclosures on invertebrates, in particular spiders. Spiders are a megadiverse arthropod order, with almost 50 000 described species (World Spider Catalog 2022). They also occupy almost all possible terrestrial microhabitats (Turnbull 1973; Foelix 2011). Ecologically, spiders are important predators (Nyffeler and Birkhofer 2017) that commonly feed on insects, rendering spiders important natural control agents (Nentwig and Kobelt 2010). Spiders also feed on small mammals such as bats (Nyffeler and Knörnschild 2013), aquatic organisms such as fish (Nyffeler and Pusey 2014), and even other spiders (Wise 2006).

Spider diversity is dependent on several factors (Foelix 2011), including vegetation structure (Baldissera *et al.* 2004; Roberson *et al.* 2016), prey availability and competitive exclusion (Dennis *et al.* 2015; Rodriguez-Artigas *et al.* 2016). Spiders possess several characteristics that make them good bio-indicators (Churchill 1997; Marc *et al.* 1999) of environmental disturbances such as fire (Pryke and Samways 2012; Haddad *et al.* 2015), habitat modification (Haddad *et al.* 2010), habitat quality (Halaj *et al.* 1998) and grazing (Fuller *et al.* 2014; Schwerdt *et al.* 2018). They have also been used to determine the influence of other environmental changes, including leaf-litter structure (Castro and Wise 2009; Butler and Haddad 2011; Podgaiski *et al.* 2013), seasonality (Niemela *et al.* 1994; Weeks and Holtzer 2000; Mineo *et al.* 2010) and rainfall gradients (Churchill 1998). According to Podgaiski *et al.* (2013), spiders have the potential to re-occupy affected habitats within less than a month, and are therefore an appropriate taxon for testing the effect of short-duration kraaling (7 days) on spider assemblages inside previously kraaled inclusions and their surroundings.

This study examined the response of spider assemblages to short-duration kraaling. It was predicted that spider assemblages would be less diverse in kraaled sites than in adjacent non-kraaled (control) sites, because of grazing and trampling by cattle. Second, we assessed whether spider assemblages varied with time since kraal occupation. We

predicted that spider assemblages between the kraaled and non-kraaled sites would be more diverse with time since disturbance because of vegetation regrowth and recolonisation by mobile spiders. Last, we sought to identify the micro-habitat variables that influence spider assemblages around previously kraaled inclusions and their control sites. We predicted that spider diversity would be more diverse in structurally more complex vegetation, mainly through varied substrates, opportunities for web attachments, and shelter from predators (Fuller *et al.* 2014).

Materials and methods

Study sites

The study was conducted on the Debshan Ranch, a privately owned commercial cattle ranch 100 km northeast of Bulawayo within Insiza district, Matabeleland North Province, Zimbabwe (Fig. 1). The Debshan Ranch (19°35'S, 29°15'E) occupies 800 km² (Huruba *et al.* 2018), and utilises a holistic management approach (Mberi 2013). Mean annual rainfall is 639 mm, the rainy season starts in November, peaks in December, averaging 144 mm, and ends in March–April. Annual average temperature is 18°C, October is the hottest month (average temperature 21°C), and July the coldest (average temperature 12.4°C). Average daily humidity is 55% (Climate-data.org 2019).

The ranch falls under agro-ecological natural region IV (Cousins 1992), a livestock production area that also cultivates drought-tolerant crops such as sorghum, millet and rapoko. It is also a semi-extensive savanna biome suitable for forestry, wildlife and tourism (Mugandani *et al.* 2012). Elevation is between 1230 and 1414 m above sea level (Dunham *et al.* 2003), and soils are coarse-grained yellowish-brown loamy sands, resulting from granite, forming soils that are usually infertile and poorly drained, ultramafic or mafic rocks that give rise to productive red soils, and dark brown clayey soils (Robertson 2013). The soils support floral types that are normally dispersed in a catenae pattern (Dunham *et al.* 2003) that comprises bushlands, grasslands, wetlands and woodlands, such as (1) *Julbernadia–Stereochlaena* woodland, (2) *Combretum hereroense–Hyparrhenia* mixed bushlands, (3) *Colophospermum* bushlands, (4) *Terminalia–Schizachyrium* bushlands, (5) Riverine woodland, and (6) *Hyperthelia vlei* grassland (Robertson 2013).

Spider sampling

Ground-dwelling spiders were collected using pitfall traps at 22 sites × 4 herds = 88 sites during the early rainy season sampling period (November 2017) and at 22 sites × 3 herds = 66 sites during the late-summer sampling period (March 2018). Herd 7 was not sampled in the late-summer sampling period because of the inaccessibility of roads caused by heavy rainfall (Appendix Table A1). The 88

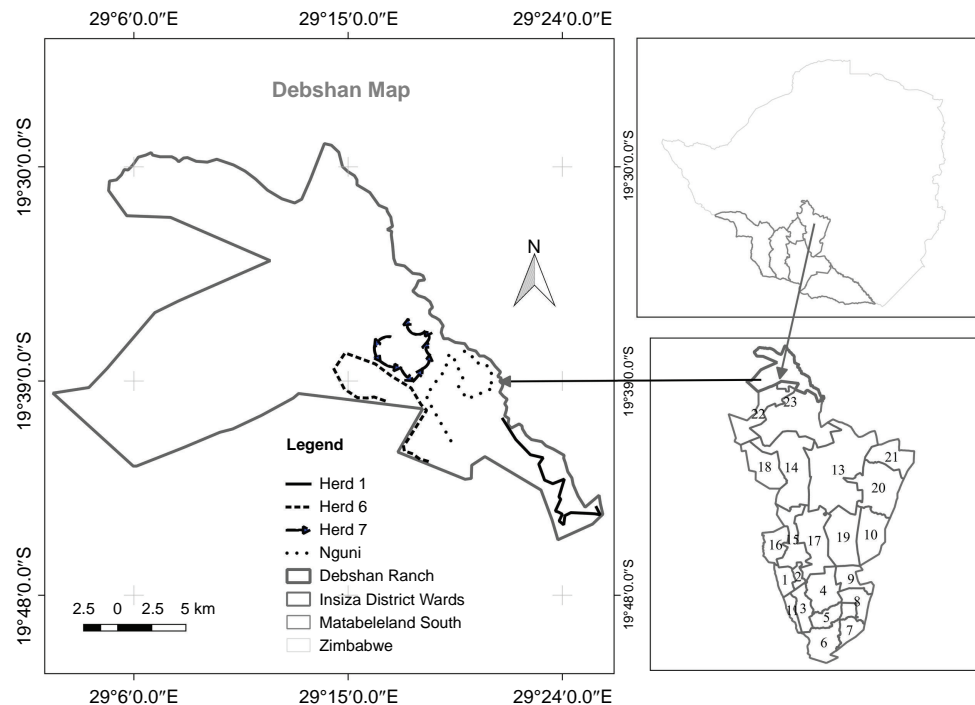


Fig. 1. Map of Debshan Ranch and its location within Zimbabwe, showing the distribution of the spider sampling points within each replicate herd (Herd 1, Herd 6, Herd 7 and Herd Nguni) during the early (November 2017) and late (March 2018) rainy seasons.

sites comprised kraaled and adjacent non-kraaled (control) plots (Fig. 1). Each herd was considered a replicate, and contained approximately 350–396 cattle (Huruba *et al.* 2018). At each site, a matched-pair design was employed, consisting of two plots, each containing five pitfall traps, with one plot inside the kraal and one outside the kraal. The pitfall traps in a plot were arranged in a cross (Fig. 2), for a total of 880 pitfall traps (22 sites \times 4 herds \times 10 traps) across all sites. Pitfall traps were 10 m apart, and the plots (kraaled and non-kraaled) were 50 m apart (Fig. 2). Pitfall traps consisted of glass bottles 14 cm deep and 9 cm wide at the mouth, filled with 100 mL of 70% propylene glycol, placed inside a plastic PVC pipe and buried to their rims. Pitfall traps were left open for 14 day sampling periods, and emptied twice in each sampling period. To reduce seasonal influences on spiders (Whitmore *et al.* 2002; Muelelwa *et al.* 2010), sampling was conducted in early summer (November 2017) and late summer (March 2018), because these are the periods when spider activity is considered to be relatively high within the savanna region (Muelelwa *et al.* 2010). At the end of each sampling period, the contents of the sampling bottles were collected, and sorted. Adult specimens were sorted into morphospecies and identified to species level where possible, with all the juveniles being identified at least to genus level. Spider identification to family level was undertaken using the keys of Dippenaar-Schoeman and Jocqué (1997), and further to morphospecies by the first and third authors. All adult spider specimens collected were

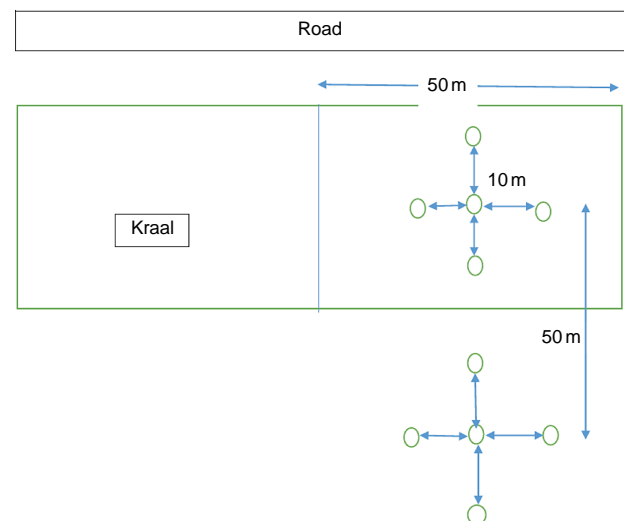


Fig. 2. Format used for the arrangement of pitfall traps used to sample spider diversity inside and outside the previously kraaled sites at Debshan Ranch, Zimbabwe. Pitfall traps were placed 10 m apart and at least 25 m from the kraal boundaries.

deposited in the Department of Arachnology, Natural History Museum in Bulawayo.

Micro-habitat variables

Micro-habitat variables were assessed by placing a 1 m \times 1 m quadrat over each pitfall trap and taking a photograph.

Each sampled pitfall trap was photographed in both November and March. Images were visually inspected and the percentage cover of the following micro-habitat variables was estimated: grass, bare ground, leaf litter, coarse woody debris (wood with a diameter > 5 cm), cow dung, and rock, by utilising the methodology of [Dethier *et al.* \(1993\)](#). In each of the 88 kraaled and adjacent non-kraaled (control) sites, a 40 m transect was established inside and outside the kraal within the plots. Along each transect, 10 grasses approximately 1 m apart were selected and marked with plastic ear tags and the tallest vertical point of each grass with the leaf blade extended was measured, and mean grass height (cm) determined at each site.

Data analysis

All statistical analyses were performed using R statistical software version 4.1.2 ([R Core Team 2021](#)). Data for spiders were pooled within a plot, i.e. catches from five pitfall traps in a plot within each 14day sampling period were pooled. Sample coverage was calculated using the iNEXT package ([Hsieh *et al.* 2016](#)), to enable estimation of the percentage of total species obtained in a sample. Its inverse counterpart is the likelihood that the following sampled individual may be a previously unsampled species ([Chao and Jost 2012](#)).

The relationships between micro-habitat structure variables were summarised using principal component analysis (PCA). By reducing data, collinearity that hinders interpretation and analysis of ecological data ([Graham 2003](#)) is avoided while retaining information from such variables. These derived variables are then included as predictors in regression models ([Ellison 2004](#)). The first component (PC1, explained variance = 41%) was moderately negatively correlated with microhabitat variables such as percentage grass cover (−0.52) and mean grass height (cm; −0.46), and positively with percentage bare ground cover (0.41; Appendix [Fig. A1a](#)). The second component (PC2, explained = 16%) was correlated positively with percentage rock cover (0.73) and negatively with percentage leaf litter cover (−0.60; [Fig. A1a](#)). The third component (PC3, explained variance = 15%) and was positively correlated with percentage coarse woody debris cover (0.44), percentage leaf litter cover (0.44) and percentage rock cover (0.49), and negatively with percentage dung cover (−0.48; [Fig. A1b](#)). Original variables that were strongly correlated with individual PCA axes with a cut-off point of 0.4 ([Legendre and Legendre 1998](#)) were utilised in the discussion of the results ([Table A2](#)).

Factors affecting spider abundance and generic richness were modelled using generalised linear mixed models with a log-link function, with either Poisson or negative binomial distributions, using the ‘glmer’ or ‘glmer.nb’ functions in the lme4 package ([Bates *et al.* 2015](#)), depending on the degree of over-dispersion of dependent variables. Candidate models were subsets of the global model that contained all predictors, namely time since kraal removal, PC 1, 2 and 3, and the paired

treatment (kraaled vs non-kraaled), as well as the interactions between treatment and these variables. A quadratic term for time since kraaling was also included to account for any non-linear responses of abundance and generic richness over time. Herds nested within survey were included as random factors. Model residuals were inspected for overdispersion, heteroscedacity and normality, as well as influential observations ([Zuur and Ieno 2016](#)). Model selection was conducted using an information-theoretic approach based on Akaike Information Criterion (AIC; [Burnham and Anderson 2002](#)). The best model was that with the lowest AIC, but we also report on those models that differed by less than 2 AIC values from the best model. To determine variation explained by fixed factors and that explained by the whole model, marginal R_m^2 and conditional R_c^2 respectively were also calculated ([Nakagawa and Schielzeth 2013](#)).

Model-based multivariate analysis using generalised linear models with negative binomial distribution and log-link functions was used to test for differences in composition between kraaling and no kraaling, time since kraaling, PC1, PC2 and PC3. This was undertaken using the R package mvabund ([Wang *et al.* 2018](#)). This approach accounts for confounding mean–variance relationships, which are common in abundance data containing many zeros ([Warton *et al.* 2015](#)). The likelihood-ratio statistics for each species were summed, resulting in a community-level measure for each predictor. The PIT-residual bootstrap method was utilised by resampling 999 rows of the dataset to derive *P*-values for the variables ([Warton *et al.* 2017](#)). Model assumptions were evaluated by visually examining plots of residuals for any non-random patterns.

Results

In total, 634 individual spiders in 63 identified species representing 44 genera and 18 families were collected ([Table A3](#)). Of these, 451 were adults identified to species level, and 183 were juveniles identified to genus level. In total, 430 individuals were collected in December 2017, and 204 in March 2018. The most common families were Lycosidae and Gnaphosidae ([Table A3](#)). Nearly one quarter of the mature spiders were either *Allocosa umtalica* (Purcell, 1903) (101 specimens) or *Asemesthes paynteri* Tucker, 1923 (61 specimens). The four most common species represented 40% of the total spiders sampled. One species is possibly new, on the basis of the identifications of specialists; 45 species were encountered only once. Sample-based rarefaction curves showed higher genera richness of spider assemblages in the unkraaled sites than in the kraaled sites, although confidence intervals did overlap ([Fig. 3](#)). Furthermore, sample coverage for both the kraaled and the adjacent non-kraaled (control) sites was relatively high (> 94%), suggesting that sampling captured a significant portion of the spider assemblages at Debshan Ranch.

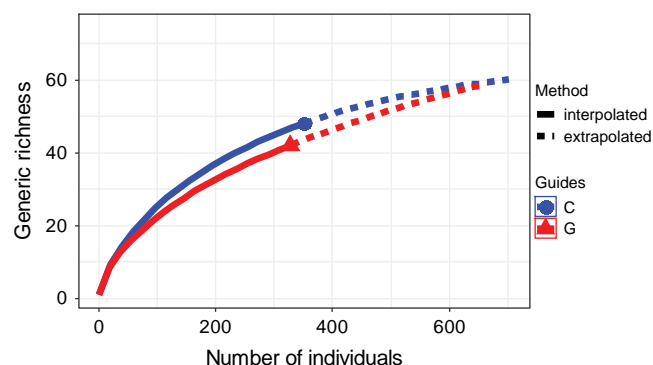


Fig. 3. Sample sized based rarefaction and extrapolation sampling curves with 95% confidence intervals based on a bootstrap method with 200 replications comparing spider genera richness between the 'unkraaled' sites (C) and the kraaled sites (G). Solid lines = rarefaction; dotted lines = extrapolation; confidence intervals = shaded areas.

Effects on spider abundance and generic richness

Spider generic richness was related to microhabitat variables, increasing with $PC1_{RICH}$ ($R_m^2 = 0.15$, $P = 0.1$; Table 1), suggesting more genera and individuals in sites that have lower vegetation cover, i.e. that are more open $PC1$ (bare ground, logs), and have more dung. However, this effect was reversed in plots that were previously kraaled, and was particularly evident for spider abundance where the interactions of kraaling with $PC1_{ABUN}$ ($R_m^2 = 0.18$, $P = 0.05$; Table 1, Fig. 4) and $PC3_{ABUN}$ ($R_m^2 = 0.18$, $P = 0.1$; Table 1, Fig. 4) affected spider abundance negatively relative to plots that were not kraaled. Furthermore, there was also an effect of time since kraal removal, with generic richness increasing with time since kraaling ($R_m^2 = 0.15$, $P = 0.1$; Table 1, Fig. 4), with a non-linear component where there is an overall decrease in richness and then a recovery.

Effects on spider assemblages

The multivariate generalised linear models showed significant effects of short-duration kraaling, but those were relatively small when compared with that of sampling season and time since kraaling on spider genera composition (Table 2). In other words, the differences among the spider assemblages were more evident between sampling season and time since kraal removal than were those observed between previously kraaled sites and their surroundings. Furthermore, there was a weak but significant effect of two interactions, namely, short-duration kraaling interacted with both $PC1$ (bare ground, logs) and also $PC3$ (dung). Most of the genera that responded significantly to short-duration kraaling had a negative response, including *Diores*, *Ranops*, *Thanatus*, *Evippomma* and *Langona*. Only *Proevippa* responded negatively to more open habitat, whereas *Ranops* and *Hermippus*, in particular, responded positively. The negative response of spider diversity to short-duration kraaling is further exemplified by the presence of several genera that generally were

less diverse within the short-duration kraaled sites with comparable microhabitat characteristics than were those found in the control (non-kraaled) plots (Fig. 5).

Discussion

Effects of short-duration kraaling

In line with our first prediction, non-kraaled (control) sites were more diverse than kraaled sites. De Keer and Maelfait (1988) observed that spiders mostly oviposit or overwinter in ungrazed areas to avoid unfavourable climatic conditions. Despite the limited variation (18%) explained by the models, even with the random factors (herd nested within survey), there were weak negative responses of spider diversity to short-duration kraaling. We found lower generic richness and abundance in the kraaled sites than in the adjacent non-kraaled (control) sites, with the greatest variation being explained by seasons. These patterns were consistent with previous studies (Gibson *et al.* 1992a; Bromham *et al.* 1999; Sebata 2020), which found less diverse spider assemblages in grazed areas. Grazing leads to the modification of vegetation by cattle through trampling (Fuller *et al.* 2014), reducing the suitability of the biotope, because structure of vegetation is a key element that affects habitat choice by most spiders (Štokmane and Spun̄gis 2016; Lafage *et al.* 2019) and other invertebrates (Crist *et al.* 2006).

Furthermore, most spiders have excellent dispersal powers, with many Lycosidae and Gnaphosidae ballooning, especially as juveniles (Mrzljak and Wiegler 2000). Ballooning is a 'tiptoe' behaviour, where an individual straightens its legs, balancing on the tips of its tarsi while raising its abdomen, thereby releasing a silken dragline in the air, while a drag-induced lift of the spider's body by wind is achieved (Weyman 1993; Zhao *et al.* 2017). Ballooning allows dispersal, but mainly over short distances (Pedley and Dolman 2014). For example, *Pardosa monticola* (Clerck, 1757) may disperse no more than 280 m over its lifetime (Bonte *et al.* 2003), with females able to balloon between 30 and 40 m per day during natal dispersal (Bonte *et al.* 2007). Several negative and positive factors that elicit ballooning behaviour have been reported (Weyman 1993), ranging from temperature, humidity, wind, vibration, light and stress. Grazing and trampling by cattle usually causes vibration that can be detected by the spider legs, and may induce ballooning of spiders away from the kraaled sites. This suggests that the small differences between the inside and outside of kraals may have been the result of the high dispersal power by either walking or ballooning (Weyman *et al.* 2002), which enabled spatial exchange among spider assemblages, because the sites among the treatments were separated by only 50 m.

Beta diversity has been generally defined as the variation in species composition of assemblages among sites (Whittaker 1960), and is determined by two different phenomena acting

Table 1. Best models for the relationship between spider generic richness and abundance and its associated predictor variables. Only the models that were within 2 AIC values of the best model and predictors that were included in these models are shown.

Variable	PCI	PC2	PC3	Time ^A	Time2	Kraal ^B	PCI × Kraal	PC3 × Kraal	d.f.	AICc	ΔAICc	Weight	R ² conditional	R ² marginal
Generic richness														
Model 1	*		n.s.	*	*	†	**	*	10	1046.28	0	0.25	0.15	0.07
Model 2				*	*				5	1046.99	0.71	0.17	0.12	0.04
Model 3	†			*	*	n.s.	*		6	1047.38	1.10	0.14	0.14	0.05
Model 4				*	*	n.s.			6	1047.58	1.3	0.13		
Model 5			n.s.	*	*				6	1047.81	1.52	0.12		
Model 6		n.s.		*	**				11	1048.12	1.84	0.1		
Averaged coefficient (full average)	0.1	-0.006	0.04	0.09*	0.12*	-0.09	-0.13	-0.09						
Spider abundance														
Model 1	†	†	n.s.	n.s.	†	n.s.	**	*	11	1237.40	0	0.37	0.18	0.1
Model 2	†		†		†	n.s.	**	*	10	1237.83	0.43	0.5	0.17	0.09
Model 3	†		n.s.	n.s.	†	n.s.	**	*	10	1238.65	1.25	0.2	0.17	0.09
Model 4	†	†				n.s.	**	**	9	1239.35	1.95	0.14	0.16	0.08
Averaged coefficient (full average)	0.23 [†]		0.17	0.05	0.07	-0.2	-0.42**	-0.37*						

^ATime, time since kraal removal.^BKraal, Kraal treatment.Significant effects: † $P < 0.1$; * $P < 0.05$; ** $P < 0.01$.

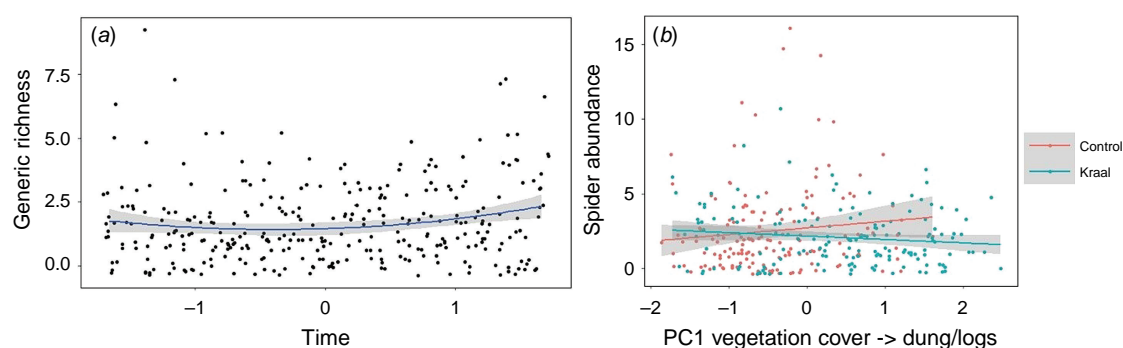


Fig. 4. (a) Response of ground-dwelling spider genera richness to time since kraaling, and (b) spider abundance response to increased cover of coarse woody debris, dung and bare ground in plots that were kraaled and those that were adjacent unkraaled (control) at Debshan Ranch, Zimbabwe, with log-regression line and 95% confidence intervals.

Table 2. Results of model-based analysis of multivariate abundance data (mvabund) of the response of ground-dwelling spider communities to kraaling treatment (inside vs outside previously kraaled inclusions), time since kraal removal (<2, 2, 4, 6, 8 and 10 months), season (early sampling season (November) vs late sampling season (March)) and PC1, PC2 and PC3 microhabitat characteristic variables.

Item	Residual degrees of freedom	d.f. diff	Deviance	P
Intercept	176			
Season	175	1	84.01	0.001**
Herd	172	3	63.36	0.04*
Kraal	171	1	29.5	0.02*
Time since kraal removal	170	1	23.76	0.11
PC1	169	1	8.96	0.87
PC2	168	1	14.89	0.41
PC3	167	1	12.92	0.57
Kraal: time since kraal removal	166	1	16.42	0.18
Kraal:PC1	165	1	25.22	0.03*
Kraal:PC2	164	1	14.04	0.16
Kraal:PC3	163	1.32	32.47	0.002**

P-values from *0.05 to 0.01; **0.01 to 0.001.

on spider assemblages, namely spatial species turnover (the changeover of species between seasons) and nestedness (the loss and gain of species across time; [Carvalho et al. 2012, 2013](#)). Whereas richness differences are determined by the net loss (or gain) of species from site to site or from one date to another, replacement refers to the substitution of species between sites or points in time. Although the contribution of both sources of dissimilarity is usually not disentangled ([Baselga 2010](#)), the dissimilarity of spider assemblages

between the short-duration kraaled sites and their surroundings is most likely due to the change in generic richness and abundance. In all likelihood, short-duration kraaled sites do not complement the unkraaled (control) sites, but are a smaller subset of the species found around the kraals.

Despite the sampling being conducted in the rainy season, seasonality was an important predictor of spider assemblages, with a lower spider abundance caught in the late rainy season (March) than in the early rainy season (December). These findings support those of [Muelelwa et al. \(2010\)](#), who recorded higher spider abundance and species richness in early summer (November) than in autumn (March). They attributed their results to maturing of overwintering juveniles and subadults, captured as adults ready for mating during the rainy season of the early summer. By the late-summer rainy season, most adults have died and assemblages are dominated by juveniles ([Foord et al. 2008; Muelelwa et al. 2010](#)). However, in this study, the differences in spider abundance may have been affected by the heavy rains that fell during the late summer season, which may have led to a reduction in spider activity, as reported elsewhere ([Haddad et al. 2015; Queiroz and Gasnier 2017](#)).

Effects of time since kraal removal

In line with our second prediction, with a U-shaped recovery, spider generic richness increased with time since kraaling. The lowest generic richness was recorded when cattle occupied the short-duration kraals, most probably a consequence of livestock trampling, which resulted in the development of bare soil ([Gibson et al. 1992a, 1992b](#)). Bare soil implies reduced raw materials for minerals and nutrients for most organisms ([Rampai 2017](#)), and has been negatively associated with spider species richness under trees ([Barton et al. 2017](#)). At the time of abandonment, short-duration kraals are usually bare and mostly covered by dung above the soil-surface layer ([Sibanda et al. 2016](#)), which indirectly leads to the subsequent increase in grass cover with time since

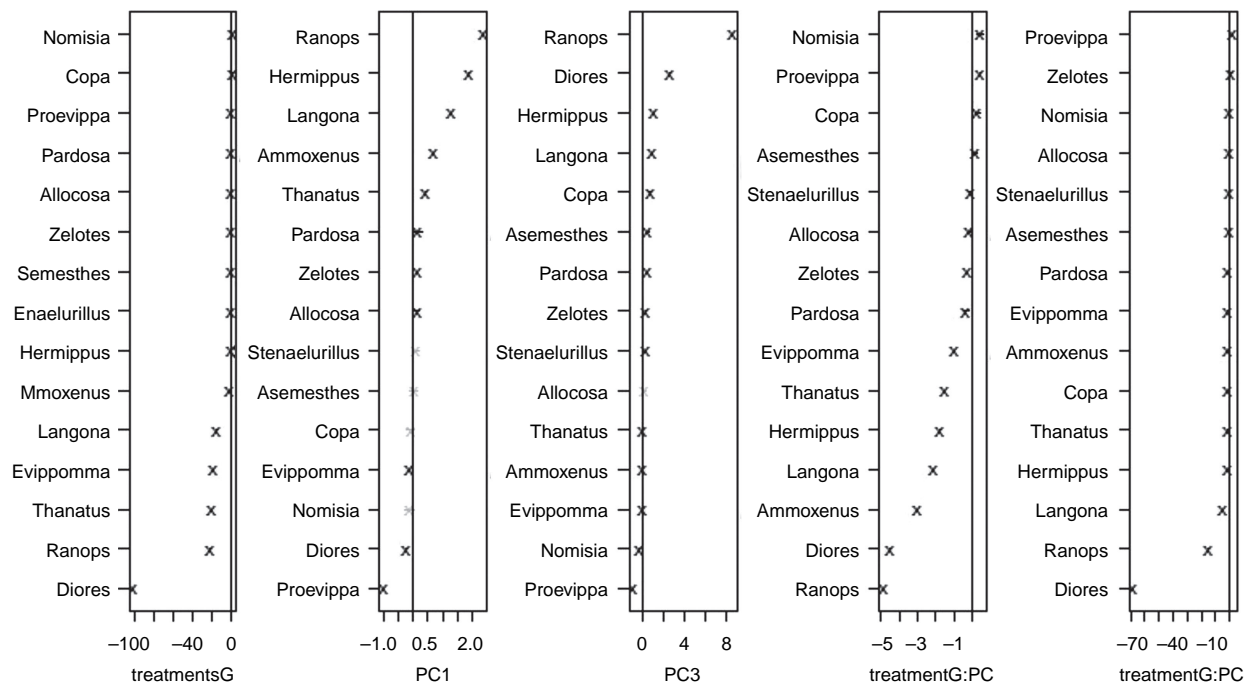


Fig. 5. Point estimates for coefficients and their 95% confidence of the predictor variables included in the best negative binomial generalised linear latent variable model.

kraal removal (Huruba et al. 2018). Similar to other studies, grass re-establishment at Debshan was rapid following kraal removal (Reid and Ellis 1995), most probably a consequence of nutrient-reserve patches (a consequence of dung and urine deposition) that develop in previously kraaled inclusions (Augustine 2003). Grass cover can increase faster during shorter periods of cattle occupation (4 and 7 day treatments) than in corals where cattle occupation was longer (14 and 28 day treatments), owing to the more hospitable conditions of moderate versus excessive cattle waste deposits (Veblen and Porensky 2019). In addition, there is usually less grass trampling in short-duration kraals, allowing for more rapid regrowth after rains than with excessive trampling in long-duration kraals. Vegetation structure such as plant height can reflect the diversity of potential invertebrate prey and habitat for spiders (Gallé et al. 2011), thereby potentially supporting the different species composition at each time interval. Spiders can benefit from higher grass cover, which provides essential services to most invertebrates (Gibson et al. 1992a, 1992b); hence, the observed increase in spider diversity recorded with time since kraal removal.

Effects of microhabitat variables

Contrary to our third hypothesis, spider genera abundance and richness did not benefit from greater vegetation structure and cover, but instead, several genera and individuals were obtained in sites that had less vegetation cover, i.e. areas of bare ground and coarse woody debris. Lycosidae

have been reported to increase in abundance with increased disturbance (Pedley and Dolman 2014). Similarly, in this study wolf spiders were sampled at higher densities inside than outside kraals, indicating a preference for increased levels of disturbance, making this group good indicators of these changes (Piacentini and Ramírez 2019). There are several possible reasons for this, namely that wolf spiders chase their prey at ground level, thereby making open habitat the optimal foraging ground. Also, because this group hunts actively by running, warmer and drier ground is usually more suitable than the unkraaled plots with usually lower numbers of suitable prey (Suominen 1999). Furthermore, the most abundant species collected belonged to Lycosidae, which are usually found in high numbers in open and disturbed habitats (Nyffeler 1999; Mallis and Hurd 2005), because they are normally the first species to inhabit disturbed lands (Pedley and Dolman 2014). For example, *Pardosa* species have been reported to achieve dense populations in open barren lands (Buddle and Rypstra 2003; Mallis and Hurd 2005). Here, two species, *P. manubriata* Simon, 1898 (15%) and *P. crassipalpis* Purcell, 1903 (5%), were the second- and third-most abundant lycosid species sampled, after *Allocosa umtalica* (32%). However, since sampling took place only within the miombo woodlands, further research in other woodland types is recommended, to determine their degree of habitat specificity and biomonitoring potential.

In conclusion, diversity and abundance of ground-dwelling spiders were enhanced in sites with more bare

ground within the miombo woodlands of the Debshan Ranch. However, this effect disappeared in sites previously kraaled. The differential response of spider assemblages to short-duration kraaling in the present study showed the importance of structurally complex habitats, essential for a wide variety of invertebrates with contrasting life traits. Despite the initial decrease in spider fauna because of short-duration kraaling, spider richness did show a U-shaped recovery, suggesting that the 10 month resting period is essential to ensure recovery of the spider diversity. Further research on the impacts of spider assemblages within a broader landscape context would contribute to the knowledge on short-duration kraaling effects on spider assemblages, and help develop management recommendations within south-western Zimbabwe.

Conservation significance and management recommendations

In Zimbabwe, conservation approaches currently consider vertebrates and plants, believing that protection given to these groups will benefit arthropods such as spiders. This approach usually does not provide for the protection of threatened and rare spider species (Lovell *et al.* 2009). Spiders contrast in their responses to disturbance, and managers may decide to protect spider communities by targeting species of concern and implementing species-specific management plans. However, such information requires long-term monitoring of spider assemblages within a region, so as to provide a complete database of all possible spiders in each biotope, which will later contribute to recognising the rare, endemic, and threatened species within that region. Species need to be ranked according to the effects of grazing and trampling of the holistic management approach.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

Conflicts of interest. The authors declare that they have no conflicts of interest.

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Appendix

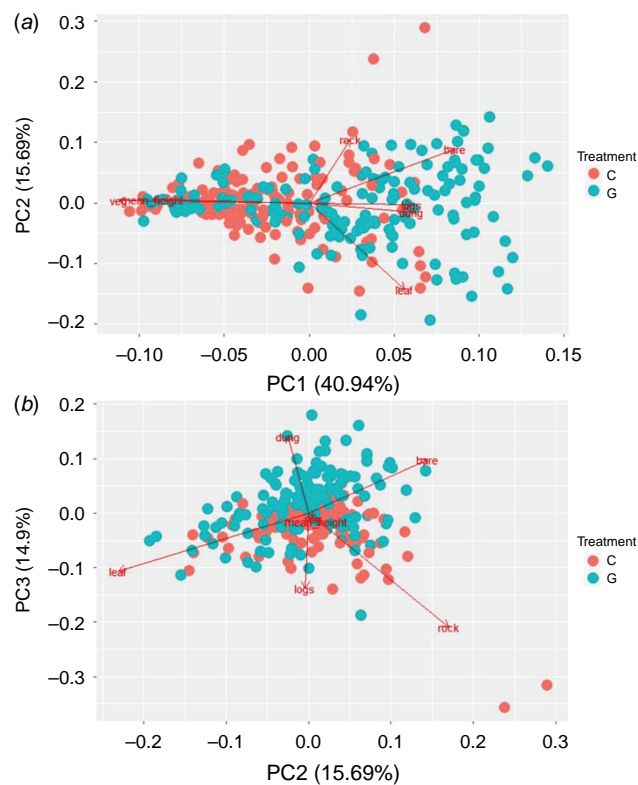


Fig. A1. Biplots of (a) PC1 and PC2, and (b) PC2 and PC3 of the principal-component analyses of micro-habitat structure variables measured inside previously kraaled inclusions and their surrounding areas at Debshan Ranch, Zimbabwe.

Table A1. Geographic coordinates of each of the 22 sites sampled in each herd at the Debshan Ranch, Shangani, Zimbabwe, in November 2017 and March 2018.

Site		Herd 1		Herd 6		Herd 7 ^A		Herd Nguni	
1	No kraaling	S 19.69107	E 29.36696	S 19.64025	E 29.28051	S 19.64025	E 29.28051	S 19.65937	E 29.30470
2	During cattle occupation	S 19.67682	E 29.35800	S 19.62839	E 29.26832	S 19.62839	E 29.26832	S 19.66359	E 29.30591
3	Cattle removed 2 weeks	S 19.70195	E 29.37732	S 19.63600	E 29.27242	S 19.63600	E 29.27242	S 19.65645	E 29.30718
4	Cattle removed 4 weeks	S 19.70400	E 29.38647	S 19.64098	E 29.28668	S 19.64098	E 29.28668	S 19.64968	E 29.31193
5	Cattle removed 6 weeks	S 19.70825	E 29.38339	S 19.64497	E 29.28898	S 19.64497	E 29.28898	S 19.64270	E 29.31764
6	Cattle removed 8 weeks	S 19.72186	E 29.39313	S 19.63866	E 29.30556	S 19.63866	E 29.30556	S 19.63724	E 29.32519
7	Cattle removed 10 weeks	S 19.71991	E 29.39707	S 19.64994	E 29.29533	S 19.64994	E 29.29533	S 19.63164	E 29.32266
8	Cattle removed 12 weeks	S 19.71873	E 29.40114	S 19.64422	E 29.30052	S 19.64422	E 29.30052	S 19.63172	E 29.32062
9	Cattle removed 14 weeks	S 19.73152	E 29.39768	S 19.64205	E 29.30202	S 19.64205	E 29.30202	S 19.69245	E 29.32191
10	Cattle removed 16 weeks	S 19.74315	E 29.42289	S 19.62868	E 29.31593	S 19.62868	E 29.31593	S 19.63012	E 29.33309
11	Cattle removed 18 weeks	S 19.73836	E 29.42373	S 19.62694	E 29.31413	S 19.62694	E 29.31413	S 19.63012	E 29.33611
12	Cattle removed 20 weeks	S 19.74376	E 29.42631	S 19.62601	E 29.31075	S 19.62601	E 29.31075	S 19.63163	E 29.33611
13	Cattle removed 22 weeks	S 19.74297	E 29.41851	S 19.63155	E 29.30695	S 19.63155	E 29.30695	S 19.63722	E 29.33861
14	Cattle removed 24 weeks	S 19.74234	E 29.40565	S 19.62930	E 29.30505	S 19.62930	E 29.30505	S 19.63723	E 29.33862
15	Cattle removed 26 weeks	S 19.74806	E 29.39758	S 19.62251	E 29.30556	S 19.62251	E 29.30556	S 19.63806	E 29.34593
16	Cattle removed 28 weeks	S 19.75067	E 29.40096	S 19.61911	E 29.30643	S 19.61911	E 29.30643	S 19.64313	E 29.35061
17	Cattle removed 30 weeks	S 19.74418	E 29.40181	S 19.61567	E 29.30366	S 19.61567	E 29.30366	S 19.65482	E 29.35157
18	Cattle removed 32 weeks	S 19.74141	E 29.39508	S 19.60712	E 29.29185	S 19.60712	E 29.29185	S 19.64731	E 29.34930
19	Cattle removed 34 weeks	S 19.74192	E 29.39731	S 19.61065	E 29.29114	S 19.61065	E 29.29114	S 19.64973	E 29.34956
20	Cattle removed 36 weeks	S 19.74323	E 29.39994	S 19.62635	E 29.26821	S 19.62635	E 29.26821	S 19.66277	E 29.33269
21	Cattle removed 38 weeks	S 19.73297	E 29.39868	S 19.61976	E 29.27555	S 19.61976	E 29.27555	S 19.65349	E 29.32700
22	Cattle removed 40 weeks	S 19.71975	E 29.38755	S 19.61897	E 29.27895	S 19.61897	E 29.27895	S 19.64792	E 29.33011

^ANot sampled in late-summer (March 2018) because of inaccessibility of roads caused by heavy rainfalls.

Table A2. Eigenvectors of PCA Axes 1, 2 and 3 (used in further analyses) for original variables characterising micro-habitat characteristics measured at each site.

Variable	PC1	PC2	PC3
Mean grass height (cm)	-0.46	0.03	-0.08
Grass cover (%)	-0.53	-0.03	0.06
Leaf-litter cover (%)	0.30	-0.60	0.44
Rock cover (%)	0.05	0.73	0.49
Coarse woody debris (%)	0.36	0.01	0.44
Dung cover (%)	0.35	-0.05	-0.48
Bare ground (%)	0.41	0.37	-0.37

PCA included the variables mean grass height, grass cover, leaf-litter cover. Cut off for important loading was 0.4.

Table A3. Family composition of the ground-dwelling spider fauna collected from Debshan Ranch, Zimbabwe.

Family	Genera and species	Functional group	Control	Kraal	Total
Ammoxenidae	<i>Ammoxenus daedalus</i>	Free-living ground dwellers	4	3	7
Araneidae	<i>Neoscona hirta</i>	Web dwellers	1	0	1
	<i>Nephila inaurata</i>	Web dwellers	2	0	2
Cheiracanthiidae	<i>Cheiracanthium furculatum</i>	Plant wanderers	0	1	1
	<i>Cheiracanthium minshullae</i>	Plant wanderers	1	0	1
Corinnidae	<i>Copa flavoplumosa</i>	Free-living ground dwellers	2	7	9
Ctenidae	<i>Afroneutria velox</i>	Free-living ground dwellers	1	0	1
Gnaphosidae	<i>Asemesthes paynteri</i>	Free-living ground dwellers	43	35	78
	<i>Ibala minshullae</i>	Free-living ground dwellers	0	1	1
	<i>Nomisia varia</i>	Free-living ground dwellers	2	6	8
	<i>Trephopoda aplanita</i>	Free-living ground dwellers	1	0	1
	<i>Trephopoda parvipalpa</i>	Free-living ground dwellers	1	0	1
	<i>Xerophaeus vickermani</i>	Free-living ground dwellers	1	0	1
	<i>Zelotes bastardi</i>	Free-living ground dwellers	1	0	1
	<i>Zelotes brennanorum</i>	Free-living ground dwellers	0	1	1
	<i>Zelotes frenchi</i>	Free-living ground dwellers	0	1	1
	<i>Zelotes tuckeri</i>	Free-living ground dwellers	1	0	1
Hersiliidae	<i>Hersilia sericea</i>	Plant wanderers	2	0	2
Locranidae	<i>Rhaeboctesis secundus</i>	Plant wanderers	1	2	3
	<i>Rhaeboctesis trinotatus</i>	Plant wanderers	2	0	2
Lycosidae	<i>Allocosa faberrima</i>	Free-living ground dwellers	1	0	1
	<i>Allocosa lawrencei</i>	Free-living ground dwellers	5	0	5
	<i>Allocosa marshalli</i>	Free-living ground dwellers	0	1	1
	<i>Allocosa schoenlandi</i>	Free-living ground dwellers	6	9	15
	<i>Allocosa umtalica</i>	Free-living ground dwellers	62	53	115
	<i>Amblyothele ecologica</i>	Free-living ground dwellers	1	0	1
	<i>Evippomma plumipes</i>	Free-living ground dwellers	1	0	1
	<i>Evippomma squamulatum</i>	Free-living ground dwellers	3	0	3

(Continued on next page)

Table A3. (Continued)

Family	Genera and species	Functional group	Control	Kraal	Total
	<i>Pardosa crassipalpis</i>	Free-living ground dwellers	6	12	18
	<i>Pardosa leipoldti</i>	Free-living ground dwellers	3	0	3
	<i>Pardosa manubriata</i>	Free-living ground dwellers	30	27	57
	<i>Proevippa albiventris</i>	Free-living ground dwellers	2	3	5
	<i>Proevippa fascicularis</i>	Free-living ground dwellers	3	0	3
	<i>Schizocosa darlingi</i>	Free-living ground dwellers	1	1	2
	<i>Trabea purcelli</i>	Free-living ground dwellers	0	1	1
	<i>Zenonina albocaudata</i>	Free-living ground dwellers	0	2	2
Oxyopidae	<i>Oxyopes dumonti</i>	Plant wanderers	0	1	1
	<i>Oxyopes hoggi</i>	Plant wanderers	1	0	1
Philodromidae	<i>Hirriusa variegata</i>	Plant wanderers	0	1	1
	<i>Suemus punctatus</i>	Free-living ground dwellers	0	1	1
	<i>Thanatus dorsilineatus</i>	Free-living ground dwellers	3	0	3
	<i>Tibellus minor</i>	Plant wanderers	0	1	1
Pisauridae	<i>Euprostenopsis armata</i>	Web dwellers	0	1	1
	<i>Maypacijs roeweri</i>	Plant wanderers	1	1	2
	<i>Perenethis simoni</i>	Web dwellers	1	0	1
Prodidomidae	<i>Theuma parva</i>	Free-living ground dwellers	0	1	1
Salticidae	<i>Euophrys purcelli</i>	Plant wanderers	0	1	1
	<i>Hyllus brevitaris</i>	Plant wanderers	0	1	1
	<i>Langona bethae</i>	Free-living ground dwellers	3	3	6
	<i>Pellenes bulawayoensis</i>	Plant wanderers	0	1	1
	<i>Pellenes tharinae</i>	Plant wanderers	1	1	2
	<i>Stenaelurillus guttiger</i>	Free-living ground dwellers	19	5	24
	<i>Stenaelurillus termitophagus</i>	Free-living ground dwellers	37	21	58
Segestriidae	<i>Ariadna corticola</i>	Web dwellers	0	1	1
Selenopidae	<i>Selenops kruegeri</i>	Plant wanderers	0	1	1
Sparassidae	<i>Olios correvoni</i>	Plant wanderers	2	1	3
	<i>Olios freyi</i>	Plant wanderers	1	0	1
	<i>Panaretella minor</i>	Plant wanderers	1	1	2
Zodariidae	<i>Capheris fitzsimonsi</i>	Free-living ground dwellers	1	0	1
	<i>Diores magicus</i>	Free-living ground dwellers	2	1	3
	<i>Hermippus loricatus</i>	Free-living ground dwellers	1	0	1
	<i>Hermippus tenebrosus</i>	Free-living ground dwellers	2	1	3
	<i>Ranops caprivi</i>	Free-living ground dwellers	4	0	4
Total number of species			45	38	63

