INFLUENCE OF GRAZING BY LARGE MAMMALS ON THE SPIDER COMMUNITY OF A KENYAN SAVANNA BIOME

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ABSTRACT. Pitfall trap and sweep net samples were taken over a period of fifteen months (2002–2003) in the Kenya Long-term Exclosure Experiment (KLEE), in which the presence of domestic and wild herbivores have been independently manipulated since 1995. ANOVA and ANCOVA showed that the exclosure treatments significantly affected plant cover, with the presence of cattle significantly reducing the relative vegetation cover and spider diversity. Herbivory by indigenous mega- and meso–herbivores did not have a significant influence on the diversity of the spider fauna, but abundance of three dominant species (*Cyclosa insulana* Costa (Araneidae), *Argiope trifasciata* Forskål (Araneidae) and *Runcinia flavida* Simon (Thomisidae)) decreased in cattle-grazed plots. In contrast, *Aelurillus* sp. became more prevalent where cattle have been grazing. Multivariate analyses revealed that the spider community responded to grazing pressure by aggregating into three groups that reflected control, cattle grazing and non-cattle grazing clusters. It was probable that the direct effects on vegetation mediated an indirect influence of herbivores on spider diversity. The relative vegetation cover was a positive predictor of spider diversity. Spider communities were found to be an indicator of the activity of mammals and could be used as indicators of land use changes and for bio-monitoring.

Keywords: Grazing, mammals, savanna, Kenya, spiders

Savanna inventories.—Little ecological work has been done on spiders of African savannas and inventories from this habitat are rare. For example, the only inventory work in Kenya was carried out by Russell-Smith et al. (1987), who reported 68 species from Kora Game Reserve. Recently, Warui et al. (2004) reported a checklist of 132 species from a black cotton soil ecosystem in Laikipia. In Tanzania, a checklist of 508 species from Mkomazi Game Reserve was published by Russell-Smith (1999). In South Africa, several surveys of spiders were undertaken in the Savanna Biome. Dippenaar-Schoeman et al. (1989) reported 98 species from Roodeplaat Dam Nature Reserve while Dippenaar-Schoeman and Leroy (2003) reported another 152 species from the Kruger National Park and Foord et al. (2002) recorded 127 species from the western Soutpansberg. Another 55 species were recorded from Rietondale, Pretoria (van

den Berg & Dippenaar-Schoeman 1991), and 268 species from Makalali Game Reserve in the Limpopo Province (Whitmore et al. 2001). Lastly Lotz et al. (1991) working on grassland biome reported 31 families of spiders from Bloemfontein. The only other works on savanna spiders apart from check-lists are those of Russell-Smith (1981), who reported 135 species from Botswana; and Blandin & Célérier (1981), who studied savanna spiders in Ivory Coast.

Current study.—This study was part of the Kenya Long-term Exclosure Experiment (KLEE), a long-term multi-species vertebrate herbivore exclusion experiment in a semi-arid savanna ecosystem in Laikipia, Kenya (Young et al. 1998). KLEE is aimed at comparing the impacts of cattle and wildlife (elephants, giraffes, buffaloes, antelopes and other savanna ungulates) on various components of the savanna biome including biodiversity. Refer-

ence is made to spiders because they inhabit a large array of microhabitats ranging from the ground layer, to the tree layer and makes them particularly suitable to integrate and evaluate activity by the different guilds of herbivores. Since the response of spiders to the particular structure of the habitat is very fine-grained (Gunnarsson 1988; Uetz 1991; Rypstra et al. 1999), it was expected that changes caused by the different guilds of herbivores, would be reflected in the spider fauna. The influence of abiotic environmental variables was also investigated for a few individual species.

Most studies on the influence of grazing and trampling concentrate on the effects on the fauna or vegetation as a whole. Outside Africa and in different ecosystems, such general investigations were carried out by Gibson et al. (1982, 1992) and Curtis et al. (1990) who found that communities of spiders were negatively affected by grazing and trampling. Abensperg-Traun et al. (1996) studied the grazing impact of mammals on invertebrates in Australian woodland and found that the abundance of the spider families Idiopidae and Lycosidae was highest in moderately disturbed woodlands. Rambo & Faeth (1998) looked at influence of grazing on plant insect communities. In Africa, Woldu & Saleem (2000) focused on plant biodiversity in Ethiopia, while Rivers-Moore & Samways (1996), Fabricius (1997), Seymour (1998), Seymour & Dean (1999) and Fabricius et al. (2002) demonstrated that grazing or trampling has effects on various groups of invertebrates in South Africa. Earlier African studies were reviewed in Skarpe (1991). Few studies are available that report the influence of grazing on spiders in particular: Churchill (1998) reported a variation in the abundance of dominant spider families along grazing and rainfall gradients in Australian tropics. Abrous-Kherbouche et al. (1997) investigated the effects of grazing in mountain grassland in North Africa. The present study is the first that studies the subject in tropical Africa and uses a large-scale experimental set-up for the purpose. This is the second paper on Kenyan savanna spiders by the author and more reference can be made to Warui et al. (2004).

METHODS

Study area.—The study was conducted at Mpala Research Centre (MRC) (00°17′N

037°52′E, 1750–1800 m asl), a 1200 ha piece of land adjacent to Mpala Ranch in the Laikipia District of central Kenya. The study site is characterized by black cotton soil (Chromic vertisols), which are heavily textured cracking clays with impeded drainage (Ahn & Geiger 1987; Taiti 1992). Its vegetation is Acacia bushed grassland (Young et al. 1998) dominated by A. drepanolobium (Harms) Sjostedt, accounting for over 95% of the woody vegetation. Rainfall averages 500–600 mm per year (Young et al. 1995, 1998). Data were collected from May 2001 to July 2002.

The KLEE study design.—The Kenya Long-term Exclosure Experiment is a set up in which the presence of domestic and wild herbivores has been independently manipulated since 1995. KLEE allows herbivory (grazing and browsing) in six combinations of three categories of herbivores. These three categories are (1) meso-wildlife (W) (or meso-herbivores: buffalo and other smaller ungulates), referred to as 'wildlife' in Young et al. (1998); (2) mega-wildlife (M) (or mega-herbivores: giraffes and elephants); and (3) cattle (C). The grazing by cattle was moderate, with one livestock unit per 5–8 ha (Young et al. 1998). The details of this design are shown in Fig. 1. The three categories of the large mammalian herbivores were managed such that (i) only cattle (C); (ii) only meso-herbivores (W); (iii) only mega-herbivores and meso-herbivores (MW); (iv) mega-herbivores, meso-herbivores and cattle (MWC); (v) only meso-herbivores and cattle (WC); and (vi) no large mammalian herbivores (control, O) were allowed to graze/browse. Each treatment plot is 200 × 200 m and is replicated three times, once in each of three blocks (north, central and south), totalling 18 plots.

Spider collection.—Spiders were collected with pitfall traps and by sweep-netting. Much has been published about advantages and limitations of pitfall traps (e.g., Greenslade 1964; Uetz & Unzicker 1976; Spence & Niemelä 1994; Green 1999; New 1999) and this study employed them to allow comparison with data from published studies. The pitfall traps consisted of two cone-shaped plastic (polyethylene) cups 9 cm wide at the mouth and 14 cm deep, one inside the other, buried to their rim. Three pitfalls per plot for each of the 18 sampling plots were used, making a total of 54 traps. The three pitfall traps were laid on a
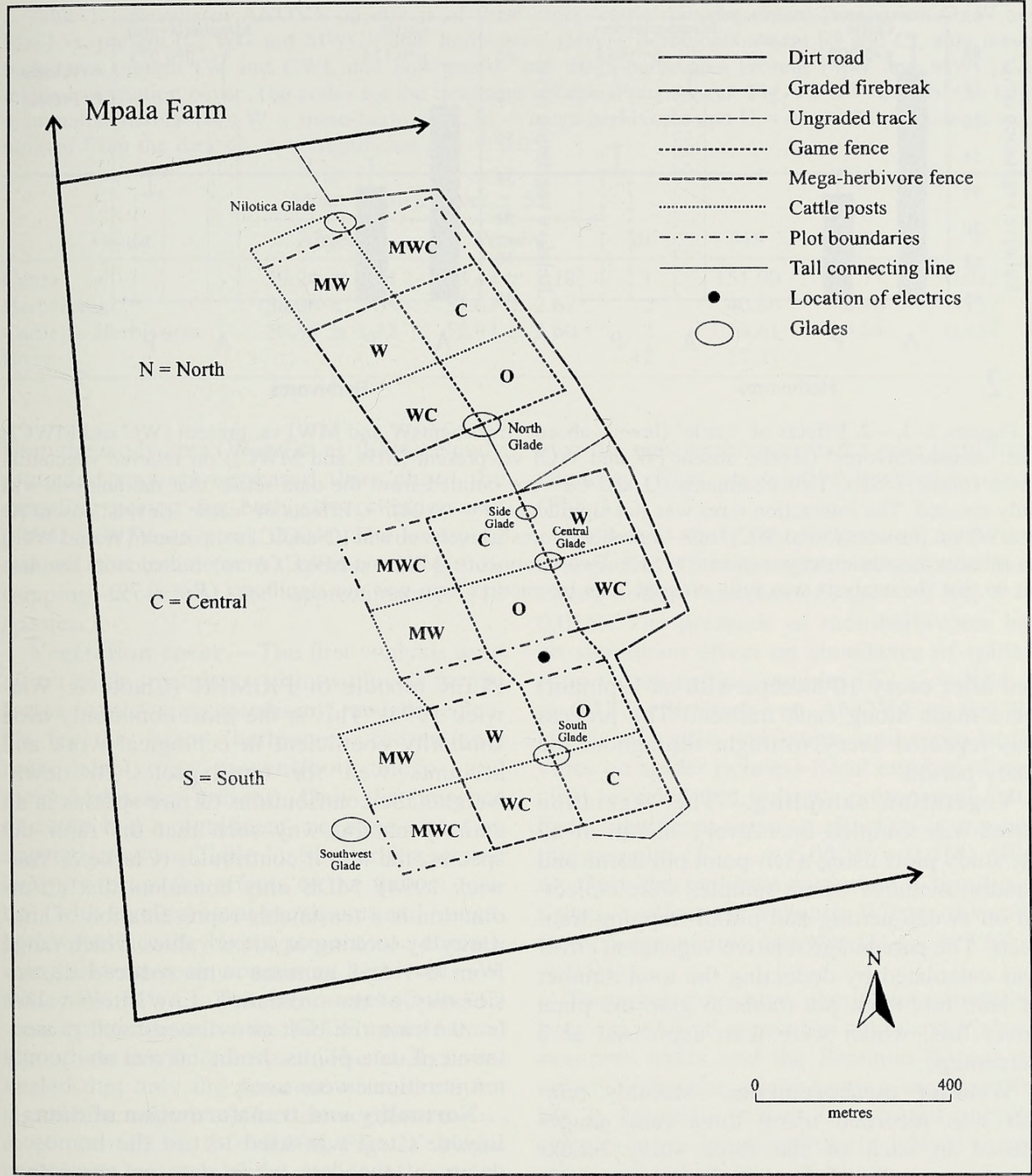
Figure 1.—Schematic representation of the experimental design of the KLEE study plots at Laikipia, Kenya. Letters in each plot represent the herbivores allowed in: C = cattle, W = meso-herbivores, M = mega-herbivores, O = control (all large mammalian herbivores excluded). N, C and S represent north, central and south blocks respectively. Each plot measures 200 × 200 m. The distance between the furthest placed plots (between north and south block) is approximately 2 km. Adapted from Young et al. (1998).

line transect every 3 m. The inner cup of each trap was filled to a third of its volume with a 2% formaldehyde solution as a preservative. Traps were left open and emptied every second week. Sweep-netting was done by walking through the herb layer swinging a sweep net (40 cm in diameter) through the vegetation for a standard number of times (Coddington et al. 1996; Scharff & Griswold 1996; Dippenaar-Schoeman et al. 1999). Sweeping was done on a randomly selected 50 m transect in each of the 18 plots. A hundred sweeps (emp-
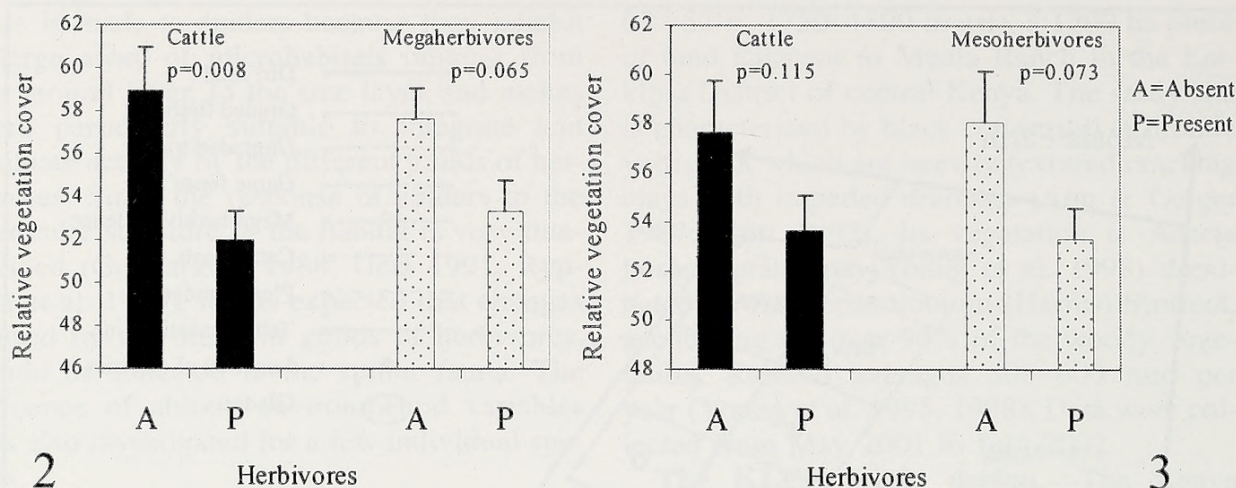
Figures 2–3.—2. Effects of 'cattle' (levels: absent [treatmentsW and MW] vs. present [WC and MWC]) and 'megaherbivores' (levels: absent [W and WC] vs. present [MW and MWC]) on relative vegetation cover (mean + SE). Two treatments (O and C) were omitted from the data set so that the analysis was fully crossed. The interaction term was not significant ($P = 0.28$). 3. Effects of 'cattle' (levels: absent [O and W] vs. present [C and WC]) and 'mesoherbivores' (levels: absent [O and C] vs. present [W and WC]) on relative vegetation cover (mean + SE). Two treatments (MW and MWC) were omitted from the data set so that the analysis was fully crossed. The interaction term was not significant ($P = 0.79$).

tied after every 10 sweeps with an aspirator) were made along each transect. The process was repeated every fortnight throughout the study period.

Vegetation sampling.—The vegetation cover was sampled once every month in all the study plots using a ten-point pin frame and quadrat methods where samples were collected on sweep-netting and pitfall-trapping transects. The percentage relative vegetation cover was calculated by deducting the total number of bare hits from pin totals to give the plant cover hits, which were then expressed as a percentage.

Weather measurements.—Monthly rainfall was recorded using three rain gauges placed in each of the three study blocks (north, central and south). The mean maximum temperature is between 24 and 27 oC (Ahn & Geiger 1987).

Statistical analyses.—Four diversity indices [Shannon-Wiener (H), Margalef (d), Pielou (J) and total species (S)] were computed using PRIMER (Clarke & Gorley 2001). Other statistical tests were performed using STATISTICA (StatSoft 1999). In this study, ordinations by non-metric multidimensional scaling (MDS) were computed in the MDS module of PRIMER, where the original abundance data matrix was first converted into a Bray-Curtis similarity matrix using the SIM-

PLER module of PRIMER (Clarke & Warwick 1994). This is the most commonly used similarity coefficient in ecological work and accounts well for rare species. It downweights the contributions of rare species in an entirely natural way such that the rarer the species, the less it contributes (Clarke & Warwick 1994). MDS only considers that an ordination is a reasonable representation of similarity by looking at stress values which range from 0-1 and increase with reduced dimensionality of the ordination. Low stress values (< 0.1) are the best two-dimensional presentation of data points. In the current study only ten iterations were used.

Normality and transformation of data.—Levene's test was used to test the homoscedacity of the data while data on percentage relative vegetation cover were arcsine-transformed before being subjected to ANOVA. Square root transformation was performed on all spider abundance data in order to make the underlying distribution normal before any ANOVA or analyses of covariance (ANCOVA) were performed. ANOVA and ANCOVA results were done only where Levene's test was not significant or there were no serious violation of the assumptions of ANOVA.

RESULTS

A total of 10,487 specimens, representing 132 species in 30 families, were collected

Table 1.—Results of ANOVA on effects of the factors 'cattle' (levels: absent [treatments O, W and MW] vs. present [C, WC and MWC]) and 'herbivores' (levels: herbivores absent [O and C], only meso-herbivores present [W and CW], and both meso- and mega-herbivores present [MW and MWC]) on relative vegetation cover. The codes for the treatment abbreviations are (cf. Fig. 1): O = control (no large mammalian herbivores); W = meso-herbivores; M = mega-herbivores and C = cattle. No treatments were omitted from the data set. * = Significant at α = 0.05.

| Factor | Mean relative cover $\pm$ SE | | df | MS | F | P |
	Absent	Present				
Cattle	59.24 $\pm$ 1.74	53.43 $\pm$ 1.18	1	151.90	8.77	0.012*
Herbivores	58.06 $\pm$ 2.08	57.61 $\pm$ 2.67	2	40.86	2.36	0.137
Cattle & Herbivores	56.35 $\pm$ 1.22	52.94 $\pm$ 2.60	2	14.61	0.84	0.454
Error			12	17.31		

from the study area (Warui et al. 2004). Newly recorded species appeared throughout the sampling period for both sweep-netting and pitfall (see Warui et al. 2004). The sweeping method accounted for 67 species and pitfall-trapping accounted for approximately 110 species.

Vegetation cover.—The first analysis used all six cattle treatments with two levels for the factor 'cattle' (present/absent), and three levels for the factor 'herbivores' (absent/only meso-herbivores present/both meso- and mega-herbivores present). Only the presence of cattle had a significant, negative effect on vegetation cover (Table 1). Similarly, a second analysis tested the effects of the factors 'cattle' (with levels present vs. absent) and 'mega-herbivores' (with levels present vs. absent), using all treatments containing herbivores (W, WC, MW, MWC). Two treatments (O and C) were omitted because the KLEE experimental layout was not fully crossed. This analysis revealed that only the presence of cattle had a significant, negative effect on vegetation cover ($F_{1, 8}$ = 12.31, P = 0.008, Fig. 2). Mega-herbivores had an almost significant negative effect on relative vegetation cover ($F_{1, 8}$ = 4.59, P = 0.065, Fig. 2). A third analysis tested the effects of the factors 'cattle' (with levels present vs. absent) and 'meso-herbivores' (with levels present vs. absent) in the four treatments that excluded mega-herbivores (O, C, W, WC). The mega-herbivore treatments (MW and MWC) were omitted because the KLEE experimental layout was not fully crossed. The results showed that there was no significant effect of cattle or meso-herbivores on relative vegetation cover and the resulting interaction was not significant (Fig. 3). How-

ever the mesoherbivores had a near significant negative effect on relative vegetation cover (Fig. 3).

Spiders.—Only the presence of cattle had a negative effect on spider abundance from sweep-netting samples ($F_{1, 500}$ = 5.84, P = 0.016). The presence of mesoherbivores had no significant effect on abundance of spiders from sweep-netting samples ($F_{1, 500}$ = 5.84, P = 0.177). Similarly, an ANOVA to test the effects of cattle and mega- and meso-herbivores on spider richness (total number of species) revealed that only the presence of cattle had a significant negative effect on sweep-netting samples ($F_{1, 332}$ = 6.05, P = 0.014), (Fig. 4). Only the presence cattle had a significant negative effect on Shannon-Wiener diversity from sweep-netting samples ($F_{1, 332}$ = 4.68, P = 0.031).

There was a positive, significant correlation between relative vegetation cover and Pielou's evenness index and the Shannon-Wiener diversity index for sweep-netting samples (Table 2). Diversity indices from pitfall-trapping samples were not significantly related to relative vegetation cover (Table 2).

Four study species were chosen for individual analysis based on the fact that they were the most numerically dominant and represented a number of different functional groups: *Cyclosa insulana* (Costa 1834), *Argiope trifasciata* (Forskål 1775) (both Araneidae), *Runcinia flavida* (Simon 1881) (Thomisidae), and *Aelurillus* sp. (Salticidae). A series of analyses of covariance (ANCOVA) were performed to establish their response to some biotic and abiotic factors, namely relative vegetation cover, total monthly rainfall and presence of large mammalian herbivores. The
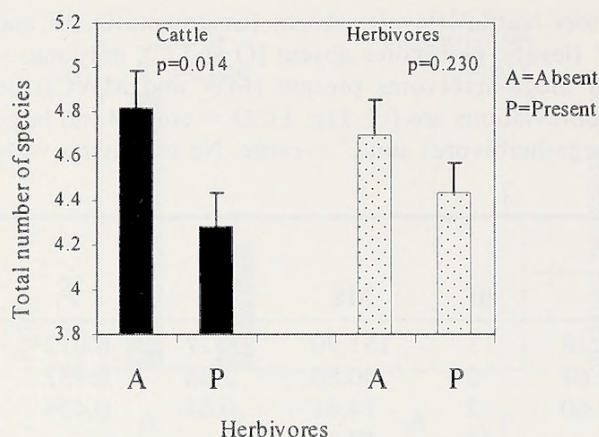
Figure 4.—Effects of 'cattle' (levels: absent [O, W and MW] vs. present [C, WC and MWC]) and 'herbivores' (levels: herbivores absent [O and C], only mesoherbivores present [W and CW], and both meso- and megaherbivores present [MW and MWC]) on total number of spider species from sweep-netting samples (mean + SE). No treatments were omitted from the data set. The interaction term was not significant ($P = 0.81$).

summarized results are shown in Table 3. The presence of cattle and meso-herbivores had significant, negative effects on the abundance of all of the species except *Aelurillus* sp., where the presence of cattle was related to an increase in the species' abundance. Only *R. flavida* and *Aelurillus* sp. were significantly affected by the amount of rainfall (Table 3).

Finally, the stress values of multidimensional scaling (MDS) ordinations for the sweep-netting (Fig. 5) and pitfall-trapping data sets were 0.15 and 0.01, respectively, which implies that the plots were reliable two-dimensional representations of the n-dimensional similarities of the samples and therefore worth interpreting (Clarke & Warwick 1994). The aim of this analysis was to show whether the spider community organised itself in pattern that reflected the intensity of grazing by different herbivore groups. The MDS ordinations for sweep-netting samples have a clearer separation into three clusters of control, cattle and non-cattle grazing, (Fig. 5) when compared to pitfall-trapping samples (not shown) which did not separate by herbivore grazing group. For sweep-netting samples, only the southern control plot was peculiar (Fig. 5) and appeared to be in the same position as the cattle grazing plots. The other two control plots are in their own well-separated cluster. Grazing and control plots are separated by meso-

Table 2.—Correlations between relative vegetation cover and four measures of diversity (Shannon-Wiener diversity index [H'], Margalef's richness index [d], Pielou's evenness index [J'] and total spider species [S]) for data sets generated at Laikipia, Kenya in 2001–2002 using sweep-netting and pitfall-trapping samples. df = 18. * = Significant at $\alpha = 0.05$.

Method	Diversity index	r-value	*P*-value
Sweep-netting samples	S	0.35	0.160
	d	3.14	0.204
	J'	0.54	0.020*
	H'	0.61	0.007*
Pitfall-trapping samples	S	0.29	0.244
	d	0.26	0.304
	J'	0.06	0.809
	H'	0.23	0.356

herbivores (W) and mega-herbivore (M) treatment plots. For the pitfall-trapping data most cattle-grazing and non-cattle grazing plots overlapped, thus no interpretation could be made.

DISCUSSION

There is considerable evidence that grazing and trampling have an influence, and in virtually all cases a negative one, on spider diversity (Gibson et al. 1982, 1992; Curtis et al. 1990; Abensperg-Traun et al. 1996; Rivers-Moore & Samways 1996; Abrous-Kherbouche et al. 1997; Fabricius 1997; Churchill 1998; Fabricius et al. 2002). Yet, this is the first paper that compares the influence of domesticated animals on spiders with that of wildlife. Our analyses (Table 1 and Figs. 2–4) support the conclusion that the presence of cattle, much more than that of other large mammalian herbivores, reduces relative vegetation cover and spider diversity and abundance, while other results (Table 2) demonstrate that diversity and species richness are correlated with relative vegetation cover. As expected, the presence of herbivores had an indirect effect on spiders, presumably by reducing the relative vegetation cover and hence the complexity of the habitat.

Spiders were significantly scarcer in the treatments with cattle compared to those with other large mammalian herbivores. However, some of the effects by mega- and meso-herbivores were close to significance suggesting
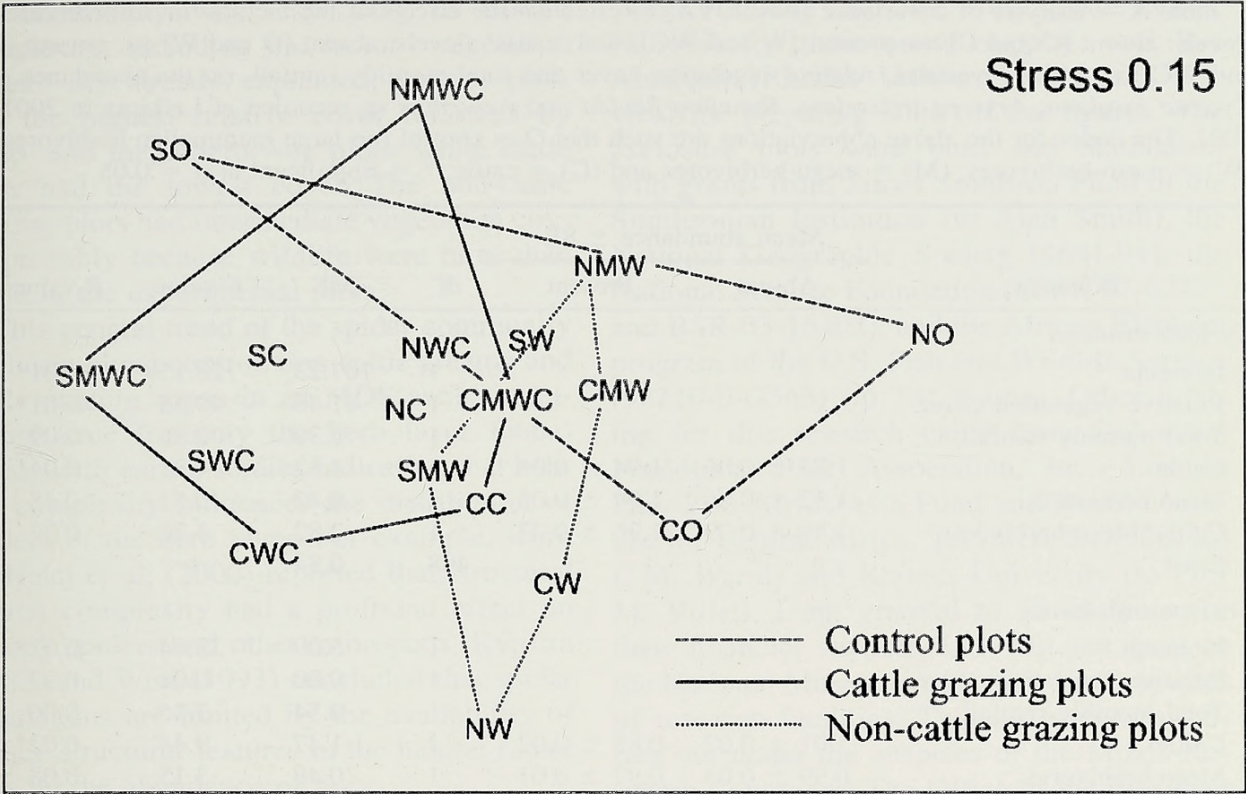
Figure 5.—Multidimensional scaling (MDS) ordination of the spider community in the sweep-netting samples of spiders collected at Laikipia, Kenya in 2001–2002, with convex hulls superimposed to enclose regions characteristic of control, cattle and non-cattle treatments. In all cases the first letter of any code represents the three study blocks, namely north (N), central (C) and south (S). All other letters represent the animals present, where O = control, C = cattle, W = meso-herbivores, and M = mega-herbivores.

that this group also had effects on spiders. Earlier research in the KLEE experiment has shown that exclosure of ungulates (control plots) resulted in a 60% increase in the total number of small mammals (Keesing 2000). In most cases, mega-herbivores (elephant, giraffe) influence the type of habitat under study by browsing its shrub and tree layer (Dublin 1995). Perhaps both mega-herbivores and meso-herbivores have little effect in the current study because they have low densities compared to cattle. It is already documented that most wildlife in Laikipia lives outside national parks (Western 1989; Mbugua 1986; LWF 1996). However, the densities of wildlife on ranches are considerably lower than that of livestock. This may be why only cattle densities were high enough to cause a statistically significant effect on the relative vegetation cover and, by extension, on the spider community.

The diversity indices from pitfall-trapping samples were not significantly related to relative vegetation cover unlike those from sweep-netting samples. Such difference between the two methods may be caused by the difference in biology of the species targeted by the two methods. It was possible that sweep-netting mainly caught foliage dwelling spiders, which were likely to be affected by changes in vegetation cover more than ground living spiders that dominated the pitfall trap samples.

The influence of experimental treatments or abiotic environmental variables could be tested for only a few abundant species. *Cyclosa insulana* reacted to changes in relative vegetation cover, while *R. flavida* and *Aelurillus* sp. were more sensitive to seasonal changes. All four species including *A. trifasciata*, were significantly affected by the presence of cattle but in different ways. *Aelurillus* sp. was more abundant in plots grazed by cattle, while the reverse was true for the other three species. The specific behavior of each species (e.g., its way of acquiring food), or the kind of habitat where it lives may explain this difference. *Aelurillus* is a ground-active jumping spider that

Table 3.—Analysis of covariance (ANCOVA) to establish the effects of the factors 'meso-herbivores' (levels: absent [O and C] vs. present [W and WC]) and 'cattle' (levels: absent [O and W] vs. present [C and WC]) and two covariates, relative vegetation cover and total monthly rainfall, on the abundance of *Cyclosa insulana*, *Argiope trifasciata*, *Runcinia flavida* and *Aelurillus* sp recorded at Laikipia in 2001–2002. The codes for the above abbreviations are such that O = control (no large mammalian herbivores); (W) = meso-herbivores; (M) = mega-herbivores and (C) = cattle. * = Significant at $\alpha = 0.05$.

| | Mean abundance $\pm$ SE | | | | | |
Effect	Absent	Present	df	MS	F-value	P-value
Cyclosa insulana						
Intercept			1	107.23	128.15	<0.01*
Relative vegetation cover			1	41.46	49.55	<0.01*
Total monthly rainfall			1	2.39	2.86	0.09
Cattle	1.73 $\pm$ 0.06	1.94 $\pm$ 0.05	1	3.52	4.21	0.04*
Meso-herbivores	1.82 $\pm$ 0.06	1.99 $\pm$ 0.05	1	0.42	0.51	0.48
Cattle*Meso-herbivores	1.89 $\pm$ 0.09	1.96 $\pm$ 0.07	1	2.82	3.36	0.07
Error			498	0.84		
Argiope trifasciata						
Intercept			1	5.09	32.64	<0.01*
Relative vegetation cover			1	0.00	0.01	0.92
Total monthly rainfall			1	0.54	3.46	0.06
Cattle	1.01 $\pm$ 0.02	0.88 $\pm$ 0.02	1	1.47	9.44	0.02*
Meso-herbivores	0.99 $\pm$ 0.03	0.92 $\pm$ 0.01	1	0.49	3.15	0.08
Cattle*Meso-herbivores	1.00 $\pm$ 0.03	1.04 $\pm$ 0.06	1	0.04	0.28	0.60
Error			498	0.16		
Runcinia flavida						
Intercept			1	6.06	25.29	<0.01*
Relative vegetation cover			1	0.58	2.43	0.12
Total monthly rainfall			1	3.75	15.64	<0.01*
Cattle	1.16 $\pm$ 0.03	1.00 $\pm$ 0.02	1	1.27	5.28	0.02*
Meso-herbivores	1.07 $\pm$ 0.03	1.08 $\pm$ 0.02	1	0.09	0.38	0.54
Cattle*Meso-herbivores	1.02 $\pm$ 0.04	1.11 $\pm$ 0.05	1	0.25	1.04	0.31
Error			498	0.23		
Aelurillus sp						
Intercept			1	8.54	37.44	<0.01*
Relative vegetation cover			1	0.02	0.09	0.77
Total monthly rainfall			1	0.89	3.89	0.04*
Cattle	1.05 $\pm$ 0.03	1.21 $\pm$ 0.03	1	2.84	12.46	<0.01*
Meso-herbivores	1.08 $\pm$ 0.03	1.15 $\pm$ 0.02	1	0.63	2.75	0.09
Cattle*Meso-herbivores	0.98 $\pm$ 0.04	1.18 $\pm$ 0.05	1	0.11	0.49	0.48
Error			498	0.23		

does not build webs to catch prey but chases and jumps onto prey. It seems likely then that it thrived well where there was more grazing and more open ground, compared to a web-builder like *Argiope* that preferred a complex habitat where it could find vegetation to anchor its web. Since *Aelurillus* is known to feed on ants, perhaps grazing makes ants more abundant and this in turn makes *Aelurillus* increase in abundance. Other related studies on individual species have shown that species

level of resolution has a limitation when used for such analysis since a single species tolerant of a perturbation might strongly influence the results (Caro and O'Doherty 1999). This was noted in the current study, where *C. insulana* was found to be very dominant.

The pattern shown by MDS analysis (Fig. 5) seems to correspond with the relative vegetation cover distribution pattern, which is found to be lower in grazing plots and higher in control plots. This could mean that the spi-

der community was responding to habitat complexity, including the factor "vegetation cover." As already explained, control plots had the highest relative cover followed by meso- and mega-herbivore plots, while cattle plots had the lowest cover. The non-cattle grazing plots had intermediate vegetation cover, probably because wildlife were rarer than cattle in the experimental plots.

This general trend of the spider community to cluster along control, non-cattle grazing and cattle grazing zones in an MDS analysis (although true for only the herb layer fauna) agrees with earlier studies indicating that habitat complexity influences the distribution of spiders of the herb layer. For example, work by Halaj et al. (2000) reported that structural habitat complexity had a profound effect on canopy spiders and other arthropods. Rypstra (1983) and Wise (1993) concluded that spider populations are limited by the availability of unique structural features in the habitat rather than by the abundance of prey.

Exclosure treatments allowed us to detect changes in plant cover, and showed them to be significant in plots with cattle grazing. Plant cover appears to significantly affect spider diversity. Overall, activity by wildlife (mega- and meso-herbivores) had less (non-significant) effect on plant cover and spider diversity compared to that of cattle. The spider fauna of the black cotton soil savanna habitat is sufficiently rich to be useful for biological monitoring work in the sense of Kremen et al. (1994), who stated that: "the importance of monitoring is to come up with indicators that respond to anthropogenic disturbances early enough before changes manifest themselves in the more complex food webs and food chains and even affect the long living organisms."

ACKNOWLEDGMENTS

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