

Abundance and guild structure of grasshoppers (Orthoptera: Acridoidea) in communally grazed and protected savanna

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This study was conducted to determine how savanna grass sward modifications caused by heavy grazing pressure influenced the abundance and guild structure of grasshoppers. Heavily grazed communal land was compared with a lightly grazed area and a mowed airstrip, in adjacent protected land, in the Mpumalanga lowveld, South Africa. Plant species composition, height, aerial cover and greenness of grass in the herbaceous stratum were measured in representative sites. Total grasshopper abundance and relative abundance of grasshopper species were also assessed in each site. Grasshoppers were assigned to feeding and habitat functional groups for comparison among the three areas. The heavily grazed area, characterised by short vegetation and low aerial cover, high greenness of grass, and high frequency of forbs, was inhabited by grasshopper species associated with bare ground or short and/or sparse grass, that were non-graminivorous or soft grass feeders. The lightly grazed area, characterised by tall vegetation and high aerial cover, low greenness of grass, and low frequency of forbs, was inhabited by grasshopper species associated with long and/or thick grass, that were mixed feeders or tough grass feeders. The mowed area, characterised by short vegetation and low aerial cover, low greenness of grass, and low frequency of forbs, exhibited lower grasshopper abundance, species richness, and diversity than either of the grazed areas.

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Grasshoppers are the predominant insect herbivores in African savannas (Gandar 1979). Most grasshopper species are highly mobile and able to choose from a wide variety of potential microhabitats. They therefore provide an opportunity for studying the influence of vegetation disturbance on the structure and abundance of insect guilds. Habitat selection among grasshoppers is affected by several habitat characteristics, including plant species composition (Isely 1938; Otte 1976; Capinera & Sechrist 1982; Joern 1986; Evans 1988a), plant nutritional quality (Ellis, Carlisle & Osborne 1965; Mulkern 1967; Gandar 1979, 1982, 1983; Grayson & Hassall 1985), plant morphological characteristics (Mulkern 1967; Joern 1983, 1986), availability of predator-free space (Isely 1938; Uvarov 1966; Joern 1986), availability of suitable oviposition sites (Isely 1937, 1938; Uvarov 1966), and microclimate (Uvarov 1966; Anderson, Tracy & Abramsky 1979; Chappell 1983; Whitman 1987). Changes to herbaceous stratum physiognomy and species composition caused by grazing and mowing that alter any of these habitat characteristics may affect grasshopper abundance and guild structure. During a preliminary investigation conducted over five days during April, 1994, we compared the abundance and guild structure of grasshoppers in three areas: (i) a protected area that had not been recently grazed; (ii) an adjacent communal grazing area subject to heavy grazing by cattle; (iii) an airstrip that had been mowed regularly for an unknown period. It was hypothesised that long-term grazing and mowing would indirectly affect grasshoppers by altering the height, aerial cover, and species composition of the herbaceous stratum, and that different species of grasshoppers would vary in their population responses to these changes.

Study site

The study site was located on the boundary between the Mhala and Phalaborwa magisterial districts in the lowveld of Mpumalanga, South Africa (mid-point = 24°31'S; 31°6'E). Sampling was conducted on protected land at Wits Rural Facility (WRF), on the farm Guernsey (550 ha), and adjoining communally owned grazing land on the farm Okkerneutboom, in former Gazankulu. The protected area was separated from the communally grazed area by an arterial road (a distance of approximately 100 m) and the two areas were similar in most respects barring grazing regime (Shackleton 1993). Mean annual rainfall was 670 mm, most of which was received in convectional thunderstorms between October and April. Mean annual temperature was approximately 22°C, and frost was rare. The areas were underlain by Basement Complex strata of the Bandelierkop Complex, typified by potassic granites and grandiorite. Sampling was conducted toward the top of the catena, where shallow sandy lithosols were characteristic. The areas were situated on the boundary of Acocks' (1988) Veldtypes 10 (Lowveld) and 11 (Arid Lowveld), with the tree stratum dominated by *Terminalia sericea*, *Acacia* species, and *Combretum* species. Dominant grasses of the herbaceous stratum included *Pogonarthria squarrosa*, *Hyperthelia dissoluta*, *Heteropogon contortus*, *Cynodon dactylon*, and several species of *Eragrostis* and *Aristida*, but these differed among the areas on the basis of grazing pressure, as will be documented below.

The communal grazing land had been zoned as such for more than 15 years (Shackleton 1993). However, scattered homesteads existed there previously, indicating that cattle

grazing had persisted in the area for several decades. The WRF property had not been grazed by cattle for over 25 years (Shackleton 1993), the only grazers being indigenous ungulate species (wildebeest, impala, warthog, and duiker) present in low numbers. Thus whereas the herbaceous stratum of the communal grazing lands had been heavily grazed for at least 15 years, grazing had been very light in the protected area of WRF for the previous two decades, resulting in an extensive accumulation of moribund grass. The airstrip was also located on WRF property, and had been maintained by regular mowing for an unknown period. These three areas are referred to below as the heavily grazed, lightly grazed, and mowed areas, respectively.

Materials and Methods

Three 30 m × 30 m census zones, located using a random number table, were sampled for vegetation and grasshoppers in each of the three areas. Census zones in the lightly and heavily grazed areas were completely out in the open, but incorporated occasional bushes (e.g. *Acacia* species or *Terminalia* species), bush cover being reduced in the communally grazed area, where widespread clearing for firewood had occurred (Shackleton 1993). However, the effects of bush cover on grass species composition appeared to be uniform across all census zones.

Vegetation sampling. Ten 0.5 m × 0.5 m quadrats were used to sample the herbaceous stratum of vegetation in each census zone. A random number table was used to position each quadrat. Vegetation attributes measured in each quadrat were height of the herbaceous stratum, plant species composition, percentage aerial cover and percentage greenness of grass. Height of the herbaceous stratum was measured with a tape, ignoring emergent grass culms. Herbaceous aerial cover and grass greenness were assessed subjectively in six categories (0–10 %, 10–25 %, 25–50 %, 50–75 %, 75–90 %, and 90–100 %), following Walker (1976). Assessment of herbaceous species composition involved the identification of all grass species present in each quadrat. The forb species present were distinguished but not identified to species level. Grass species nomenclature follows Gibbs Russell, Watson, Koekemoer, Smook, Barker, Anderson & Dallwitz (1991).

Grasshopper sampling. Grasshoppers were sampled between 10:00 and 15:00 by means of two separate methods. The line transect method (Laake, Burnham & Anderson 1980) was used to estimate total grasshopper abundance (density.m⁻²), as it provides an accurate estimate in a short period of time (Brower & Zar 1984). Four line transects, each 30 m in length and 6 m apart, were walked per census zone. Sighting distance for flushed grasshoppers was measured by tape as the distance from the observer to the point where the grasshopper appeared. Sighting angle was measured with a compass as the angle from the transect line. Transect width was chosen to be unbounded, for it was found to be impractical to impose a limit on the sighting distance, given the distance at which certain individuals would emerge from the herbaceous stratum. No distinction was made between species or age classes, owing to the fact that individuals could not be captured without flushing others from the surrounding area.

Random sweeping with a canvas net was used to assess the

species composition and relative abundance of grasshoppers. A sweep was taken at each step by traversing an arc of 180° with the net through the herbaceous stratum. After twenty such sweeps, the contents of the net were examined, and all grasshoppers removed and killed in ethyl acetate. Twenty sets of 20 sweeps each (i.e. 20 samples) were taken per census zone. Grasshopper samples, preserved in ethanol, were identified subsequent to field sampling. Suprageneric classification follows the taxonomic scheme of Scholtz & Holm (1986). The keys of Dirsh (1965) were employed for classification to genus. Species were identified by reference to a collection of grasshoppers from Pullen Farm, Mpumalanga, identified by Dr H.D. Brown (collection housed at the Zoology Museum, University of the Witwatersrand), most species of which also occurred at WRF. Species not represented in the Pullen Farm collection were identified by reference to the Transvaal Museum collection. Two species could not be identified beyond generic level. A collection of voucher specimens of all species collected during the study has been lodged with the Curator of Entomology, Transvaal Museum, Pretoria. As no difficulty was experienced in associating nymphs with adults for any particular species, nymph and adult counts for each species were combined for the purpose of the analyses.

Sweeping is recognised as a problematic means of sampling (Hughes 1955; Southwood 1978), but remains the only practical means of sampling a large number of sites in areas of tall and/or thick grass in a short period of time (Evans 1988a, 1988b). Evans, Rogers & Opfermann (1983) found that sweeping provided poor estimates of absolute abundance of grasshopper species, but good estimates of the relative abundance. Therefore, sweep sampling is considered suitable for discriminating potential differences in grasshopper species composition and relative abundance (Kemp 1992).

Data analysis

Bartlett's test for homogeneity of variances was performed on all data sets to test for heteroscedacity, which would violate the assumptions of parametric statistics, and normal probability plots were constructed to establish whether the data were normally distributed. One-way ANOVA or Kruskal-Wallis nonparametric ANOVA by ranks was then performed to determine how much of the variation in the data could be explained by differences among the three study areas. Post tests, viz. Dunn's multiple comparisons tests and Tukey-Kramer multiple comparisons tests, were used to assess which areas differed significantly.

Vegetation analysis. Midpoints of each percentage category were used to calculate mean aerial cover and grass greenness for each area, following Walker (1976). Frequency of forbs was calculated for each quadrat by dividing the number of forb species in a quadrat by the total number of herbaceous plant species, and a mean obtained for each area. The number of grass species recorded in each census zone was averaged to calculate the mean species richness, *S*, of grasses in each of the three study areas. The total number of grass species recorded in each area represented the total species richness, *S*, of grasses. In addition, a 'frequency index' was assigned to each grass species in each area, calculated by tallying the number of quadrats where that species was present and dividing by 10 (since there were only 10 quadrats per census zone).

Grasshopper analysis. Relative abundance of the grasshopper species in each study area was calculated by dividing the number of individuals of each species caught by the number of individuals of all species caught. A similar formula (replacing species with family or subfamily) was used to determine the relative abundance of higher taxonomic groups of the Acridoidea. These proportions were converted to percentages.

Grasshoppers were classified into functional groups (Appendix 1), following Evans (1988a), based on feeding preferences (preferred diet) and habitat preferences (preferred 'environment' (Mulkern 1967)). Most information relating to particular species was obtained from Gandar's (1979, 1982, 1983) detailed physiological and ecological research on the grasshoppers of Nylsvley Nature Reserve, Northern Province. Additional information was obtained from Scholtz & Holm (1986). Where information was not available for a species, it was placed in a functional group on the basis of taxonomic affinity. For example, Pyrgomorphidae are obligately non-graminivorous (Scholtz & Holm 1986) and, hence, *Plerisca* sp. (Pyrgomorphidae) was assumed to be non-graminivorous. Morphology was also found to be informative for placement into habitat functional groups. Most species could be assigned to both a feeding and a habitat functional group by these means. However, species which could not be assigned to any functional group were ignored in the analyses. Feeding and habitat functional groups were largely mutually exclusive. The following six feeding functional groups were distinguished: non-graminivorous (forbivorous) species; mixed feeders; graminivorous species; soft grass feeders; tough grass feeders; soft and tough grass feeders (generalists). The following five habitat functional groups were distinguished: geophilous species; short and/or sparse grass species; long grass species; thick grass species; long and short grass species (generalists). The graminivorous species group was retained, despite the existence of three distinct functional groups of graminivores, because it was useful for comparison with the non-graminivorous and mixed feeder functional groups. The two 'generalist' functional groups were included on the null hypothesis that they would be unaffected by changes in the community structure of the herbaceous layer. A bush and forb habitat functional group was omitted since most savanna grasshoppers shelter and/or roost on grass culms, even if obligately non-graminivorous (Mulkern 1967).

The number of grasshopper species recorded in each census zone was averaged to calculate the mean species richness, S , of grasshoppers in each of the three study areas. The total number of grasshopper species recorded in each area represented the total species richness, S , of grasshoppers. Simpson's and Brillouin's indices of species diversity were calculated for each census zone, following Morris & Lakhani (1979), and averaged to calculate mean indices in each of the three study areas. Simpson's index, D_s , was chosen because it is an unbiased estimate of the probability that two individuals drawn from the population belong to the same species and is thus particularly useful for samples taken from the field (Zar 1984). The Brillouin index, H , is an estimate of the more widely used Shannon-Wiener index, except that it is superior where species abundance data is considered to be a non-random sample (Zar 1984), as may be

the case with sweep sampling.

The program TRANSECT (Laake *et al.* 1980) was used to obtain total grasshopper abundance (density.m⁻²) in each of the three study areas. Data (perpendicular distances) were sorted in ascending order and grouped to overcome the effect of 'heaping': a humped pattern in the data distribution caused by flushing of grasshoppers ahead of the observer on the line transect, which then land characteristically between 0.3 and 0.8 m from the line. The χ^2 goodness of fit test was used to test the null hypothesis that the model provided an adequate fit to the grouped perpendicular distance data. All series that fitted the χ^2 model (χ^2 probability > 0.05) were selected, and the series with the lowest percentage confidence intervals chosen from these. Accordingly, the exponential power series was used to estimate total grasshopper density in the lightly grazed area, whereas the Fourier series was used to estimate density in the heavily grazed area and in the airstrip.

Correspondence analysis (CA), was used to reveal associations of grasshopper species with census zones. CA is an ordination technique that summarises data from a species-site matrix such that individual species and sites (census zones) are arranged in a low-dimensional space (two dimensions in the present study) that reflects as much as possible of the variation among species and sites. Increasing distance between any two points is indicative of decreasing similarity. The program CANOCO (Ter Braak, 1987) was used for the analysis.

Results

Vegetation features. Vegetation was significantly taller in the lightly grazed than in both the heavily grazed and mowed areas, and significantly taller in the heavily grazed area than in the mowed area (Table 1). Aerial cover was also significantly greater in the lightly grazed area than in both the heavily grazed and mowed areas, but did not differ significantly between the heavily grazed and mowed areas. In contrast, percentage greenness of grass was significantly greater in the heavily grazed area than in both the lightly grazed and mowed areas, and significantly greater in the mowed area than in the lightly grazed area. Frequency of forbs was also significantly greater in the heavily grazed area than in both the lightly grazed and mowed areas, but did not differ significantly between the lightly grazed and mowed areas.

The species richness, S , of grasses did not differ between study areas, but the species composition altered markedly,

Table 1 Comparative features of the herbaceous stratum in three areas subjected to different management regimes ($n = 90$ quadrats). Tukey-Kramer test: *** = significant difference, where $p < 0.001$. Dunn's test: ** = significant difference, where $p < 0.01$; *** = significant difference, where $p < 0.001$

Feature	Lightly grazed area (mean \pm SD)	Heavily grazed area (mean \pm SD)	Mowed area (mean \pm SD)
Height (m)	0.9 \pm 0.4***	0.3 \pm 0.2***	0.1 \pm 0.1***
Aerial cover (%)	76.0 \pm 14.5***	41.3 \pm 7.2***	30.8 \pm 5.8
Greenness of grass (%)	61.4 \pm 8.2***	86.7 \pm 21.7**	73.7 \pm 12.9***
Frequency of forbs	0.0***	0.2 \pm 0.2	0.1 \pm 0.1**

with certain species almost exclusively restricted to certain areas (Table 2). Only three species (*A. congesta* var. *barbicollis*, *P. patens*, and *P. squarrosa*) were shared by the three areas.

Grasshopper abundance. Total grasshopper abundance (density.m⁻²) was lower in the mowed area than in either the lightly grazed or heavily grazed areas, but similar in the lightly grazed and heavily grazed areas (Table 3). Twenty-nine grasshopper species, belonging to three families, were recorded in the study (Table 4). Both species richness, *S*, and

Brillouin (*H*) diversity of grasshoppers were significantly lower in the mowed area than in the lightly grazed and heavily grazed areas (Table 3). Simpson (*D*_s) diversity of grasshoppers did not differ significantly among the three areas.

Whereas seven species of grasshopper were restricted to the heavily grazed area, only two were restricted to the lightly grazed area, and none was restricted to the mowed area (Table 4). Ten species occurred in both the lightly grazed and heavily grazed areas, but not the mowed area, whereas two species occurred in both the heavily grazed and mowed areas,

Table 2 Frequency indices and richness of grass species recorded in three areas subjected to different management regimes

Tribe	Species	Lightly grazed area	Heavily grazed area	Mowed area
Aristideae	<i>Aristida congesta</i> Roem. & Schult. subsp. <i>barbicollis</i> (Trin. & Rupr.) De Winter	0.4	0.3	0.4
	<i>Aristida stipitata</i> Hack. subsp. <i>graciliflora</i> (Pilg.) Meld.	–	0.4	–
Pappophoreae	<i>Schmidtia pappophoroides</i> Steud.	0.4	–	–
Chlorideae	<i>Cynodon dactylon</i> (L.) Pers.	–	0.4	0.9
	<i>Dactyloctenium aegyptium</i> (L.) Willd.	–	–	0.1
	<i>Eragrostis ciliaris</i> (L.) R. Br.	–	0.1	–
	<i>Eragrostis patens</i> Oliv.	–	–	0.3
	<i>Eragrostis racemosa</i> (Thunb.) Steud.	–	–	0.0
	<i>Eragrostis rigidior</i> Pilg.	0.7	–	–
	<i>Eragrostis superba</i> Peyr.	–	–	0.4
	<i>Eragrostis trichophora</i> Coss. & Dur.	–	–	0.4
	<i>Perotis patens</i> Gand.	0.7	0.8	0.5
	<i>Pogonarthria squarrosa</i> (Roem. & Schult.) Pilg.	0.4	0.8	0.3
Paniceae	<i>Trichoneura grandiglumis</i> (Nees) Ekman	0.1	–	0.1
	<i>Digitaria eriantha</i> Steud.	–	0.3	–
	<i>Digitaria ternata</i> (A. Rich.) Stapf	–	–	0.2
	<i>Panicum maximum</i> Jacq.	0.6	0.0	–
	<i>Panicum natalensis</i> Hochst.	0.2	0.1	–
	<i>Urochloa mossambicensis</i> (Hack.) Dandy	0.1	–	–
Andropogoneae	<i>Urochloa panicoides</i> Beauv.	–	0.2	0.6
	<i>Heteropogon contortus</i> (L.) Roem. & Schult.	0.0	–	–
	<i>Hyperthelia dissoluta</i> (Steud.) Clayton	0.2	0.4	–
Total species richness (<i>S</i>) of grasses		11	11	12
Mean species richness (<i>S</i>) of grasses (<i>n</i> = 9 census zones)		8.0 ± 2.0	7.7 ± 1.2	9.3 ± 1.5

Table 3 Species richness (*S*), Brillouin species diversity (*H*), Simpson species diversity (*D*_s), and total abundance (density.m⁻²) of grasshoppers in three areas subjected to different management regimes. Tukey-Kramer test: † = significant difference, where *p* < 0.05; †† = significant difference, where *p* < 0.01; ††† = significant difference between treatments, where *p* < 0.001

Variable	<i>n</i>	Lightly grazed area	Heavily grazed area	Mowed area
Total species richness (<i>S</i>)	–	18	27	7
Mean species richness (<i>S</i>)	9 census zones	15.3 ± 1.5	21.7 ± 4.0††	5.0 ± 1.0†††
Mean Brillouin species diversity (<i>H</i>)	9 census zones	0.9 ± 0.0	1.0 ± 0.2†	0.5 ± 0.1††
Mean Simpson species diversity (<i>D</i> _s)	9 census zones	0.8 ± 0.0	0.9 ± 0.1	0.8 ± 0.0
Total grasshopper abundance	409 flushings	0.3 ± 0.5	0.3 ± 0.7	0.1 ± 0.1

Table 4 Relative abundance of grasshopper species in three areas subjected to different management regimes, expressed as a proportion of the total number of grasshoppers caught by sweeping ($N = 1380$ individual grasshoppers)

Family	Subfamily	Species	Code*	Lightly grazed area (%)	Heavily grazed area (%)	Mowed area (%)		
Pamphagidae	Porthetinae	<i>Lamarckiana nasuta</i> (Saussure)	1	0.2	9.1	0		
Pyrgomorphidae		<i>Chrotogonus hemipterus</i> Schaum	2	0	3.0	0		
		<i>Plerisca</i> sp.	3	0	7.7	0		
Acrididae	Hemiacridinae	<i>Leptacris pretoriae</i> (Miller)	4	0.3	0	0		
	Calliptaminae	<i>Acorypha pallidicornis</i> (Stål)	5	0	0.3	0		
	Euryphyminae	<i>Amblyphymus rubripes</i> Dirsh	6	1.0	3.5	0		
	Eyrepreocnemidinae		<i>Cataloipus cognatus</i> (Walker)	7	2.9	0.3	0	
			<i>Heteracris speciosa</i> (Sjöstedt)	8	20.1	0.6	0	
			<i>Tylotropidius gracilipes</i> Branchsik	9	7.3	0.2	0	
	Catantopinae		<i>Catantops melanostictus</i> Schaum	10	5.4	3.3	0	
			<i>Phaeocatantops decoratus</i> (Gerstaecker)	11	0.8	0.6	0	
	Cyrtacanthacridinae	<i>Cyrtacanthacris tatarica</i> (Linnaeus)	12	1.7	4.3	3.8		
	Acridinae		<i>Acrida acuminata</i> Stål	15	3.7	6.5	15.1	
			<i>Acrotylus bilobatus</i> Miller	13	0	1.4	0	
			<i>Acrotylus junodi</i> Schulthess	14	0	7.6	0	
			<i>Anaeolopus socius</i> (Stål)	16	0	3.3	0	
			<i>Humbe tenuicornis</i> (Schaum)	17	0.8	0.3	1.9	
			<i>Morphacris fasciata</i> (Thunberg)	18	0	0.2	1.9	
			<i>Oedaleus carvalhoi</i> I. Bolivar	19	0	22.2	28.3	
			<i>Orthochtha dasyncnemis</i> (Gerstaecker)	20	29.3	5.8	24.5	
		Truxalinae		<i>Mesopsis laticornis</i> (Krauss)	21	4.2	4.1	0
				<i>Truxaloides braziliensis</i> (Drury)	22	0	0.8	0
	Gomphocerinae		<i>Pseudourcyptera cephalica</i> (I. Bolivar)	23	6.8	0.6	0	
			<i>Leva</i> sp. (I. Bolivar)	24	4.1	2.7	0	
			<i>Paragymnobothrus rectus</i> Karny	25	0	0.5	0	
			<i>Dnopherula cruciata</i>	26	1.4	2.5	0	
			<i>Pnorisa squalus</i> Stål	27	9.8	5.5	24.5	
			<i>Rhaphotittha carvalhoi</i> (I. Bolivar)	28	0	3.0	0	
	Tropidopolinae	<i>Afroxyrrhepes procera</i> (Burmeister)	29	0.2	0	0		

* = numbers corresponding to grasshopper species shown in Figure 1.

but not the lightly grazed area. Despite their proximity, and spatial separation from the heavily grazed area, the lightly grazed and mowed areas did not share any species that did not also occur in the former. Five species were widely distributed among the three areas.

Higher taxonomic groups of grasshoppers also showed noticeable patterns (Table 5). Almost all pamphagids, all pyrgomorphids, and all calliptamine acridids were restricted to the heavily grazed area. All hemiacridine and tropidopoline acridids were restricted to the lightly grazed area. No higher taxonomic group was restricted to the mowed area. Four acridid subfamilies (Euryphyminae, Eyrepreocnemidinae, Catantopinae and Truxalinae), that occurred in both the lightly grazed and heavily grazed areas, were not found in the mowed area. Eyrepreocnemidine acridids, in particular, were noticeably more abundant in the lightly grazed area than in the heavily grazed area.

Geophilous grasshoppers and grasshoppers favouring short and/or sparse grass were significantly more abundant in the

heavily grazed area than in both the lightly grazed and mowed areas (Table 6). In contrast, grasshoppers favouring long grass were significantly more abundant in the lightly grazed area than in the mowed area. Grasshoppers favouring thick grass were significantly more abundant in the lightly grazed area than in both the heavily grazed and mowed areas. Relative abundance of habitat generalists did not differ significantly among the three areas.

Obligately non-graminivorous grasshoppers, obligately graminivorous grasshoppers and soft grass feeders were significantly more abundant in the heavily grazed area than in both the lightly grazed and mowed areas (Table 7). Mixed feeders were significantly less abundant in the mowed area than in the lightly grazed area, whereas tough grass feeders were significantly less abundant in the mowed area than in both the lightly grazed and heavily grazed areas. Relative abundance of generalist grass feeders did not differ significantly among the three areas.

Table 5 Relative abundance of higher taxonomic groups of Acridoidea in three areas subjected to different management regimes, expressed as a proportion of the total number of grasshoppers caught by sweeping ($N = 1380$ individual grasshoppers)

Family	Subfamily	Lightly grazed area (%)	Heavily grazed area (%)	Mowed area (%)
Pamphagidae	Porthetinae	0.2	9.8	0
Pyrgomorphidae		0	10.7	0
Acrididae	Hemiacridinae	0.3	0	0
	Calliptaminae	0	0.3	0
	Euryphyminae	1.0	3.5	0
	Eyprepocnemidinae	30.3	1.1	0
	Catantopinae	6.3	3.9	0
	Cyrtacanthacridinae	1.7	4.3	3.8
	Acridinae	33.8	47.3	71.7
	Truxalinae	4.2	4.9	0
	Gomphocerinae	22.0	14.8	24.5
	Tropidopolinae	0.2	0	0

Table 6 Number of individual grasshoppers caught in three areas subjected to different management regimes, represented in five habitat functional groups. Tukey-Kramer test: † = significant difference between treatments, where $p < 0.05$; †† = significant difference between treatments, where $p < 0.01$. Dunn's test: * = significant difference between treatments, where $p < 0.05$

Habitat functional group	n	Lightly grazed area (mean \pm SD)	Heavily grazed area (mean \pm SD)	Mowed area (mean \pm SD)
Geophilous species	168	2.3 \pm 3.2 [†]	53.7 \pm 24.6	0 ^{††}
Short and/or sparse grass species	369	30.0 \pm 29.5 [†]	83.3 \pm 18.9	9.7 \pm 3.1 [†]
Long grass species	369	97.3 \pm 87.4	20.7 \pm 16.3*	5.0 \pm 7.0
Thick grass species	508	131.7 \pm 54.6 [†]	32.7 \pm 18.3 ^{††}	5.0 \pm 8.7
Long and short grass species	123	22.3 \pm 17.5	15.7 \pm 22.0	3.0 \pm 4.4

Grasshopper guild structure. In the CA, the primary axis (axis 1) explained approximately 56% of the total sample variation, whereas the secondary axis (axis 2) explained approximately 19%. The three census zones of the lightly grazed area (CZ1, CZ2, and CZ3) were grouped close together (Figure 1), revealing a strong similarity in grasshopper species composition, as were the three census zones of the mowed area (CZ7, CZ8, and CZ9). However, the three census zones of the heavily grazed area (CZ4, CZ5, and CZ6) were less closely associated. The census zones of the lightly grazed and heavily grazed areas occurred at opposite ends of axis 1, suggesting a strong dissimilarity in grasshopper species composition. The mowed census zones were more closely associated with the heavily grazed census zones than with the lightly grazed census zones.

Grasshopper species associated with the lightly grazed area (association A) were primarily mixed feeders, and generalist grass feeders, showing a habitat preference for either long grass, thick grass, or both. Grasshoppers associated with the heavily grazed area (association B) were primarily non-graminivorous species, and feeders on soft grass, which were geophilous, or showed a habitat preference for short and/or sparse grass. Grasshopper species not associated with these

groups included mixed feeders, soft grass feeders, tough grass feeders, and generalist grass feeders. Among these species were habitat specialists, preferring long and/or thick grass, or short and/or sparse grass, and generalists, found in both long and short grass. *M. fasciata*, a soft grass feeder with a habitat preference for short and/or sparse grass, was the only species associated with the census zones of the mowed area.

Discussion

Grazing and mowing generally alter the physiognomy and species composition of the herbaceous stratum by altering the height and cover of grasses and forbs, and the amount of bare ground in a habitat (Johnston, Dormaar & Smoliak 1971; Smoliak, Dormaar & Johnston 1972; Gandar 1980; Belsky 1986). Altered physiognomy and species composition may, in turn, lead to changes in the guild structure of herbivorous insects (Morris 1967, 1969, 1979; Morris & Lakhani 1979).

The effect of altered vegetation physiognomy. In the Nylsvley study, Gandar (1982: 370) found physiognomy to be 'more significant than species composition as a determinant of habitat selection' by grasshoppers in the herbaceous stratum. The results of the present study indicated that the lightly grazed area, characterised by tall vegetation and high aerial cover,

Table 7 Number of individual grasshoppers caught in three areas subjected to different management regimes, represented in six feeding functional groups. Tukey-Kramer test: † = significant difference between treatments, where $p < 0.05$; †† = significant difference between treatments, where $p < 0.01$; ††† = significant difference between treatments, where $p < 0.001$. Dunn's test: * = significant difference between treatments, where $p < 0.05$

Feeding functional group	<i>n</i>	Lightly grazed area (mean ± SD)	Heavily grazed area (mean ± SD)	Mowed area (mean ± SD)
Non-graminivorous species	207	12.7 ± 16.1 [†]	56.3 ± 14.2	0 ^{††}
Mixed feeders	297	73.0 ± 72.4	25.0 ± 18.5*	0.7 ± 1.2
Graminivorous species	873	79.0 ± 45.2 ^{††}	195.0 ± 16.7	17.0 ± 10.6 ^{†††}
Soft grass feeders	351	14.3 ± 24.8*	97.3 ± 42.7	5.3 ± 8.4*
Tough grass feeders	244	43.7 ± 13.8	33.3 ± 12.1 [†]	4.3 ± 1.9 [†]
Soft and tough grass feeders	302	66.7 ± 92.5	26.7 ± 21.5	7.3 ± 6.0

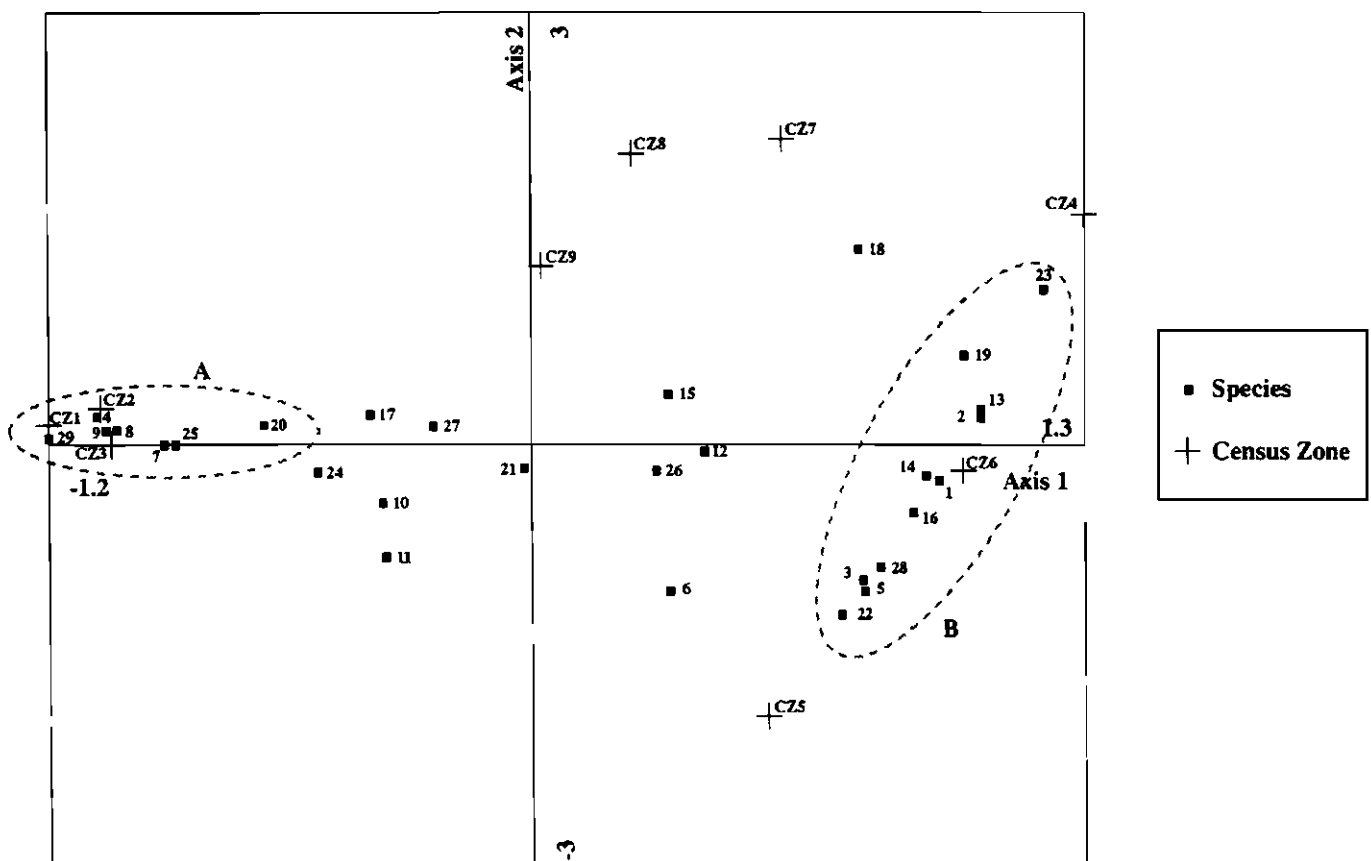


Figure 1 CA ordination plot of 9 census zones and 29 grasshopper species, showing grasshopper associations A and B. Eigenvalues for CA axes 1 and 2 are 0.560 and 0.186, respectively. CZ1–CZ3 are lightly grazed zones, CZ4–CZ6 are heavily grazed zones, and CZ7–CZ9 are mowed zones. Codes for grasshopper species are shown in Table 4.

was inhabited by grasshopper species associated with long and/or thick grass. In contrast, the heavily grazed area, characterised by short vegetation and low aerial cover, was inhabited by grasshopper species associated with bare ground or short and/or sparse grass. These findings are similar to those of studies in British calcareous grassland (Morris 1967; Grayson & Hassall 1985), North American mixed-grass prairie (Quinn & Walgenbach 1990), and southern African savanna (Gandar 1979, 1982, 1983), where grasshopper species negatively associated with bare ground were more abundant in ungrazed areas, whereas those positively associated with bare

ground were more abundant in grazed areas.

Preferences of grasshopper species for particular vegetation physiognomy may reflect a preference for enemy-free space or optimal microclimate. For example, the cryptic colouration of many geophilous grasshopper species, and the importance of birds as major predators, suggests that grasshoppers may have habitat preferences for particular substrata (Isely 1938; Uvarov 1966). Quinn & Walgenbach (1990) indicated that the affinity of many cryptic Gomphocerinae for bare-ground habitats in grazed mixed-grass prairie may be an anti-predation mechanism. Accordingly, the absence of any

association between grasshoppers and the mowed area may be related to the high risk of bird predation in this area of low aerial cover. Cryptic geophilous species (e.g. *C. hemipterus*, *A. pallidicornis*, *A. rubripes*, and *Acrotylus* species) were associated with bare ground in the heavily grazed area, whereas cryptic long-bodied species (e.g. *M. laticornis* and *L. pretoriae*) were associated with the long grass (e.g. *Hyperthelia dissoluta*) of the lightly grazed area. Johnston *et al.* (1971) have shown that very heavy grazing in fescue grassland creates a drier microclimate with increased soil temperature and decreased soil moisture. These conditions may favour some stages of grasshopper development, as shown by the greater survivorship of eggs and hatchlings of *Chorthippus brunneus* in grazed chalk grassland (Grayson & Hassall 1985). Correspondingly, a recent study assessing the effects of fertilizer on grasshopper abundance and guild structure in chalk grassland in the Netherlands (van Wingerden, van Kreeveld & Bongers 1992) showed that the greater biomass and denser physiognomy of the vegetation in fertilized fields resulted in a lower air temperature at the soil surface. This caused lower rates of nymphal development, adult maturation, and egg production, and also retarded egg development.

Preference for particular oviposition sites may also influence habitat selection (Isely 1937, 1938; Uvarov 1966). Quinn & Walgenbach (1990) found that species which prefer to oviposit in bare ground were more common in grazed areas, whereas those which prefer to oviposit in clumps of vegetation were more abundant in ungrazed areas. The low relative abundance of grasshoppers in the mowed area may be related to the hard compacted soil in this area (caused by tractors and aeroplanes), which is unsuitable for oviposition.

Altered physiognomy may also affect feeding requirements. Both grazing and mowing tend to reduce the quantity of standing dead/moribund grass in a savanna-grassland (Gandar 1980; Shackleton 1993). In view of the fact that the diet of a generalised grasshopper has been found to be 'overwhelmingly green leaf' (Gandar 1979: 34), areas with a greater percentage greenness of grass may attract more graminivorous grasshoppers. Green grass is more nutritious than dead/senescent grass, which may retard the growth and development of grasshoppers (Ellis *et al.* 1965). Food selection is suggested as an explanation for greater relative abundance of soft grass feeders in the heavily grazed area, where grass was greenest, than in the lightly grazed and mowed areas, where grass was less green. This may also explain the predominance of tough grass feeders in the lightly grazed area. Generalist grass feeders may have occurred in similar abundance in all three areas because of their ability to tolerate senescent grass when nutritious green grass is less readily available. Generalist feeders were unaffected by grazing intensity in the study of Holmes, Smith & Johnston (1979). Lower greenness in the mowed area may also explain the absence of geophilous soft grass feeders (*Acrotylus* species) from otherwise suitable habitat (low aerial cover and height). The finding that obligately graminivorous feeders showed the same pattern as soft grass feeders may be attributed to the fact that soft grass feeders (especially species such as *O. carvalhoi*) formed the bulk of the graminivorous species, in terms of number of individuals.

The effect of altered plant species composition. In addition to altering the physiognomy of the herbaceous stratum, grazing and mowing may alter the species composition (Coppock, Detling, Ellis & Dyer 1983; Belsky 1986; Archer, Garrett & Detling 1987; Gibson 1988) and, thus, the availability of preferred plant species for food and shelter. However, it is often unclear to what extent insect species richness and composition are determined by the taxonomic composition *per se* of associated plant communities versus the physiognomy of the habitat, which derives largely from the former (Evans 1988a).

The results of the present study indicated that although the species richness of grasses remained constant in the three study areas, species composition changed markedly. Both short grass species and taller, tussock-forming species were characteristic of the heavily grazed area, which contained the greatest number of grasshopper species that preferred short and/or sparse grass or bare soil between grass tussocks (geophilous species). The association between these grasses and the grasshopper species of the heavily grazed area is thus probably related to their influence on the physiognomy of the herbaceous stratum. Similarly, in the lightly grazed area, *P. maximum* and *E. rigidior* tended to form dense stands that were associated with grasshopper species favouring long, and especially thick, grass. This association may thus be attributable to the influence of these two grasses on the physiognomy, as opposed to food availability, of the herbaceous stratum. The fact that such stands were commonly associated with bush cover (e.g. *Acacia* species) may provide an explanation for the greater relative abundance of species such as the eyreopocnemidine acridids and *O. dasynemis* in the lightly grazed area than in the heavily grazed area, where extensive bush clearing had taken place (Shackleton 1993).

However, feeding requirements may explain why obligately non-graminivorous (forbivorous) species (notably *L. nasuta*, *C. hemipterus*, and *Plerisca* sp.) were most abundant in the heavily grazed area, where frequency of forbs was highest. Holmes *et al.* (1979) have shown that forb feeders and mixed feeders with a preference for forbs are most abundant in moderately to heavily grazed fields of Canadian fescue grassland. In the semi-desert grassland of Arizona, Jepson-Innes & Bock (1989) found that herb-feeding melanopline acridids exerted preference for grazed areas. In Nyls-vley, *C. hemipterus* was found by Gandar (1982: 376) to be 'one of the few examples of distribution influenced by food availability ... only [being] common in disturbed areas where there were both bare patches and a high proportion and diversity of forbs'. Food limitation may explain why the mowed area, which provided an equally suitable habitat for geophilous species (aerial cover equal to the grazed area), but had a lower frequency of forbs, supported neither *C. hemipterus* nor *L. nasuta*.

Conclusions

Changes in guild structure associated with grazing or mowing in an area cause changes in the abundance, species richness and diversity of grasshoppers. Total grasshopper abundance has been found to increase (Smith 1940; Uvarov 1966; Southwood & van Emden 1967; Holmes *et al.* 1979; Morris & Lakhani 1979) or decrease (Morris 1967; Capin-

era & Sechrist 1982; Grayson & Hassall 1985; Quinn & Walgenbach 1990) in response to grazing and mowing. Similarly, species richness and diversity of grasshoppers have also been found to increase (Morris 1967, 1969, 1979; Morris & Lakhani 1979; Morris & Rispin 1987) or decrease (Quinn & Walgenbach 1990) in relation to these disturbances.

Gandar (1979, 1982, 1983) and Jepson-Innes & Bock (1989) suggested that the impact of grazing or mowing on grasshoppers depends on season, location, and taxonomic composition of the grasshopper fauna. Thus it may be difficult to compare the findings of studies conducted at different times of the year in areas as diverse as semi-arid grassland, mixed-grass prairie, and fescue grassland, each with its own distinctive assemblage of species.

In the present study grasshopper abundance, species richness, and Brillouin diversity were all lowest in the mowed area, indicating that this area was the most unfavourable for grasshoppers in general. This may be due to low greenness of grass, low frequency of forbs, short vegetation and low aerial cover. These features of the mowed area may be linked to others such as enhanced predation, unfavourable microclimate and unsuitability for oviposition, perhaps acting in concert. The heavily grazed area was a favourable habitat by comparison, owing to high greenness of grass and high frequency of forbs, but the lightly grazed area, with tall vegetation and high aerial cover, was also favourable, though for a different assemblage of species. Thus, although both of the grazed areas favoured different species, a similar number of species and a similar number of individual grasshoppers were attracted to each, taken overall. Accordingly, both areas were characterised by high total grasshopper abundance, high species richness, and high Brillouin diversity.

Our findings suggest that, in savanna, heavy grazing results in a change in the guild structure of grasshoppers, supporting a different assemblage of species from those that predominate in lightly grazed areas, but does not reduce grasshopper abundance and diversity overall. However, owing to the preliminary nature of this investigation, and the seasonality of Acridoidea in particular, these findings may vary during the course of a single year, or between years with contrasting rainfall patterns (and their implications for the physiognomy and species composition of the herbaceous stratum). Kemp (1992) has shown that although some species are separated to an extent by differences in phenology, there is considerable overlap of species at a given site during the course of the summer. More comprehensive research programmes, extended over a longer time period, are needed to address the issue fully.

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See following page for Appendix 1

Appendix 1 Grasshopper species assigned to six feeding functional groups and five habitat functional groups on the basis of feeding and habitat preferences. NGF = non-graminivorous; MF = mixed feeding; GF = graminivorous; SGF = soft grass feeding; TGF = tough grass feeding; STGF = soft and tough grass feeding; G = geophilous; SSG = short and/or sparse grass; LG = long grass; TG = thick grass; SLG = short and long grass; x = presence of trait; ? = no information was available

Grasshopper species	Feeding functional groups						Habitat functional groups				
	NGF	MF	GF	SGF	TGF	STGF	G	SSG	LG	TG	SLG
<i>Lamarckiana nasuta</i> (Saussure)	X					X					
<i>Chrotogonus hemipterus</i> Schaum	X						X				
<i>Plerisca</i> sp.	X						?	?	?	?	?
<i>Leptacris pretoriae</i> (Miller)	?	?	?	?	?	?			X		
<i>Acorypha pallidicornis</i> (Stål)		X					X				
<i>Amblyphymus rubripes</i> Dirsh		X					X				
<i>Cataloipus cognatus</i> (Walker)		X							X	X	
<i>Heteracris speciosa</i> (Sjostedi)		X								X	
<i>Tylotropidius gracilipes</i> Branckisik		X		X					X	X	
<i>Catantops melanostictus</i> Schaum	X									X	
<i>Phaeocatantops decoratus</i> (Gerstaecker)	X						?	?	?	?	?
<i>Cyrtacanthacris tatarica</i> (Linnaeus)		X								X	X
<i>Acrida acuminata</i> Stål				X			X				X
<i>Acrotylus bilobatus</i> Miller			X	X			X				
<i>Acrotylus junodi</i> Schulthess			X	X			X				
<i>Anaeolopus socius</i> (Stål)			X	X				X			
<i>Humbe tenuicornis</i> (Schaum)			X			X					X
<i>Morphacris fasciata</i> (Thunberg)			X	X				X			
<i>Oedaleus carvalhoi</i> I. Bolivar			X	X				X			
<i>Orthochtha dasycnemis</i> (Gerstaecker)			X			X			X	X	
<i>Mesopsis laticornis</i> (Krauss)			X		X					X	
<i>Truxaloides braziliensis</i> (Drury)			X				?	?	?	?	?
<i>Pseudoarcyptera cephalica</i> (I. Bolivar)			X		X			X			
<i>Leva</i> sp.		X					?	?	?	?	?
<i>Paragymnobothrus rectus</i> Karny			X				X				
<i>Dnopherula cruciata</i> (I. Bolivar)			X		X			X			
<i>Pnorisa squalus</i> Stål			X		X			X			
<i>Rhaphotittha carvalhoi</i> (I. Bolivar)			X		X			X			
<i>Afroxyrrhopes procera</i> (Burmeister)	?	?	?	?	?	?				X	

Sources: Gandar (1979, 1982, 1983) and Scholtz & Holm (1986).