Ecological notes and annotated checklist of the grasshoppers (Orthoptera: Acridoidea) of the Savanna Ecosystem Project Study Area, Nylsvley

74

Ecological notes and annotated checklist of the grasshoppers (Orthoptera: Acridoidea) of the Savanna Ecosystem Project Study Area, Nylsvley

Author's address

Mr M V Gandar
Institute of Natural Resources
University of Natal
P O Box 375
Pietermaritzburg
3200

GAcsir 24H4278*8311

PREFACE

The Savanna Ecosystem Project of the National Programme for Environmental Sciences is one of several national scientific programmes administered by the CSIR. The National Programme is a cooperative undertaking of scientists and scientific institutions in South Africa concerned with research related to environmental problems. It includes research designed to meet local needs as well as projects being undertaken in South Africa as contributions to the international programme of SCOPE (Scientific Committee on Problems of the Environment), the body set up in 1970 by ICSU (International Council of Scientific Unions) to act as a focus of non-governmental international scientific effort in the environmental field.

The Savanna Ecosystem Project being carried out at the Nylsvley Provincial Nature Reserve is a joint undertaking of more than fifty scientists from the Department of Agriculture, the Transvaal Provincial Administration, the CSIR, the Transvaal Museum, and seven universities. As far as possible, participating laboratories finance their own research within the project. The shared facilities at the study area and the research of participating universities and museums are financed from a central fund administered by the National Committee for Environmental Sciences and contributed largely by the Department of Environment Affairs.

The research programme of the Savanna Ecosystem Project has been divided into three phases - Phase I (mid-1974 to mid-1976) - a pilot study of the Nylsvley study area, in particular the description and quantification of structural features of the ecosystem, Phase II (mid-1976 to 1979) - studies of the key components and processes including the development of mathematical models, and Phase III (1979 to 1984) - extension to other sites and the study of management strategies for the optimal utilization of Burkea savanna ecosystems.

ACKNOWLEDGEMENTS

ABSTRACT

An annotated checklist is given of 60 species of Acridoidea which were found on the Nylsvley Nature Reserve.

The density of a species may change greatly over small distances, altering the population species composition. Vegetation structure seems to be the main determinant of this. Changes also occur with time because of different breeding strategies. Most species are univoltine but exhibit considerable flexibility and asynchrony in breeding.

All species examined are polyphagous but diets can be distinguished according to the physical characteristics of the preferred food plants. The amount of grass production removed by grasshoppers in a year varied between 9 and 24%. The effect of feeding and the extent to which grasshoppers were in competition with other grazers was less than these figures suggest.

The passage of a grass fire in spring caused only a 30% loss of grasshopper biomass but post-fire mortality of nymphs was high.

SAMEVATTING

'n Geannoteerde oorsiglys van 60 Acridoidea spesies wat in die Nylsvley Natuurreservaat gevind is, word aangegee.

Die bevolkingsdigtheid van 'n spesie kan baie verander oor kort afstande, wat dan die spesiesamestelling van die populasie verander. Dit wil voorkom asof plantegroeistruktuur die vernaamste bepalende faktor hiervan is. Veranderinge in tyd vind ook plaas as gevolg van verskillende broeistrategieë. Die meeste spesies broei net een keer in die broeiseisoen maar toon groot buigsaamheid en ongelykheid daarin.

Alle spesies wat ondersoek was, is polifaag maar diëte kan onderskei word na aanleiding van die fisiese kenmerke van die voorkeur-plantvoedsel. Die jaarlikse hoeveelheid grasproduksie deur sprinkane verwyder, het gewissel vanaf 9 tot 24%. Die effek van voeding en die mate waarin sprinkane met ander grasvreters wedywer, was minder as wat hierdie persentasies voorstel.

'n Grasvuur in die lente het slegs 'n 30% verlies van sprinkaanbiomassa veroorsaak maar die na-vuurse dodetal van nimfe was hoog.

TABLE OF CONTENTS

INTRODUCTION

Between 1976 and 1979 a study was carried out on the energetics, population dynamics, distribution and food preferences of the phytophagous insects in the herb layer of the Savanna Ecosystem Project study area on the Nylsvley Provincial Nature Reserve, northern Transvaal. Research concentrated on the grasshopper populations which were identified as the main phytophagous insects of the herb layer, accounting for over 75% of the biomass of this trophic group (Gandar 1982a). In calculating the energy flow through the grasshopper populations, data on feeding and energetics were related to an hypothetical generalized grasshopper population based on population averages of the most abundant species (Gandar 1982b), though the community in fact consists of more than 60 species.

During the course of this study, information on habitat and food preferences, breeding cycles, interactions with other consumer groups, and with fire, was obtained for a number of species, together with some incidental information on other Orthoptera. Differences were noted in the breeding cycles of some grasshopper species from those reported for the same species in different habitats. Evidence was also obtained for considerable flexibility in breeding and feeding strategies. Since this flexibility may relate to the frequent occurrence of fires and drought in savannas, this information has been brought together in the form of an annotated checklist of the grasshoppers of the Savanna Ecosystem Project study area, to provide an ecological background to the more detailed studies of the energetics of the grasshopper population. In this report the checklist is preceded by some general ecological notes on the grasshoppers.

STUDY AREA

The study area of the South African Savanna Ecosystem Project lies in the eastern part of the Nylsvley Provincial Nature Reserve (24°29'S, 28°42'E). The study area covers about 745 ha and borders on a seasonally flooded grassland. The climate is semi-arid with three distinct seasons: a hot, dry season from August to October; a hot, wet season from November to April, and a cool, dry season from May to July. Mean annual temperature is 18,6°C, and mean annual rainfall, 630 mm, falling mainly from October to March (Huntley and Morris 1978). Considerable variation was recorded in annual rainfall during the period of this study. In 1976/1977 rainfall was only 1,6% below average; in 1977/1978, 25,6% above average, though the early part of the rainy season from mid-October to mid-December was very dry with only 80 mm of rain falling compared with 200 mm over the corresponding period the previous year. Rainfall in 1978/1979 was 31,5% below normal. The grasshopper population declined in these last two years and small changes in species structure were also evident.

The soils of the study area are coarse and well drained. Details are given by Harmse (1977) and Huntley and Morris (1978). Associated with the different soil types are three broadly defined vegetation types:

1. <u>Burkea africana</u>-<u>Eragrostis pallens</u> savanna, referred to as <u>Burkea</u>. The main trees are <u>Burkea africana</u>, <u>Ochna pulchra</u> and <u>Terminalia sericea</u>. The commonest grasses are <u>Eragrostis pallens</u> and <u>Digitaria eriantha</u>. Some areas are characterized by tall tussock grasses of the subfamily Andropogoneae, especially <u>Trachypogon spicatus</u>. Another variation occurs where <u>Setaria perennis</u> is locally plentiful, creating a lower, more even sward than the Andropogoneae. Tree canopy cover is 27% and <u>Panicum maximum</u> sometimes occurs in almost pure stands under canopy. Grass makes up between 70% and 95% of the herbaceous biomass.

2. <u>Acacia</u> savanna. Within the <u>Burkea</u> savanna are interspersed patches of microphyllous savanna dominated by <u>Acacia</u> spp particulary <u>A tortilis</u>, <u>A nilotica</u>, <u>A karroo</u> and <u>A burkei</u>. The main grasses are <u>Eragrostis rigidior</u> and <u>Eragrostis lehmanniana</u>. The small woody plant, <u>Solanum panduraeforme</u> is very common in the herbaceous layer and forms dense stands.

3. <u>Diplorhynchus condylocarpon</u>-<u>Barleria bremekampii</u> savanna on a rocky outcrop known as Maroela Kop. This vegetation type was not sampled for grasshoppers.

A detailed description of the vegetation has been given by Coetzee <u>et al</u> (1977).

ECOLOGICAL NOTES

1. Density and biomass

1.1 Mean over a year

A drop-tent was used in the sampling of grasshoppers (Gandar 1982b). Sampling was conducted in the middle of each month from September 1976 to August 1977 on five grids each consisting of 25 sampling points. Each grid was distinctive in its composition of herbaceous species. Three were in Burkea, one in Acacia and one in an intermediate area.

Grid 1: Burkea: Eragrostis pallens, Setaria perennis
Grid 2: Burkea: E pallens, Andropogoneae
Grid 3: Burkea: E pallens, Digitaria eriantha
Grid 4: Acacia: E rigidior, Solanum panduraeforme
Grid 5: Intermediate: High plant diversity

The recorded density and biomass for the grids averaged over the year are given in Table 1.

Table 1.   The mean density and biomass of grasshoppers from September 1976 to August 1977.

	Density number m^{-2}	Biomass kg ha^{-1}
Mean for grids 1, 2 and 3[a]	1,93	0,73
Grid 4[b]	10,20	2,28
Grid 5[c]	3,57	0,86

[a]Grids 1, 2 and 3 were in Burkea
[b]Grid 4 was in Acacia
[c]Grid 5 was in an intermediate area

There was no significant difference between population density and biomass in the three Burkea grids. The population on the Acacia grid was significantly larger than in all other grids in all months ($p < 0,01$). The average density and biomass in the intermediate area was only slightly higher than in Burkea, but these differences were significant at $p < 0,05$.

In Burkea, the grasshopper population contributed 76% to the biomass of phytophagous insects in the grass layer. The corresponding figure for Acacia was 93% (see Table 2).

Table 2.   Average biomass of groups of phytophagous insects at Nylsvley, 1976/77.

	Burkea		Acacia	
	Biomass kg ha^{-1}	Percent of total	Biomass kg ha^{-1}	Percent of total
Acridoidea	0,76	76	2,32	93
Other Orthoptera	0,06	6	0,02	1
Lepidoptera	0,05	5	0,03	1
Hemiptera	0,08	8	0,08	3
Others	0,05	5	0,05	2
Total	1,00		2,50	

1.2 Fluctuations

The biomass of grasshoppers in winter was between a third and a half of that in summer.   Other insect groups tend to fluctuate much more during the year.   The relatively high biomass of grasshoppers in winter was due to overwintering adults.

However, there are wide fluctuations from year to year.   The Burkea grids were sampled every three months after the intensive study which ended in August 1977.   The results are shown in Table 3.   The biomass in January 1978 was only one quarter of that in January 1977.   This was due to a halving of both the density and the average dry mass of individual grass-hoppers.

White (1976) has suggested that the survivorship of locusts is correlated with rainfall which exerts its influence through food quality and that mortality in times of drought is heaviest on young nymphs.   There was a severe dry spell from mid-October to mid-December in 1977 with only 80 mm rainfall compared to 200 mm in the corresponding period of 1976, so the change in population is consistent with the above theory.   The nymphs which emerged in that period suffered heavy mortality (hence the low density) while those which emerged after the rain in December and were still very small had survived much better (hence the low mean individual dry mass). Rodell (1977) concluded from studies by various authors that weather is the most important influence on the size of grasshopper populations.

Table 3.   The biomass of the grasshopper population in <u>Burkea</u> savanna. Units are kg ha^{-1}.

	January	April	July	October
1976		0,75[a]	0,60[b]	0,68
1977	0,96	0,86	0,54	0,44[c]
1978	0,24	0,48	0,34	0,50
1979	0,36	0,57		
Significant differences	77/78 p<0,0001 77/79 p<0,001	77/78 p<0,01	77/78 p<0,05	None

[a],[b]Rough estimates based on a preliminary survey.
[c]No sample was taken in October 1977. The entry in the table is the nearest (August) value.

2.   Populations in Burkea and Acacia

2.1 Species differences

The structure of the grasshopper populations in <u>Burkea</u> and <u>Acacia</u> differ from one another with some species occurring predominantly in one type or the other.

(i)   <u>Species in both types</u>:
Many species are found in both, and this includes the majority of common species. For example:

<u>Pnorisa</u> <u>squalus</u> (<u>Acacia</u>)
<u>Pseudoarchyptera</u> <u>carvalhoi</u>
<u>Acrida</u> <u>acuminata</u> (<u>Acacia</u>)
<u>Acorypha</u> <u>pallidicornis</u>
<u>Acrotylus</u> <u>diana</u> (<u>Burkea</u>)
<u>Dnopherula</u> spp
<u>Tylotropidius</u> <u>gracilipes</u>
<u>Parga</u> <u>xanthoptera</u> (<u>Burkea</u>)
<u>Platypternodes</u> <u>brevipes</u> (<u>Acacia</u>)

In some cases a slight preference for one type or another was evident and these are shown in brackets. <u>P</u> <u>squalus</u> was the commonest species in both types but its dominance in <u>Acacia</u> was more pronounced.

(ii)   Burkea species:
        Mesopsis laticornis
        Humbe tenuicornis
        Orthochtha dasychnemis
        Spathosternum nigrotaeniatum

        O dasychnemis and S nigrotaeniatum were found exclusively in
        Burkea. M laticornis and H tenuicornis were very occasionally seen
        in Acacia.

(iii)   Acacia species:
        Oedaleus carvalhoi
        Phaeocatantops decoratus

        These two common species exhibit strong preferences for Acacia,
        although they are both found in Burkea as well.

Species diversity was higher in Burkea. In the intermediate area (Grid 5)
where plant diversity was high, grasshopper diversity was also high. Both
Acacia and Burkea species were found there. Chrotogonus hemipterus was
very common there but scarce in both Acacia and Burkea.

2.2 Size structure

The size structure of the two populations also differ. Acacia is charac-
terized by extremely high densities of small nymphs in December followed by
high mortality rates. The density on Grid 4 in December was 50 per square
metre, a whole order of magnitude higher than Burkea. This is the reason
why mean density on Grid 4 over the year is 5,3 times that in Burkea while
biomass is only 3,1 times that in Burkea (see Table 1).

Both emergence and maturation were earlier in Acacia than Burkea. This was
true even for species which were found in abundance in both types, so the
difference in timing was a function of habitat, not differences in the
population.

3. Breeding cycles

Breeding cycles were determined from population dynamics, dissection of
females, records of observed copulation and observations of egg-laying by
captive grasshoppers.

Since the life cycles of different species do not necessarily coincide, the
species structure of the population changes continually. There are three
strategies in the life cycles of grasshoppers, but these are flexible and
most species have life cycles which can change slightly with habitat and
climatic factors.

(i)   Overwintering adults - one generation per year:
        Catantops melanostictus, Pnorisa squalus, Tylotropidius gracilipes
        and Dnopherula spp overwinter as non-breeding adults. Females
        became gravid in September or in some instances late August.
        Nymphs emerged from early November and became adult in late summer.

(ii)   Overwintering eggs - one generation per year:
         Orthochtha dasychnemis, Gastrimargus africanus, Humbe tenuicornis
         and Acrida acuminata have only one generation per year. Nymphs
         emerged from mid October. Gravid females were found from March to
         May. Adults died off during winter.

(iii)   Overwintering eggs - two generations per year:
         Here was evidence that Pseudoarchyptera carvalhoi, Spathosternum
         nigrotaeniatum, Acrotylus spp and Oedaleus carvalhoi could complete
         two generations in a year if conditions are good. Nymphs emerged
         in mid October and gravid females were found in January and Febru-
         ary. A second generation emerged in February and gravid females,
         presumably from this generation, were found as late as June. I was
         not able to estimate what proportion of the first generation
         managed to produce a second generation in that season, but it
         certainly was not all of them.

These strategies are not adhered to rigidly. Some of the exceptions and
anomalies are listed below:

(i)   P carvalhoi often overwintered as non-breeding adults in Burkea
         possibly because it was not able to complete the second generation
         in time. These individuals were able to breed at the beginning of
         the following season. S nigrotaeniatum also overwintered as non-
         breeding adults or late instar nymphs when the second generation
         was not completed in time.

(ii)   The growth rate of P squalus was greater in Acacia than in Burkea
         and it had no difficulty completing its cycle in the former. How-
         ever, in Burkea a small proportion of individuals had to overwinter
         as late instar nymphs. These did not undergo final moult until the
         following season and breeding females were found as late as Jan-
         uary. These were probably the late maturing individuals of the
         previous season and the nymphs they produced would be unlikely to
         complete their development before winter. The possibility exists
         of a partial separation of a section of the population of P squalus
         through asynchronization of the breeding cycle, though this was not
         verified. There is no doubt that the effect is habitat dependent.
         It was never detected in Acacia, and was much commoner on Grid 2
         than elsewhere.

(iii)   Gravid females of Acorypha pallidicornis were found in late
         summer. Non-breeding adults were found throughout winter and these
         began breeding at the beginning of the following season. I do not
         know whether this implies that A pallidicornis can overwinter
         either as egg or as adult, or whether it means that an individual
         can come into breeding condition twice.

(iv)   H tenuicornis generally fitted into the second class above, but
         sometimes it overwintered as non-breeding adult or as young nymph.
         This asynchrony was far more obvious in 1978 than previously.

In an area such as Nylsvley, this flexibility is an obvious advantage. Rainfall is variable in both quantity and distribution, and prolonged dry spells are common. The flexibility allows exploitation of optimal conditions, and the slight asynchrony helps to protect a species from the effects of a drought which causes severe mortality of young nymphs in particular.

There is evidence of breeding cycles varying geographically. For example, P squalus at Nylsvley has a single generation per year with overwintering adults. But in East Africa this species has two generations per year (Phipps 1966) and in the Rukwa Valley in Tanzania it has one generation per year, but lays its eggs before the dry season (Robertson and Chapman 1962).

A severe fire could eliminate a nymphal population completely if intense enough (Note 11). A well synchronized population would therefore be vulnerable to a widespread spring fire.

4. Consumption by grasshoppers

From a study of the dynamics, energetics and feeding of grasshoppers (Gandar 1982b) I deduced that grasshoppers in Burkea savanna ingested 94 kg ha^{-1} of plant material in the 12 months from September 1976 to August 1977. This means that a grasshopper ingests about one third of its body weight in food per day. In addition a further 36 kg ha^{-1} of grass was wasted in the course of feeding, so total offtake was 130 kg ha^{-1}.

Ninety two percent of consumption was grass. Thus grasshoppers removed 24% of grass production in that year (based on unpublished data of J O Grunow on herbaceous production). The following year herbaceous primary production increased despite an early season drought which drastically reduced the grasshopper population (Note 1.2) and only about 9% of grass production was removed by grasshoppers.

5. The effects of feeding

From September 1976 to August 1977, green blades of grass were picked monthly inside a 3 ha game fence exclosure. Any mechanical damage to these was attributed to insects. Ten species of grass were examined. Blades were sorted according to estimates of size and percentage of green material missing in order to calculate a damage index. This approximates to the percentage of green blade which had been eaten or destroyed by insects. By June and July it became difficult to estimate damage because of the winter die-back. There may have been natural die-back at other times of the year too. For example the lower leaves of Perotis patens seemed to die off as growth progressed. This might be confused with insect caused damage. The insect damage is due mainly to grass-feeding insects. However in some cases, blades would constrict at a point, severing the distal portion. This was assumed to be a reaction to feeding by a plant-sucking anthropod but this was not verified. This type of damage was particularly severe in the case of Aristida argentea.

Table 4 gives damage indices for 10 species of grass. The percentage of green matter missing is not necessarily proportional to the rate of utilization of the plant by insects because the percentage is also a function of the rates of growth and senescence. The apparent damage at any one time is roughly what might be expected from the grasshopper feeding rates above.

Table 4. An index of damage to green blades by insects was determined monthly for certain species of grass. The index expresses the percentage of green material missing at any one time.

	1[a]	2[b]	3[c]	4[d]	5[e]	6[f]	7[g]	8[h]	9[i]	10[j]
Sept	30,1	21,2	8,7	6,9	29,3	12,1	3,8	41,3	17,8	18,7
Oct	28,5	13,7	19,7	8,5	24,0	10,4	2,2	33,7	14,5	15,1
Nov	21,3	10,8	7,2	9,3	9,7	4,6	1,7	21,3	19,0	16,7
Dec	14,4	10,1	13,0	10,8	7,8	8,1	1,7	11,1	15,1	15,1
Jan	14,7	10,1	11,0	7,5	12,8	6,7	2,7	30,8	16,5	19,7
Feb	14,7	8,9	11,3	6,8	14,3	6,8	1,6	22,3	13,8	16,2
Mar	12,9	4,9	4,3	5,9	8,1	10,8	1,6	25,2	7,1	11,8
Apr	19,9	7,1	2,8	2,9	10,7	4,7	1,6	23,6	11,1	10,7
May	19,2	8,9	3,8	3,1	8,3	5,2	1,0	28,1	14,0	10,5
June		22,2	2,0	2,9		5,2	1,0		22,0	8,4
July		20,9	5,2			7,9	1,9		18,0	

[a]Eragrostis pallens
[b]Digitaria eriantha
[c]Diheteropogon amplectens
[d]Schizachyrium jeffreysii
[e]Perotis patens

[f]Rhynchelytrum repens
[g]Brachiaria serrata
[h]Aristida argentea[l]
[i]Setaria perennis
[j]Panicum maximum

It is interesting to note that Eragrostis pallens which is regarded as unpalatable to large herbivores is quite heavily grazed by insects especially in September and October, while palatable Brachiaria serrata is almost untouched. Brachiaria nigropedata (not in table) is similarly ignored by grazing insects. Diheteropogon amplectens and Schizachyrium jeffreysii which are Andropogoneae are utilized less and less by insects as the season progresses. The utilization of Digitaria eriantha on the other

[1]The indices for A argentea are not reliable. It was difficult to decide whether damage was caused by insects or not.

hand is very much higher in winter. These observations correspond well with what is known about the food selection of grasshoppers (Note 7.3). Damage to the flowering parts and seeds (Gandar 1979) were not attributable to grasshoppers.

The implication of this intensity of grazing by insects is not straight-forward. An exclusion experiment (Gandar 1980) compared the performance of certain grasses in the field under the following conditions:

    no exclusion
    large mammals excluded
    large mammals and insects excluded

This showed that the exclusion of insects had no consistent effect, but E pallens and D eriantha appeared to be stimulated by grazing by insects.

The species of grass which seemed to respond to grazing by insects were those which are heavily utilized. Grasshoppers could possibly increase grass production in grassland (Andrzejewska and Wojcik 1970). Dyer and Bokhari (1976) report that grasshoppers feeding on grass in hydroponic solution trigger processes which result in an increase in energy transport within the plant. The energy flow responses of material within the plant may be larger than the amounts of energy ingested.

6. Food preferences of selected species of grasshoppers

The food preferences of different species were compared by examining the content in the crops of grasshoppers captured by hand-netting on a limited and relatively homogeneous area of Burkea savanna. Crop contents were treated in acid, rinsed, stained and identified under a microscope from the epidermal characteristics (Gandar 1982b).

Much has been written about factors which govern the food preferences of grasshoppers and how these factors operate. The evidence suggests that there are three stimulus-response mechanisms operating, one associated with foraging, one with biting and one with feeding.

The stimuli for foraging are partly physiological and partly climatic. The foraging activity of grasshoppers is basically haphazard (Mulkern 1967 and 1969). Grasshoppers are attracted to vertical patterns (Williams 1954; Wallace 1958) and sight may be important in locating plants, but the selection of a favoured host plant probably does not take place until the grasshopper bites the plant (Mulkern 1969). Then the grasshopper, respond-ing to both the physical characteristics of the plant and to a number of chemostimulants, either feeds or resumes its haphazard foraging.

The chemostimulants are generally nutritionally unimportant although their action may be enhanced by the nutritional status of the plant (Williams 1954; Dadd 1963; Thorsteinson and Nayer 1963; Mulkern and Toczek 1970). Because food selection involves trial and error, traces of a large number of food plants were found in the crops of all grasshoppers examined although the degree of selectivity varied from species to species. Humbe tenuicornis, with 80% of D eriantha in the diet, came closest to monophagy.

Diets of individual grasshopper species fell roughly into five classes according to the toughness of the grass selected, and to the amount of non-grass in the diet. Toughness is taken as the resistance to penetration by a pin (Gandar 1979). The aim was only to describe the diets qualitatively and the data are insufficient for a precise quantitative description. The five classes are listed here:

(i)   Feeders on predominantly tough grass.
        This includes Pseudoarchyptera carvalhoi, Pnorisa squalus and Mesopsis laticornis, which may also eat grass sheath.

(ii)   Feeders on both tough and soft grass.
        This includes Acrida acuminata, Gastrimargus africanus and Orthochtha dasychnemis.

(iii)   Feeders on predominantly soft grass.
        This includes Parga xanthoptera, Humbe tenuicornis and Acrotylus diana.

(iv)   Feeders on grass and non-grass.
        This includes Ornithacris cyanea, Acanthacris ruficornis and Tylotropidius gracilipes.

(v)   Feeders on non-grass.
        This includes Acorphya pallidicornis, which also eats plant litter and, after a fire, ash. Also included are Catantops melanostictus, which may eat traces of grass in spring. Zonocerus elegans, Phaeocatantops decoratus, Phymateus baccatus, Pyrgomorpha granulata and Chrotogonus hemipterus. Although non-graminivores are represented by many species, they are not a large portion of the whole population.

Pyrgomorphidae were all non-graminivorous. Of the Acrididae, Catantopinae were mainly non-graminivorous while Truxalinae and Acridinae were purely graminivores except for Leva sp (Acridinae), which sometimes ate forbs. In the Nylsvley population, the feeders on tough grass tended to Truxalinae, while Acridinae seemed to prefer softer grasses. More details of food preferences are given in the annotated checklist.

7.   Food preferences of the whole grasshopper population

Although the diets of different species differ from one another, it is convenient to consider the diet of a generalized grasshopper which is representative of the whole population. When the composition of this diet is compared to the relative amounts of available food items in the field, the degree to which different items are selected for or avoided can be seen.

7.1   The diet of a generalized grasshopper

The diet was analyzed every two months by identification of epidermal characteristics of the crop contents of between 200 and 1 000 grasshoppers which were caught in a handnet. The crop contents of all grasshoppers of different ages and species were thoroughly mixed. Four hundred fragments were recorded by grid sampling on microscope slides giving relative surface

areas which were then connected to relative dry mass using ratios determined by Zimmermann (1978).

It should be noted that this is not a measure of diet composition, only an estimate. A number of untested assumptions have been made. For example it is assumed that catching grasshoppers in a handnet provides a representative sample of the population. It is also assumed that the quantity of material in the crop is proportional to the rate of consumption. An added complication is the fact that about 15% of the epidermal fragments were unidentified grass. Some of these may have been of minor grasses not included in the reference material. The variability of epidermal characteristics within one grass species also contributed to the high proportion of unidentified fragments. Some grasses had a more distinctive epidermis than others, so one cannot ignore the unknowns on the assumption that they have the same proportions of species as the rest of the diet. A discussion of this method and some of the inherent difficulties is given elsewhere (Gandar 1979).

7.2 The availability of food

Estimates of food availability were confounded by the imprecise concept of what is actually available to grasshoppers. The diet is overwhelmingly leaf, with grass sheath and litter present in negligible quantities. In summer, grasshoppers essentially eat only green material. In June and July only 30% of the diet was brown leaf although there was seventeen times more brown than green leaf in the standing crop. In August and September 15% of the diet was brown leaf. Accordingly, available food was taken as green leaf alone although there is an additional supply of standing dead which can be, and is, utilized in times of shortage. Availability of non-grass was not considered since it is not known to what extent shrubs and trees are utilized in addition to forbs. Non-grass only makes up 8% of the diet on average.

Availability was found by using the equation: mass per unit ground area = mass per unit basal area (a) x basal cover (b) and determining a and b for each grass species or group of species (Gandar 1982b). This is shown, together with the diet composition in Table 5.

7.3 Food preferences

The percentages in the diet given for each group of grasses are minimal, because unidentifiable fragments were recorded separately. Consequently, direct comparisons between utilization and availability are not strictly valid, but some patterns are still apparent.

Eragrostis pallens, which is one of the first grasses to produce new shoots in spring, was eaten in large quantities in October and November particularly. In April and May, it is still readily eaten when the green material has died off. Although E pallens then provided less than 1% of available green material, it was still 30% of grass standing crop. Digitaria eriantha was always common in the diet. It stayed palatable longer than other species, and was increasingly selected into the dry season.

Table 5. The relative utilization of food items by grasshoppers and the relative availability of the items are expressed as percentages[a].

	Oct/Nov		Dec/Jan		Feb/March		April/May		June/July		Aug/Sept	
	Util	Avail	Util	Avail	Util	Avail	Util	Avail	Util	Avail	Util	Avail
E pallens	36,3	46,9	19,8	30,5	11,5	11,7	13,4	0,7	0,0	0,1	24,7	17,5
D eriantha	19,5	21,3	19,2	20,2	26,9	21,4	29,4	11,8	30,9	12,5	37,2	15,5
Andropogoneae	16,3	23,4	31,7	40,0	31,5	56,0	31,4	78,4	37,7	64,3	18,1	43,4
S perennis	3,7	3,8	4,0	4,9	8,8	6,2	3,8	5,2	4,2	19,2	5,4	13,7
Aristida spp	3,3	1,3	1,9	1,4	2,1	1,3	2,9	1,3	1,5	0,4	+	3,6
Others	1,4	3,1	2,5	3,5	+[b]	4,1	2,6	2,6	+	3,5	+	6,2
Unknown	29,9		21,0		19,3		16,8		24,6		14,5	

[a]Only grasses are considered here. Utilization is based on the relative dry mass of grasses in the crops of grasshoppers; availability is based on the relative dry mass of green leaf per unit area of ground.
[b]+ denotes traces in the diet of less than 1%.

These preferences are also reflected by the estimates of insect feeding damage to grass (Table 4) even though these sets of data come from slightly different areas of Burkea savanna.

E pallens suffers great damage early in the growing season. The increase in percentage damage to D eriantha in winter parallels the shift in the grasshoppers diet. As mentioned earlier, the damage to Aristida was difficult to interpret. However the extensive damage to A argentea (Table 4) may reflect the fact that percent utilization generally exceeds percent availability (Table 5). The main eater of Aristida was Pseudoarchyptera carvalhoi which declined markedly during winter, hence the low utilization of Aristida in August/September.

8. The influence of vegetation structure and composition on the distribution of grasshoppers

8.1 Distribution of a generalized grasshopper

The data collected in the intensive survey included estimates of the maximum height of edible vegetation and aerial cover, and a ranking of the three main plant species for each 1 m² drop-tent sample. The following discussion is based on an analysis of these data:

> The average number of grasshoppers m⁻² changed with cover and with height of vegetation as shown in Figure 1. The record, cover and species apply to individual samples of 1 m² and do not represent average values for an extended area. Only trapping data from the three Burkea grids was analyzed because the other grids were relatively homogeneous with respect to structure.

> The number of grasshoppers m⁻² increased with the height of vegetation to a maximum, then dropped slightly (Figure 1). The initial increase was probably because greater height often implies greater quantity of available food and more shelter. However, the upper values for grass height frequently resulted from the presence of tall, densely tussocked grass such as Trachypogon spicatus or Cymbopogon spp which harboured fewer grasshoppers than a lower, more even sward. The variation with aerial cover was not as well defined as with height, but it is clear that grasshopper density was highest where cover was highest. On the Acacia grid the herbaceous stratum consisted typically of an even sward of 30 to 60 cm maximum leaf height and high aerial cover. That is, it tended towards optimal conditions for grasshoppers indicated by both the lines in Figure 1 so structure may contribute to the high density of grasshoppers on the Acacia grid.

8.2 Distribution of selected species

The above refers to the whole population, however, and the distribution of a single species does not necessarily coincide with this. Clarke (1948) and Williams (1954) report that vegetation structure is more important than composition in determining the distribution of grasshoppers. Food preferences and the availability of food plants can nevertheless be an important determinant of the distribution of grasshoppers (Anderson 1964), though

Table 6. The relationship between some common species of grasshoppers found in each 1 m² sample and the vegetation height and cover and the plant species in that sample were worked out from the trapping data. Chi squared tests were used to check significance of differences in numbers caught in samples in various classes according to height or cover or the product of both, or according to the relative abundance of various plant species. The results are summarized below, together with some speculative remarks.

Species	Vegetation structure	Vegetation composition	Remarks
Pnorisa squalus	Adult distribution not correlated with height, but nymphs are more common in tall than short grass (P<0,001). Prefers middle range of aerial cover.	Nymphs associated with grasses of the subfamily Andropogoneae, (P<0,05) particularly Trachypogon spicatus (P<0,01). There is no correlation with Eragrostis pallens (most favoured food in summer) or with Digitaria eriantha (most favoured food in winter) nor is any seasonal change indicated. Nymphs are negatively correlated with Setaria perennis on Grid 2 (P<0,01) but not Grid 1.	Common in Acacia and Burkea which are characterized by different grass species. In Burkea it is not necessarily associated with its favoured food, but shows slight avoidance of S perennis which is not one of its favoured food plants. The association of nymphs with Andropogoneae, which are tall tussock grasses, relates to their preference for tall grass where they are not so exposed.
Pseudoarchyptera carvalhoi	Generally favours a wide middle range of vegetation quantity (height x cover) (P<0,05). Evidence of avoidance of both very tall grass and very high cover, especially by adults, and avoidance of very open spaces, especially by nymphs.	Avoidance of S perennis by adults (P<0,01) and nymphs (not significant). Adults associated with Aristida spp (P<0,001). Positive association with D eriantha (P<0,05 for adults, P<0,05 for nymphs, P<0,01 for both) Negative association with non-grass (P<0,01).	Aristida spp are eaten in large quantities which explains why adults are associated. The reason nymphs are not correlated with Aristida spp is that these grasses grow in open areas which are avoided by nymphs. S perennis is seldom eaten and non-grasses are not eaten at all.

Species	Vegetation structure	Vegetation composition	Remarks
Mesoposis laticornis	Strongly and positively correlated with vegetation height (P<0,001 for adults and P<0,01 for nymphs). No significant correlation with cover but tends to avoid areas of low aerial cover.	Positive but not significant, correlation with Andropogoneae. Negative correlation with non-grasses (P<0,05).	This slender straw-coloured species clings to the stems of tall grass where it is well camouflaged. Although Andropogoneae form a significant part of its diet, the main determinant is structure. It will not return to a burnt area until the grass has recovered its height even though the required food plants are present. It is purely graminivorous but distribution is not related to other favoured grasses eg E pallens.
Humbe tenuicornis	Significant bimodality of distribution with respect to cover (P<0,01) with high and low values preferred to intermediate. Slight (not significant) preference for tall grasses.	No significant correlations with any plant species.	80% of its diet is D eriantha but no significant correlation was found with this grass; if anything it was slightly negative. Bimodality with respect to cover results from its preference for areas with clumped and generally tall grass in which it often uses the open spaces between clumps. Acacia areas lack both the structure and D eriantha, and H tenuicornis avoids such areas.
Tylotroptidius gracilipes	Adults are very evenly spread with respect to cover and height but they avoid very open areas. Nymphs density correlates positively with height (P<0,001) and cover (P<0,001).	Adults show no correlation with any species, but nymphs are negatively correlated with D eriantha (P<0,001) and Aristida spp (P<0,05).	Adults of this species are very mobile and widespread. Nymphs avoid open, exposed sites. It is in such sites that D eriantha and Aristida spp are often relatively common, hence the negative correlations despite the fact that D eriantha is the main food plant.

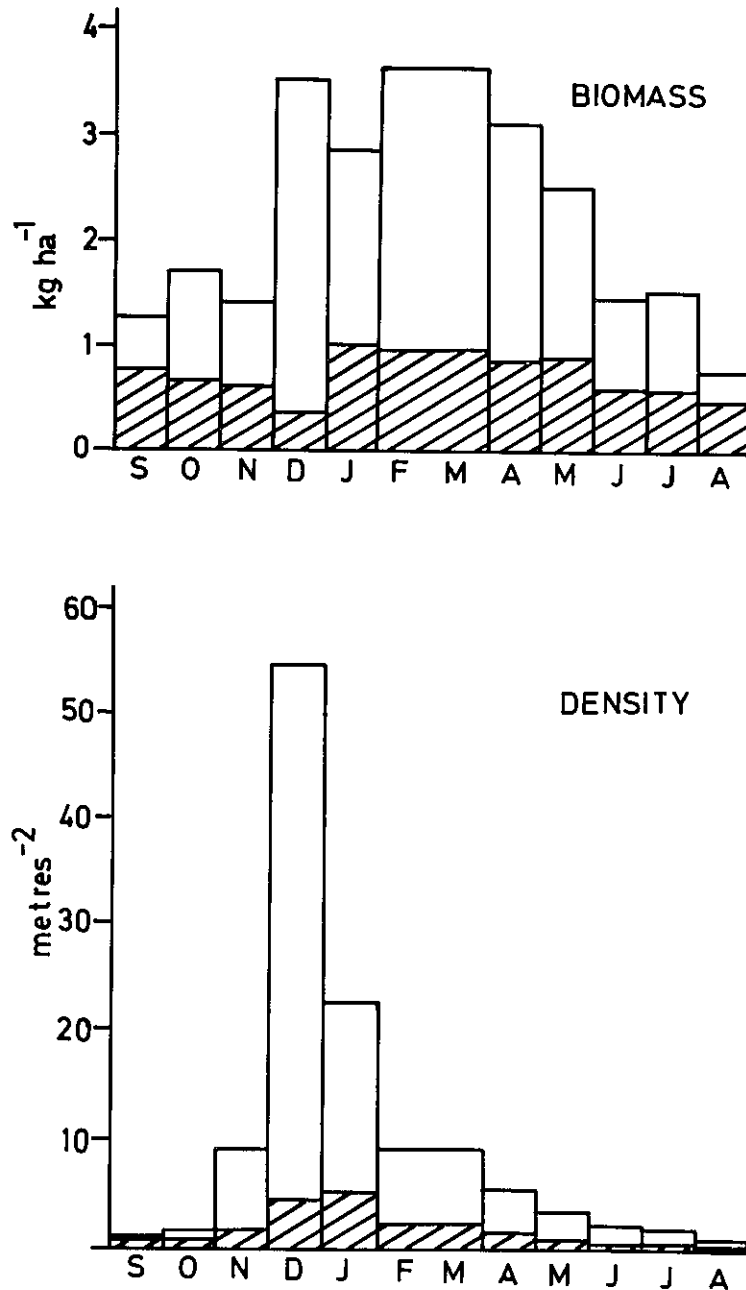| Species	Vegetation structure	Vegetation composition	Remarks
Oedaleus carvalhoi	Mainly found in Acacia where it is strongly and negatively correlated with height (F<0,001) and shows a strong preference for middle ranges of cover (P<0,001). Insufficient data from Burkea.	Insufficient data from Burkea.	It prefers a low even grass sward, and these conditions are more often encountered in Acacia than in Burkea. The fact that it is also found in Burkea when the structure is suitable implies that it is the structure of the vegetation and not composition which determines its distribution.
Orthochtha dasychnemis	Strong positive correlations with both height (P<0,001) and cover (P<0,001) for both adults and nymphs.	Negative correlation with D eriantha.	Favours tall grass and is commonest on Grid 2 which is characterized by tall Andropogoneae. It readily eats some of the shorter grasses, especially S perennis and D eriantha, but is not obviously associated with them.
Dnopherula crassipes	Widespread with respect to cover and height but avoids the extremes of very short grass (P<0,05) and tall dense vegetation (P<0,05). Generally prefers open areas of slightly less than average cover.	Negative association with Andropogoneae (P<0,001) and positive association with Aristida (P<0,05).	Association with Aristida spp results from preference for open areas where Aristida spp grow; it does not feed on these grasses. It generally avoids tall densely tussocked Andropogoneae although it will feed on these grasses. In Burkea its main food item is the short grass, D eriantha. It is common in both Acacia and Burkea so is obviously not dependent on D eriantha.

Figure 1. Comparison of density and biomass of grasshoppers in Burkea (shaded) and Acacia (not shaded).

polyphagous species can alter their diets to fit a variety of habitats. Indications are that vegetation structure is far more important than food availability in determining the distribution of a grasshopper species within Burkea savanna. Significant associations (either positive or negative) occurred with both structural aspects of the vegetation and grass species, as seen from the tabulated summary of these relationships (Table 6). Correlations with grass species were often most easily explained in terms of the growth form or ecology of the plants. This is illustrated, for example, by the species Dnopherula crassipes, which had two significant associations with respect to grasses. It was negatively associated with grasses in the subfamily Andropogoneae ($p < 0,01$) upon which it sometimes feeds, yet

it was positively associated with Aristida spp (p<0,05) upon which it never feeds (Table 6). The reason is that it preferred open areas of slightly less than average cover and avoided tall dense vegetation (p<0,05). Aristida spp tend to grow in bare areas, while most of the Andropogoneae are tall, densely tussocked grasses.

In some cases, nymphs were found to favour tall vegetation and/or high percentage cover presumably for protective reasons, while adults of the same species were more widespread, for example Pnorisa squalus, Pseudo-archyptera carvolhoi and Tylotropidius gracilipes (Table 6). Some species are morphologically adapted to a particular structural type of vegetation. For example, Mesopsis laticornis, with a thin straw-like body, was associated with tall straight grass (p< 0,01).

Two species not in Table 6, Acrotylus diana and Chrotogonus hemipterus make an interesting comparison. Both have flattened bodies and cryptic colour-ation and are adapted to open sandy areas and are found only when ground cover is very low. A diana is a feeder on a wide variety of grasses and may be found on any bare parts of the study area. C hemipterus is forbi-vorous and is locally common only on areas which have low cover and high forb diversity such as the heavily grazed and trampled area near a cattle water trough. This is the clearest case of distribution being affected by food availability although structure was equally important. Such examples are rare but the association between P carvalhoi adults and Aristida spp may relate to food preferences (Table 5) and Phaeocatantops decoratus a widespread forbivorous species, is only common on areas where there is a lot of Solanum panduraeforme on which it feeds readily.

It is noteworthy that the grasshoppers which exhibit greatest plasticity with respect to height, and cover (P squalus, P carvalhoi, T gracilipes and D crassipes) are common in both Acacia and Burkea. The diets of these species are no more diverse than those of Oedaleus carvalhoi, Orthochtha dasychnemis and M laticornis which are closely associated with certain structural characteristics and consequently are largely confined to either Acacia or Burkea (see Note 2). The very low density of H tenuicornis in Acacia may relate to structure or the absence of D eriantha (which compris-es 80% of its diet in Burkea) from Acacia. However, H tenuicornis is found in many parts of Africa (Dirsh 1965) and is clearly not dependent on that particular grass.

9. Open and canopied subhabitats

Since the composition, growth rate and structure of the herbaceous layer differs between open and canopied subhabitats, certain research projects at Nylsvley have examined the subhabitats separately. It was therefore appro-priate to investigate the grasshoppers in each. However, there was no evidence of a significant difference between the density of grasshoppers in the open or under canopy. However, the variability of the closed subhabit-ats made comparison difficult. These carried from Grewia flavescens and Ochna pulchra thickets with a dense layer of leaf litter and very little grass, to thick patches of the grass Panicum maximum under larger trees. The former contained very few grasshoppers while P maximum sometimes had very large numbers on it. Tylotropidius gracilipes in particular and others such as Acrida acuminata were frequently very common here. Where P maximum was kept short by large mammals Oedaleus carvalhoi was often common.

No single trapping method was completely satisfactory and different ones in different situations were used. Paired samples from open and closed subhabitats were taken at different times of year.

The total catch was:

	Open	Under canopy
Adults	68	62
Nymphs	84	106
Total	152	168

I have no evidence either that the distribution between these subhabitats changes during the year. Any movement between the subhabitats is likely to take place on a much shorter time scale with changes in insolation, temperature and wind speed.

If there is any quantitative difference between the two it is too small to warrant the painstaking sampling which would be required to detect it.

10. Interaction with grazing mammals

10.1 Dietary overlap

Competitive interaction between cattle, impala and grasshoppers was weaker than energy turnover suggests because of differences in food preferences. Brachiaria nigropedata and Brachiaria serrata are palatable to large mammals (Zimmermann 1978; Monro 1979) but were almost untouched by grasshoppers. Eragrostis pallens, which is unpalatable to mammals except in the first spring flush, was eaten readily by grasshoppers throughout summer. Although Digitaria eriantha was favoured by cattle, impala and grasshoppers, it was eaten proportionately less by mammals in winter than in summer, while the proportion in grasshopper diet increased in winter.

Dead material made up 12% of cattle diet in summer and 95% in winter (Zimmermann 1978) but negligible amounts of the grasshopper diet in summer and only about 25% in winter.

10.2 Density relationships

Grasshopper density was monitored over a period of a year inside and immediately outside a 3 ha plot which was protected against large mammals. Figure 2 shows the percentage of the total catch which was inside the exclosure. In winter there were more grasshoppers outside the exclosure than inside. The situation was reversed in summer. About 200 cattle were grazed in the study area outside the exclosure from January to May. They prevent a build up of standing dead (Gandar 1980) and this may help to prolong the growing season outside the exclosure by promoting young growth after the vegetation inside the exclosure has become choked. However, I did not check whether there was a greater supply of green leaf outside the exclosure in winter. In summer the grasshoppers were possibly attracted to

the exclosure by habitat factors such as greater cover, rather than food availability which was unlikely to be limiting anywhere.

Since the exclosure was small, these findings did not necessarily represent a change in the grasshopper population as a whole in response to the presence of large herbivores. It was probably simply a localized diffusion to a temporarily more favourable area. There was no noticeable difference in the species composition of the grasshopper population inside and outside the exclosure.

In the longer term heavy grazing by large herbivores can affect the composition of the grasshopper populations. Near sampling Grid 2 there was a localized area which had been overutilized where there had previously been a fence separating two grazing camps. Grass species composition was not much affected, but herbaceous cover was much lower and there were large bare patches of sand. In April the grasshopper numbers were only very slightly lower here compared to Grid 2, but Tylotropidius gracilipes and Orthochtha dasychnemis were less common and Acrotylus spp were very common although very seldom encountered on Grid 2 only 30 m away.

It is noteworthy that the drop in the grasshopper population (Note 1) by a factor of three between 1977 and 1978 coincided with the termination of cattle grazing. In Canadian grassland, grasshopper biomass was found to be three times as much on grazed as on protected areas (Riegert and Varley 1973). Although the climatic factor mentioned earlier is probably the main agent of change in the Nylsvley case, the absence of grazing may have contributed.
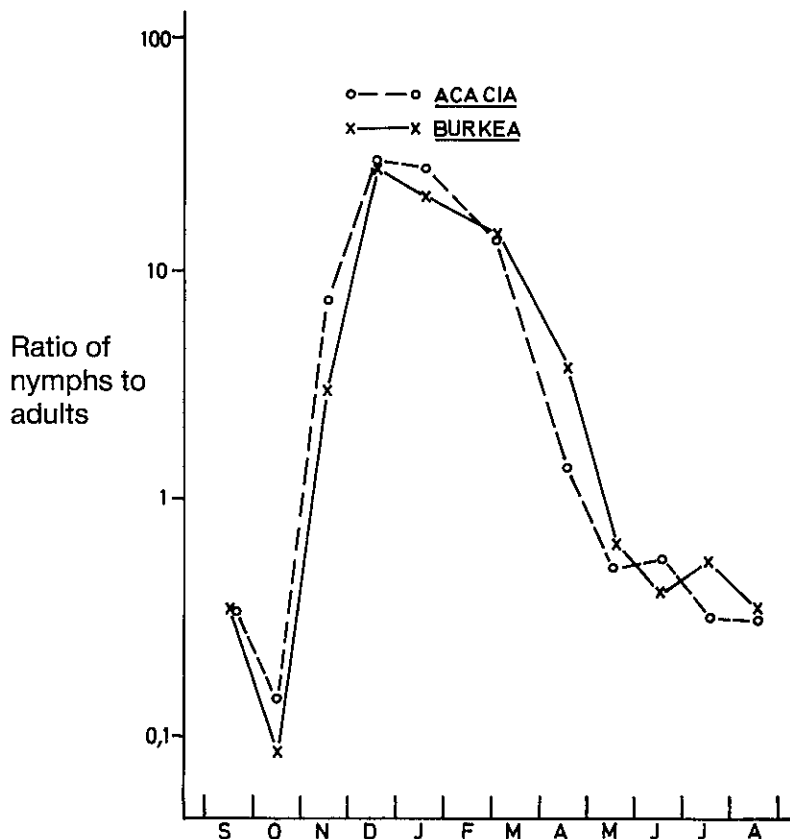

Figure 2. Monthly changes in the ratio of nymphs: adults for eleven grasshopper species on a logarithmic scale.

11. The effect of a grass fire on grasshoppers

On 5 September 1978, 180 ha of the study area were burnt. The effect on Orthoptera was studied in an area of Burkea. The fire had been very patchy, and unburnt patches, some only two metres across, amounted to 21% of the area. Immediately after the fire, there were very high concentrations of grasshoppers on the unburnt patches with negligible numbers on the burnt area. The biomass on these patches was over three times pre-fire levels (Gandar 1979).

The biomass of grasshoppers on the unburnt patches remained higher than on the burnt until January 1979, four months after the fire, when they were the same (Figure 3).

The average biomass for the entire mosaic of burnt and unburnt patches was calculated. Immediately after the fire this average biomass was 70% of that of unburnt savanna. Instead of catching up, the grasshopper biomass on the burnt mosaic was 44% of unburnt Burkea after six weeks and 42% after four months.

Egg pods of grasshoppers and stick insects (Phasmidae) in the soil survived the fire but the mortality of nymphs emerging onto the bare burnt areas in October was high. Also, predation was probably high as insectivores exploited the exposed situation of insects on the burn. There was an obvious concentration of grey hornbill, Tockus nasutus, which feed on grasshoppers, around the burn for a few weeks after the fire. There was a noticeable darkening of the cuticles of grasshoppers on the burn which may have offered some protection. One specimen of Parga xanthoptera, which is normally straw-coloured, was completely black. The fire had occurred after the final moult so this was an actual darkening as opposed to the development of a new darker cuticle. The effect has been documented by Burtt (1951) and Hocking (1964).

Only 30% of grasshopper biomass was lost in the fire. It is not known what percentage of the loss was mortality and what was flight. Mortality depends on several factors:

(i)   Time of year:
        In early September the grasshoppers were mostly adults which could dodge the flames more effectively.

(ii)   Patchiness of the fire:
        The path of the fire was sometimes uncertain and the fire front uneven. Mobile insects can escape through breaks in the fire front and shelter in unburnt patches.

(iii)   Speed and intensity:
        D Gillon (1972) reports that mobile insects can flee in front of a flame front moving at 500 m hr^{-1} (data from Ivory Coast savanna). Three measurements of the rate of spread of the Nylsvley fire ranged from 430 m hr^{-1} to 24 000 m hr^{-1} (Gandar 1982c). Gillon also reports that temperatures inside tufts may remain as low as 50°C and at this level fire is not necessarily destructive to insects. Harrison (reported in Gandar 1982c) measured temperatures just above tufts, not inside them. Of 30 tufts, all but one generated

temperatures in excess of 260°C. At least one nymph which was almost certainly too small to dodge the flames survived on a burnt patch. Reported nymphal mortalities range from 4,5% (Y Gillon 1972) in Ivory Coast savanna to 100% in rangeland in USA (Hunter 1905).

(iv)   Time of day:
Hunter (1905) states that grasshopper mortality is much greater in fires on cool windy nights when insects are less active and the fire moves faster. This fire passed through the area of study at about 20h00. Temperature was 15,1°C and mean wind speed was 1,8 m s⁻¹. On the other hand, a night fire would protect grasshoppers from insectivorous birds which are attracted to a fire where they catch fleeing insects on the wing (Komarek 1969; Y Gillon 1972). The forktailed drongo, Dicrurus adsimilis, is the commonest at fires in this area (Paintin 1965; W Tarboton, personal communication, 1978).

Acrotylus diana and Acorypha pallidicornis were the first to reinvade from the first week after the fire. A diana is a cryptically coloured grasshopper which favours open habitats. A pallidicornis is a mixed feeder eating grass, forbs and litter. On the burnt areas they fed regularly on ash. The crop of one specimen caught on the burn contained only ash. After about three weeks Pnorisa squalus, Dnopherula spp and Parga xanthoptera were also found on the burnt areas. Phaeocatantops decoratus and Catantops melanostictus followed in small numbers in mid October. These two species are forb-feeders and it was at this time that forbs reappeared. Spathosternum nigrotaeniatum and Mesopsis laticornis which were common on the unburnt areas, were never found on the burn. Tylotropidius gracilipes and Orthochtha dasychnemis were uncommon on the burn. Grasshoppers on the burnt areas fed less selectively than usual.

12.   Predation on grasshoppers

The role of predation as a regulating factor on the grasshopper population was not investigated. A few observations which relate to predation are listed.

Small running spiders preying on nymphs have been observed and this is possibly the main source of predation on small nymphs. Mantids are also common in the grass layer and may also prey on nymphs. Larger web-spinning spiders feed mostly on Coleoptera judging by the remains in the webs. I have not found grasshopper remains in these but J G Ferreira (personal communication, 1977) reports finding the remains of small adult grasshoppers in the webs of Nephila spp. Ground-dwelling spiders probably take more grasshoppers than these. Monitoring other insects using black-box traps (Gandar 1979) indicated that ground-dwelling spiders were four times more numerous in Burkea than in Acacia. This somewhat surprising discovery is probably related to vegetation structure rather than food supply. The spiders seem to be associated with densely tussocked grass such as is found in Burkea. The possibility that these spiders may contribute to the fact that grasshopper numbers are lower in Burkea is worth investigating.
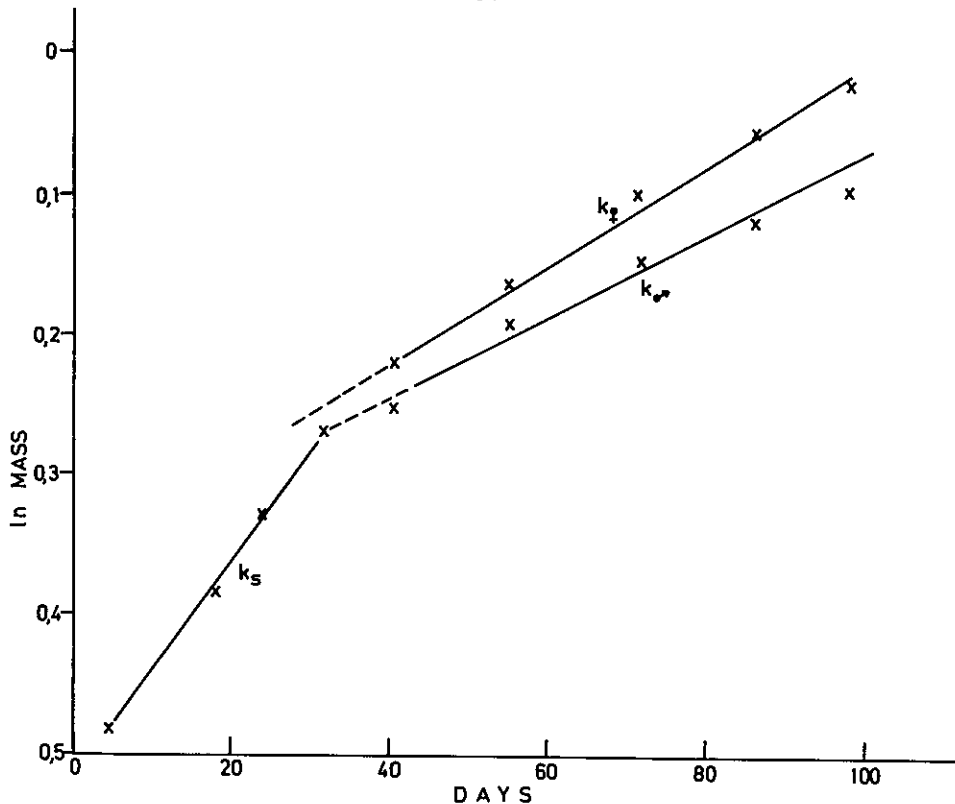
Figure 3. Average number of grasshoppers per m² plotted against the maximum height of available food, (ie green leaf), estimated for each drop-tent sample. All height estimates of 800 mm or more were lumped together.

The wasp _Liris_ sp (Laridae) was also observed taking grasshoppers. It will prey on more than one species and take either adult or final instar nymph. Prey included _Machaeridea billineata_ and _Pnorisa squalus_.

Grasshoppers are often seen to carry external parasitic mites. Their effect on mortality is not known, but grasshoppers seem to be able to carry heavy loads of these. Parasitic Diptera are known to parasitize grasshoppers but I saw no evidence of this in any of the dissected grasshoppers so it is probably unimportant.

The other main source of predation is the small vertebrates. After the fire at Nylsvley grey hornbills were noted exploiting insects, including grasshoppers, in the exposed post-fire environment.

Egg predation has been suggested as an important controlling factor in grasshopper populations (Nakamura et al 1971) but this was not investigated at Nylsvley.

13. Other Orthoptera

Phasmidae (stick insects) and Tettigoniidae (long horn hoppers) are the most important of the remaining phytophagous Orthoptera. Tettigoniidae feed mostly on dicotyledons: Phasmidae eat mostly grass. They are only present in measurable numbers from November to May though individuals may

Table 7.   Biomass of Phasmidae and Tettigoniidae, averaged over the period November 1976 to May 1977. Values in kg ha^{-1}.

	Burkea Grid 1,2,3	Acacia Grid 4	Intermediate Grid 5
Phasmidae	0,08	0,01	0,09
Tettigoniidae	0,04	0,02	0,05
Total	0,12	0,03	0,14

occasionally be found outside this period. Table 7 gives the average biomass from November 1976 to May 1977. In the year of the intensive survey, these two families amounted to 8% of the biomass of grasshoppers in Burkea. In Acacia it was less than 1%. At night I noted that the nocturnal Tettigoniidae were patchily distributed with small pockets of higher density particularly in Acacia. The estimate of the average biomass of Tettigoniidae in Acacia may be an underestimate by a factor of two or three, but they would still be insignificant compared to grasshoppers. In Burkea the population of Tettigoniidae dropped in the 1977/78 and the 1978/79 seasons as did grasshoppers. The densities then were too low for drop-tenting to give a meaningful estimate. The phasmid population was approximately halved in 1977/78 but in 1978/79 it was back to nearly 0,08 kg ha^{-1}. I also noted the presence of the Tetrigidae (pygmy grasshoppers), but their biomass was immeasurably small.

Amongst the mixed feeders, Gryllidae (crickets) are the commonest and Blattidae (roaches) are sometimes found. Their combined masses were in the order of 0,007 kg ha^{-1} based on drop-tent trap data, but this is likely to be an underestimate since they are easily overlooked. For the moment they can safely be ignored. A number of Gryllotalpidae (mole crickets) were caught in pitfall traps. These feed mainly on insect larvae. Mantidae, which are also insectivorous were common but I have no data on the density or biomass of these two families.

CHECKLIST

FAMILY   Eumasticidae
Subfamily   Thericleinae

Thericles sp
  Small uncommon apterous species. A specimen was found on Dichapetalum cymosum but it is not known whether it actually feeds on this poisonous plant. Mainly, possibly purely, a feeder on dicotyledons.

FAMILY   Charilaidae

Charilaus carinatus Stål
  Medium sized. Widespread, but uncommon in most parts. Local concentrations occur, particularly in short grass transitional zones between Acacia and Burkea in Camp 2. Mainly graminivorous. Overwinters in egg stage.

FAMILY   Pamphagidae
Subfamily   Porthetinae

Lamarckiana punctosa Walker
  Heavy sluggish insects. Females very large and wingless and found on the ground. Adult males smaller with large wings. Only one adult male found, on a branch of Terminalia sericea where it was well camouflaged. Nymphs not uncommon, but adults very uncommon implying high nymphal mortality. Non-graminivorous.

Lobosceliana brevicornis Bolivar
  Very large sluggish insects similar to L punctosa above. Also uncommon.

Transvaaliana distanti Saussure
  Medium to large sluggish apterous grasshopper. Uncommon. Non-graminivorous.

FAMILY   Pyrgomorphidae

Chrotogonus hemipterus Schaum
  Small robust flattened geophilous species with vestigal wings. Both adults and nymphs sit on bare sand in the sun where their flattened bodies and cryptic colouration make them difficult to spot. Locally common in a heavily utilized area near the watertrough in Camp 2 where ground cover is low and forb diversity is high. Feeds entirely on non-grass. Overwinters in the egg stage.

Phymateus baccatus Stål
  Large sluggish green adults. Not very common. Nymphs are black and gregarious, actively moving in groups of up to 40. Found in both Burkea and Acacia. Frequently seen feeding on Solanum panduraeforme in Acacia. Sometimes seen on Grewia flavescens in Burkea. Non-graminivorous. One generation per year. Nymphs emerge early in November, adults die off in winter and overwintering is in the egg stage.

Phymateus morbilosus L
Large grasshopper with small non-functional wings. Very uncommon. Only one individual recorded, on Solanum panduraeforme.

Phymateus viripides Stål
Very uncommon. Appears to be ecologically similar to P baccatus above.

Pyrgomorpha granulata Stål
Small grasshopper occurring in either green or brown form. Fairly common and widespread in both Burkea and Acacia. Adults are present from January to November. Entirely non-graminivorous.

Taphronota stali Bolivar
Medium sized uncommon grasshopper. Two specimens found on small woody plants near the grass vlei.

Zonocerus elegans Thunberg
Medium sized colourful grasshopper with short non-functional wings. Widespread and fairly common. Often on Solanum panduraeforme in Acacia but also locally common in long grass in Burkea. Less common in 1977 to 1979 than in the previous two seasons. Non-graminivorous. Overwinters in egg stage.

FAMILY   Acrididae
Subfamily   Hemacridinae

Hemiacris femoralis Kirby
Medium sized. Not common. Adults were only found in April and May so this species probably overwinters as eggs.

Leptacris pretoriae
Uncommon. Two specimens found in tall Hyperthelia dissoluta in Acacia-Burkea transition zone, and a third in Burkea.

Spathosternum nigrotaeniatum Stål
Small grasshopper. Very common in Burkea, fairly common in Acacia. Usually keeps well concealed in grass tussocks. Declined relatively less in dry years (1977 to 1979) than most other species. Purely graminivorous. Possibly two generations per year. It may overwinter as egg or late instar nymph or adult. Eliminated from an area by veld fire, and is one of the last species to return after a fire.

Subfamily   Coptacridinae

Eucoptera paupercula Kirby
Small. Uncommon.

Subfamily   Calliptaminae

Acorypha pallidicornis Stål

Medium sized, robust grasshopper. Widespread and common in both Burkea and Acacia. Prefers open areas and is common on freshly burnt areas. Has very mixed diet of grass (5 to 10% of diet), non-graminaceous herbs, plant litter, arthropod remains and ash. One generation per year. Overwinters as adults which breed in the spring. Nymphs emerge in October/November becoming adult from February onwards.

Subfamily   Euryphyminae

Aneuryphemus cf rhodesianus Uvarov

Medium sized. Uncommon.

Calliptamulus sp

Medium sized. Uncommon.

Rhodesiana maculata Dirsh

Medium sized. Uncommon. Prefers open sandy areas.

Subfamily   Eyprepocnemidinae

Cataliopus cognatus Walker

Medium to large grasshopper. Uncommon but possibly widespread. Found mainly in long grass near the grass vlei.

Tylotropidius gracilipes Stål

Medium to large grey and black grasshopper with long distinctive hind femora. Active and highly mobile, sometimes moving several hundred metres in a day. Common and widespread in Acacia and Burkea. Nymphs favour tall grass and high aerial cover while adults have greater plasticity but still avoid bare patches. Mixed feeder on grass forbs, preferring the softer grasses such as Digitaria eriantha. However trapping data shows a negative correlation between the numbers of this species caught and the relative abundance of D eriantha, its main food item. This is probably because D eriantha is relatively more abundant than other grass species in the open short grass areas which tend to be avoided by T gracilipes. It is less selective for green plant material in winter than most other grasshoppers, when it consumes much brown D eriantha. Sometimes it is locally very abundant on dense stands of Panicum maximum. In Acacia, it will feed on Solanum sp. It has one generation per year and overwinters as adult, breeding in the spring. Copulation was observed from September to early November. It is susceptible to veld fire, being totally absent from recently burnt areas, but it is probably a powerful enough flier to flee from most fires. It is one of the last species to reinvade after a fire.

Subfamily   Catantopinae

Catantops cf humeralis Thunberg

Very uncommon. Only one specimen found.

Catantops melanostictus Schaum

Medium sized. Common and widespread in Acacia and Burkea. Often in well-grassed areas where it feeds on forbs, but it is tolerant of open areas. It will return to a recently burnt area with the first flush of forbs. It is also often associated with shrubs and was sometimes recorded on young Burkea africana and on Grewia flavescens. Non-graminivorous for most of the year. In spring, grass makes up 25% of the diet and was observed on Panicum maximum under shrubs. One generation per year. Most overwinter as adults which breed in November, although a few breed in late summer and lay overwintering eggs.

Catantops spissus Walker

Not common. Recorded in Acacia areas with large shrubby component.

Catantops zernyi Ramme

Only one specimen found.

Phaeocatantops decoratus Gerstaecker

Medium sized grasshopper, easily identified by single black dot on hind femur. Common in Acacia, not very common in Burkea. Feeds mainly on forbs in the grass layer, particularly Solanum panduraeforme in Acacia. One generation per year. Most overwinter as adults but some females lay overwintering eggs in May.

Subfamily   Cyrtacanthacridinae

Acanthacris ruficornis Fabricius

Large. Not very common. Usually found in long grass. Mixed feeder on grass and non-grass. One generation per year. Probably breeds late summer, overwintering in egg stage.

Acridodares sp

Large. Uncommon. Found in long grass.

Ornithacris cyanea Stoll

A very large, strong-flying grasshopper. Fairly common, favouring areas of Burkea with tall, densely tussocked grass (Eragrostis pallens-Trachypogon spicatus veld) or moderately tall grass with high percentage aerial cover (Eragrostis pallens-Setaria perennis veld). Usually keeps low in the grass but flies into trees when flushed out. Sometimes seen in trees and may feed there; recorded in Acacia tortilis and Burkea africana. Diet is usually about 50% grass dropping to 10 to 20% in mid- and late summer. Solanaceous epidermal cells were found in crops of this species, implying that it also feeds in the grass layer in Acacia. One generation per year. Adults overwinter and breed in spring.

Subfamily   Acridinae

Acrotylus angulatus Stål
Not very common. Small cryptically coloured grasshopper found in sandy areas. Similar to A diana below, but prefers slightly more cover. Appeared to decline in 1977 to 1979.

Acrotylus diana Karny
Small cryptically coloured grasshopper. Common in Burkea and Acacia, particularly the former. Appeared to increase relative to the whole grasshopper population in 1977 to 1978. Found in open sandy areas with low percentage grass cover. Always keeps close to the ground. Adults often rest on bare sand in the sun; nymphs prefer more sheltered sub-habitats. Purely graminivorous, feeding largely on Digitaria eriantha. Usually overwinters as adult laying eggs in spring, but some females were breeding in May 1977. Overwintering adults feed almost entirely on green grass which is generally only found low down inside tufts in winter. It was the first species to reinvade after a veld fire.

Acrotylus furcifer Saussure
Uncommon. Found in sandy areas of Burkea with scattered tall grass tussocks, especially between Camps 3 and 4.

Acrida acuminata Stål
Medium to large slender grasshopper, usually green, but a striped brown form is also found. Common in thick grass in both Acacia and Burkea. High densities sometimes found locally on Panicum maximum under canopy. Purely graminivorous, feeding on a broad spectrum of grasses. Egg-laying was recorded in April but breeding is asynchronous and probably takes place over much of the year.

Aiolopus thalissinus Fabricius
Medium sized. Uncommon. Found in Acacia and Burkea.

Gastrimargus africanus Saussure
Large grasshopper with green and brown forms as adult, but nymphs were always green. Strong flier. Fairly common in the well-grassed areas of Burkea with either tall tussocked grass or shorter even swards. It is less common in Acacia. Near the laboratories at Nylsvley (not on the study area) it can be found in shrubby thicket. The contradictory reports in the literature on the preferred habitat types of this species testify to its plasticity. Graminivorous, feeding on a wide variety of grasses but showing a slight preference for those of the subfamily Andropogoneae. One generation per year. Breeds in late summer and overwinters in the egg stage.

Gymnobothrus sp
Small. Very uncommon. Appears to favour bare areas of Burkea.

Humbe tenuicornis Schaum
Medium large grasshopper. Its humped pronotum is particularly dist-inctive in nymphs. Widespread in Burkea. Common in tall grass Burkea where it keeps low in the grass, but it is also found in open sandy areas of Burkea. When density is compared to the quantity of grass

(ie height x cover), a bimodal distribution is indicated for adults, but nymphs are evenly distributed. Uncommon in Acacia. Graminivorous, with a strong preference for Digitaria eriantha which forms 80% of its diet. Of all the grasshoppers whose diets were examined, this species came closest to monophagy. Its distribution can be explained in terms of food preference since D eriantha is a grass of Burkea savanna. It breeds in late summer and autumn, and nymphs emerge in November. Adults live on through the winter, sometimes until the following December. A further period of breeding in spring is possible but was not established. Robertson and Chapman (1962) report complicated breeding cycles for this species.

Locusta migratoria L

Large. Uncommon. Occasionally found near the grass vlei. A breeding population exists in the grass vlei (H D Brown, personal communication, 1976).

Machaeridea bilineata Stål

Slender medium sized grasshopper. Fairly common in Burkea, slightly less common in Acacia. Common in 1975/1976 season, but relatively fewer in subsequent three years. Density is positively correlated to height and cover of grass. Graminivorous, favouring Digitaria eriantha especially in winter when it seeks out green leaves. Locally common on Panicum maximum. One generation per year. Overwinters as adult or final instar nymph. Breeds in spring.

Morphacris fasciata Thunberg

Medium sized. Widespread and generally uncommon but locally common near the main weather station. Often rests in sunshine on patches of sand or on roads and paths near the weather station. Graminivorous.

Oedaleus carvalhoi Bolivar

Small to medium sized grasshopper. Common in Acacia and fairly common in Burkea. Both green and brown forms, with the green form more common in Acacia than Burkea. Often found in areas which have been heavily grazed, and avoids areas of tall grass. Graminivorous. Breeding takes place from January to June and there may be two generations per year.

Orthochtha dasychnemis Gerstaecker

Medium sized grasshopper found only in Burkea. Common in areas of tall grass and also locally common on patches of Setaria perennis which forms a major part of its diet. Its density is strongly and positively correlated to the height and cover of grass. Also feeds readily on Andropogoneae in Eragrostis pallens-Trachypogon spicatus veld. Graminivorous. One generation per year. Overwinters in egg stage.

Paracinema tricolor Thunberg

Medium sized. Only one specimen found. Reported to prefer wet habitats (Phipps 1966, Golding 1934, Pinhey 1965) so it was probably a stray from a wetter part of the reserve and non-breeding on the study area.

Parga xanthoptera Stål

Small to medium slender straw-coloured grasshopper with distinctive paired spurs on the hind knee. Common on grass in Burkea. Also occurs in Acacia. Graminivorous, with a strong preference for Setaria perennis. Also readily eats Digitaria eriantha but tends to avoid the tough grasses such as Eragrostis pallens. One generation per year. Overwinters as adult. Breeds in spring.

Rhabdoplea cf munda Karsch

Small. Fairly uncommon in 1975 to 1977; very common 1977 to 1979. Graminivorous. Probably widespread.

Subfamily   Truxalinae

Brachychrotaphus tryxalicerus Fischer

Uncommon. Apparently localized in Burkea areas near the grass vlei.

Dnopherula rotundifrons Bolivar

Uncommon.

Dnopherula cf dorsata Bolivar

Uncommon.

Dnopherula cruciata Bolivar

Fairly common. Very difficult to distinguish from D cracipes in the field.

Dnopherula crassipes Uvarov

Small. Very common. Widespread in Acacia and Burkea. Shows slight preference for short grass but avoids very open sandy areas. Graminivorous, eating mainly Digitaria eriantha when in Burkea. May have two generations per year in favourable conditions at Nylsvley; only one generation in dry years. Overwinters as adult, breeding in spring.

Leva sp 1

Very small. Fairly common and widespread. Mainly graminivorous, but will also eat dicotyledons.

Leva sp 2

Easily confused with species 1. Probably less common.

Mesopsis laticornis Krauss

Long thin straw-coloured adult. Clings to stems of tall grass where it is well camouflaged. Small nymphs are greenish and shelter inside tufts. Distribution strongly related to grass height, especially for adults. Absent from bare sandy areas. Restricted to Burkea where it is common. Graminivorous. Nymphs feed mainly on the tussocks in which they shelter, usually grasses of the subfamily Andropogoneae. Adults are also frequently associated with these grasses and feed on them also, eating sheath as well as leaf. This was the only species examined which regularly ate grass sheath. Adults also feed readily on Eragrostis pallens, which is normally the main food item. These grasshoppers do

not feed much on Digitaria eriantha and trapping data indicates a negative correlation between numbers of this grasshopper and relative abundance of D eriantha. It is totally absent from burnt veld and will not begin to return until at least a year after the fire. Asynchronous generations with one, or one and a half, generations per year. Population overwinters as adults, small nymphs and possibly also eggs.

Paragymnobothrus rufipes Uvarov

Small. Uncommon. Geophilous.

Platypternodes brevipes Stål

Medium sized. Fairly common in Acacia, less common in Burkea. Tends to be localized, favouring areas of high percentage aerial cover. Graminivorous. One generation per year. Adults die off in autumn. Eggs overwinter.

Pnorisa squalus Stål

Active medium sized grasshopper. Very common and widespread in open grassland. Commonest grasshopper in Acacia and Burkea, with dominance more pronounced in Acacia. Found in both short and tall grass. Nymphs often shelter inside tussocks. There are two forms: the first is light brown with a dark sidestripe and sometimes two thick black stripes on the dorsum of the pronotum, and orange legs; the other form is plain greyish brown. As a general rule, the striped form is found in Acacia and the plain form in Burkea. The plain form in Burkea takes longer to develop than the striped form in Acacia and is very slightly heavier as an adult. Graminivorous, eating mainly tough grass. In Burkea it eats mainly Eragrostis pallens in summer, switching gradually to Andropogoneae in autumn and increasing its relative intake of Digitaria eriantha in winter. Numbers caught correlate negatively with the relative abundance of D eriantha in summer, but not in winter. One generation per year. Overwinters as adult in Acacia. In Burkea it sometimes fails to complete its development in time and overwinters as a final instar nymph. It breeds in spring in both savanna types.

Pseudoarchyptera carvalhoi Bolivar

Small black and white grasshopper. Very common and widespread in Burkea and Acacia. Adult males often climb grass stems from which they stridulate loudly. Found in a wide range of tall and short grass and in both well-covered and moderately bare areas, but avoided very tall dense grass. Appeared to have a slight preference for medium to short grass with 40 to 50% aerial cover. They were much less often found under tree canopy than in the open. Graminivorous. Feeds mainly on tough grasses such as Aristida spp and Eragrostis pallens, with which its distribution is positively correlated. Asynchronous breeding, probably with two generations per year. Many breed in late summer and die off in winter leaving overwintering eggs. Some adults and late instar nymphs are found throughout the winter. These breed in spring. Copulation has been observed in September and egg-laying in December.

Truxaloides braziliensis Drury

Large slender grasshopper easily distinguished from the next species, T constrictus, by the magenta wings. Uncommon.

Truxaloides constrictus Schaum

Large slender grasshopper. Not very common. Appears to favour Acacia.

DISCUSSION

Some authors (eg Robertson and Chapman 1962, Phipps 1966, Ueckert and Hanson 1971) have discussed habitat or food preferences or breeding strategies of different families and subfamilies, and shown that taxonomic groupings sometimes also roughly defined ecologically distinct groups. The study area at Nylsvley was not large enough nor varied enough to come to conclusions about habitat preferences of the different groups. As for breeding cycles, the only grasshoppers found throughout winter were Acrididae although some of this family overwinters as eggs. As far as could be ascertained, all non-Acrididae overwintered as eggs.

As mentioned above, some taxonomic groups had distinct diets. Amongst the Acrididae, the two subfamilies best represented, Acridinae and Truxalinae, were purely graminivorous except for Leva sp for which forbs made up only a small percentage of the diet. There was one clear distinction between these two subfamilies at Nylsvley in that the Truxalinae on the whole were consumers of tough grass, while the Acridinae selected the soft grasses. The Catantopinae were almost entirely non-graminivorous. The other subfamilies were not studied in detail. They appear to be mostly mixed feeders on grass and non-graminaceous plants except for Spathosternum nigrotaeniatum, the only Hemacridinae examined, which was purely graminivorous. Non-Acrididae fed on non-graminaceous plants with the one exception of Charilaus carinatus.

REFERENCES

Anderson N L 1964. Some relationships between grasshoppers and vegetation. Annals of the Entomological Society of America 57, 736-742.

Andrzejewska L and Wojcik W Z 1970. The influence of Acridoidea on the primary production of a meadow (field experiment). Ekologia Polska 18, 89-109.

Anonymous 1978. Nylsvley - A South African savanna ecosystem project : objectives, organization and research programme. South African National Scientific Programmes Report 27, 37 pp.

Burtt E 1951. The ability of grasshoppers to change colour on burnt ground. Proceedings of the Royal Entomological Society, London 27, 45-48.

Clarke E J 1948. Studies in the ecology of British grasshoppers. Transactions of the Royal Entomological Society, London 99, 173-222.

Coetzee B J, van der Meulen F, Zwanziger S, Gonsalves P and Weisser P J 1977. A phytosociological classification of the Nylsvley Nature Reserve. South African National Scientific Programmes Report 20, 31 pp.

Dadd R H 1963. Feeding behaviour and nutrition in grasshoppers and locusts. Advances in Insect Physiology I, 47-109.

Dirsh V M 1965. The African genera of Acridoidea. Cambridge University Press, 579 pp.

Dyer M I and Bokhari U G 1976. Plant animal interactions: studies of the effects of grasshopper grazing on blue grama grass. Ecology 57, 762-772.

Gandar M V 1979. Studies on the insects of the herbaceous layer of the Nylsvley savanna. Final Report to the National Programme for Environmental Sciences. Typescript, 69 pp.

Gandar M V 1980. The short term effects of the exclusion of large mammals and of insects in broad-leaf savanna. South African Journal of Science 76, 29-31.

Gandar M V 1982a. Trophic Ecology and Plant/Herbivore Energetics. In B J Huntley and B H Walker (Eds). Ecology of tropical savannas, Springer-Verlag, Berlin, pp 514-534.

Gandar M V 1982b. The dynamics and trophic ecology of grasshoppers (Acridoidea) in a South African savanna. Oecologia 54, 370-378.

Gandar M V 1982c. Description of a fire and its effects in the Nylsvley Nature Reserve: A Synthesis Report. South African National Scientific Programmes Report 63, 39 pp.

Gillon D 1972. The effect of bushfire on the principal pentatomid bugs (Hemiptera) of an Ivory Coast savanna. Proceedings of the Tall Timbers Fire Ecology Conference II, 377-417.

Gillon Y 1972. The effect of bushfire on the principal acridid species of an Ivory Coast savanna. Proceedings of the Tall Timbers Fire Ecology Conference II, 419-471.

Golding F D 1934. On the ecology of Acrididae near Lake Chad. Bulletin of Entomological Research 25, 263-303.

Harmse H J van M 1977. Grondsoorte van die Nylsvley-natuurreservaat. South African National Scientific Programmes Report 16, 64 pp.

Hocking B 1964. Fire melanism in some African grasshoppers. Evolution 18, 332-335.

Hunter J S 1905. Studies in grasshopper control. Agricultural Experimental Station Bulletin, Berkeley California 170, 8 pp.

Huntley B J and Morris J W 1978. Savanna Ecosystem Project: Phase I summary and Phase II progress. South African National Scientific Programmes Report 29, 52 pp.

Komarek E V 1969. Fire and animal behaviour. Proceedings of the Tall Timbers Fire Ecology Conference 9, 160-207.

Monro R H 1979. Study on the growth, feeding and body condition of impala, Aepyceros melampus (Lichtenstein 1912). MSc thesis. University of Pretoria, 122 pp.

Mulkern G B 1967. Food selection by grasshoppers. Annual Review of Entomology 12, 59-78.

Mulkern G B 1969. Behavioural influences on food selection in grass-hoppers (Orthoptera: Acrididae). Entomologia Expirementalis & Applicata 12, 509-523.

Mulkern G B and D R Toczek 1970. Bioassays of plant extracts for growth promoting substances for Melanoplus femurrubrum (Orthoptera: Acrididae). Annals of the Entomological Society of America 63, 272-284.

Nakamura K, Ito Y, Nakamura M, Matsumoto T and Hayakawa K 1971. Estimat-ion of population productivity of Parapleurus alliaceus Germar (Orthoptera: Acrididae) on a Miscanthus sinensis Anders. grassland. I. Oecologia 7, 1-15.

Nolte D J 1939. A comparative study of seven species of Transvaal Acrididae with special reference to the chromosome complex. Journal of southern Africa 2, 196-260.

Paintin E H 1965. Drongoes gather prey at fire. African Wildlife 19, p 231.

Phipps J 1966. The habitat and seasonal distribution of some East African grasshoppers (Orthoptera, Acridoidea). Proceedings of the Royal Society, London 41, 25-36.

Pinhey E 1965. Checklist of the short horned grasshoppers of Syringa Farm, Turk Mine, Southern Rhodesia. Arnoldia 2(1), 20 pp.

Riegert P W and Varley J L 1973. Aboveground invertebrates: II Populat-ion dynamics and biomass production of grasshoppers. Matador Project Tech-nical Report (Canadian Committee for the IBP) 16, 134 pp.

Rodell C F 1977. A grasshopper model for a grassland ecosystem. Ecology 58, 227-245.

Robertson I A D and Chapman R F 1962. Notes on the biology of some grass-hoppers of the Rukwa Valley, South West Tanganyika. Eos, Madrid 38, 51-114.

Thorsteinson A J and Nayer J K 1963. Plant phospholipids as feeding stimulants for grasshoppers. Canadian Journal of Zoology 41, 931-935.

Ueckert D N and Hansen R M 1971. Dietary overlap of grasshoppers on sand-hill rangeland in Northern Colorado. Oecologia 8, 276-295.

Wallace G K 1958. Some experiments on form perception in the nymphs of the desert locust Schistocerca gregaria Forska. Journal of Experimental Biology 35, 765-775.

White T C R 1976. Weather, food and plagues of locusts. Oecologia 22, 19-134.

Williams L H 1954. The feeding habits and food preferences of Acrididae and the factors which influence them. Transactions of the Royal Entomolog-ical Society, London 105, 423-454.

Zimmermann I 1978. The feeding ecology of Afrikander steers (Bos indicus) on mixed bushveld at Nylsvley Nature Reserve, Transvaal.   MSc Thesis, University of Pretoria.   204 pp.

TITLES IN THIS SERIES

1. A description of the Savanna Ecosystem Project, Nylsvley, South
    Africa. December 1975. 24 pp.

2. Sensitivity analysis of a simple linear model of a savanna ecosystem
    at Nylsvley. W M Getz and A M Starfield. December 1975. 18 pp.

3. Savanna Ecosystem Project - Progress report 1974/1975. S M Hirst.
    December 1975. 27 pp.

4. Solid wastes research in South Africa. R G Noble. June 1976.
    13 pp.

5. *Bibliography on marine pollution in South Africa. D A Darracott
    and C E Cloete. June 1976. 131 pp.

6. *Recycling and disposal of plastics waste in South Africa.
    R H Nurse, N C Symington, G R de V Brooks and L J Heyl.
    June 1976. 35 pp.

7. *South African Red Data Book - Aves. W R Siegfried, P G H Frost,
    J Cooper and A C Kemp. June 1976. 108 pp.

8. *South African marine pollution survey report 1974-1975. C E Cloete
    and W D Oliff (editors). September 1976. 60 pp.

9. Modelling of the flow of stable air over a complex region.
    M T Scholtz and C J Brouckaert. September 1976. 42 pp.

10. Methods and machinery for pulverising solid wastes. M J Simpkins.
    October 1976. 29 pp.

11. *South African Red Data Book - Small mammals. J A J Meester.
    November 1976. 59 pp.

12. Savanna Ecosystem Project - Progress report 1975/1976.
    B J Huntley. March 1977. 41 pp.

13. Disposal and recovery of waste paper in South Africa.
    G R de V Brooks. April 1977. 35 pp.

14. South African Red Data Book - Fishes. P H Skelton. July 1977.
    39 pp.

15. A checklist of the birds of the Nylsvley Nature Reserve.
    W R Tarboton. September 1977. 14 pp.

16. *Grondsoorte van die Nylsvley-natuurreservaat. H J von M Harmse.
    September 1977. 64 pp.

17. *Description and manual for the use of DRIVER - an interactive
    modelling aid. P R Furniss. September 1977. 23 pp.

18. *South African Red Data Book - Large mammals. J D Skinner, N Fairall and J du P Bothma. November 1977. 29 pp.

19. Introducing you to satellite operated Data Collection Platforms (DCP's). C C Stavropoulos. September 1977. 9 pp.

20. A phytosociological classification of the Nylsvley Nature Reserve. B J Coetzee, F van der Meulen, S Zwanziger, P Gonsalves and P J Weisser. December 1977. 31 pp.

21. *An annotated checklist of the amphibians, reptiles and mammals of the Nylsvley Nature Reserve. N H G Jacobsen. December 1977. 65 pp.

22. *Cooperative National Oceanographic Programme. SANCOR. January 1978. 19 pp.

23. South African Red Data Book - Reptiles and amphibians. G R McLachlan. February 1978. 53 pp.

24. *Guidelines for the disposal of dangerous and toxic wastes so as to minimize or prevent environmental and water pollution. R T Rudd. January 1978. 12 pp.

25. *Richards Bay mesometeorological data. Vertical profiles of air temperature and wind velocity and surface wind statistics. M T Scholtz, E T Woodburn, C J Brouckaert and M Mulholland. March 1978. 104 pp.

26. *Studies of mineralization in South African rivers. G C Hall and A H M Gorgens (editors). March 1978. 24 pp.

27. Nylsvley - A South African Savanna Ecosystem Project: objectives, organization and research programme. March 1978. 37 pp.

28. *A description of the Fynbos Biome Project. June 1978. 25 pp.

29. Savanna Ecosystem Project - Phase I summary and Phase II progress. B J Huntley and J W Morris. July 1978. 52 pp.

30. *Review of Coastal Currents in Southern African Waters. T F W Harris. August 1978. 106 pp.

31. *Report of the Task Group on Fermentation Technology. R J Andrews, J A de Villiers, P M Lategan, F G Neytzell-de Wilde, J P van der Walt and Professor D R Woods. September 1978. 16 pp.

32. *South African programme for the SCOPE mid-term project on the ecological effects of fire. September 1978. 36 pp.

33. Fire in South African ecosystems: an annotated bibliography. G U Schirge and A H Penderis. October 1978. 114 pp.

34. Inland water ecosystems in South Africa : a review of research needs. R G Noble and J Hemens. November 1978. 150 pp.

35. *South African Antarctic Research Programme, 1978-1982. SASCAR. December 1978. 39 pp. Out of print but partially replaced by No 50.

36. *Aboveground biomass subdivisions in woody species of the Savanna Ecosystem Project Study Area, Nylsvley. M C Rutherford. January 1979. 33 pp.

37. *Marine Line Fish Research Programme. SANCOR. April 1979. 17 pp.

38. *The Southern Ocean - South African Cooperative Research Programme. SANCOR. May 1979. 26 pp.

39. The Transfer of Pollutants in Two Southern Hemispheric Oceanic Systems. Proceedings of a workshop held at Plettenberg Bay, South Africa, 23-26 April 1979. October 1979. 188 pp.

40. Fynbos ecology : a preliminary synthesis. J Day, W R Siegfried, G N Louw and M L Jarman. December 1979. 166 pp.

41. *Bibliography of Marine Biology in South Africa. D A Darracott and A C Brown. February 1980. 250 pp.

42. Advances in understanding phosphorus cycling in inland waters - their significance for South African limnology. A J Twinch and C M Breen. March 1980. 22 pp.

43. Terrestrial ecology in South Africa - project abstracts for 1978. February 1980. 92 pp.

44. A manual of methods for use in the South African Marine Pollution Monitoring Programme. R J Watling. July 1981. 82 pp.

45. Threatened plants of Southern Africa. A V Hall, M de Winter, B de Winter and S A M van Oosterhout. May 1980. 244 pp.

46. South African legislation with respect to the control of pollution of the sea. André Rabie. January 1981. 73 pp.

47. Terrestrial ecology in South Africa and South West Africa - project abstracts for 1979. May 1981. 107 pp.

48. A bibliography of seabirds in the waters of southern Africa, the Prince Edward and Tristan Groups. J Cooper and R K Brooke. December 1981. 297 pp.

49. National Geoscience Programme. The Evolution of Earth Resource Systems. SACUGS. June 1981. 42 pp.

50. South African Antarctic Biological Research Programme. SASCAR. July 1981. 54 pp.

51. South African Marine Pollution Monitoring Programme 1979-1982. R J Watling and C E Cloete (editors). July 1981. 52 pp.

52. Structural characterization of vegetation in the Fynbos Biome. B M Campbell, R M Cowling, W J Bond and F J Kruger in collaboration with D P Bands, C Boucher, E J Moll, H C Taylor and B W van Wilgen. August 1981. 19 pp.

53. A bibliography of fynbos ecology. M L Jarman, R M Cowling, R Haynes, F J Kruger, S M Price and G Moll. August 1981. 73 pp.

54. A description of the Benguela Ecology Programme 1982-1986. SANCOR: (W R Siegfried and J G Field editors). March 1982. 39 pp.

55. Trophic Ecology of Lepidoptera Larvae associated with woody vegetation in a Savanna Ecosystem. C H Scholtz. June 1982. 29 pp.

56. Man and the Pongolo floodplain. J Heeg and C M Breen. June 1982. 117 pp.

57. An inventory of plant communities recorded in the western, southern and eastern Cape Province, South Africa up to the end of 1980. C Boucher and A E McDonald. September 1982. 58 pp.

58. A bibliography of African inland water invertebrates (to 1980). B R Davies, T Davies, J Frazer and F M Chutter. September 1982. 418 pp.

59. An annotated checklist of dung-associated beetles of the Savanna Ecosystem Project study area, Nylsvley. S Endrödy-Younga. September 1982. 34 pp.

60. The termites of the Savanna Ecosystem Project study area, Nylsvley. P Ferrar. September 1982. 42 pp.

61. Conservation of Ecosystems: Theory and Practice. A report on a workshop meeting held at Tsitsikama, South Africa, September 1980. Edited by W R Siegfried and B R Davies. September 1982. 97 pp.

62. *A description of the Grassland Biome Project. Edited by M T Mentis and B J Huntley. October 1982. 29 pp.

63. Description of a fire and its effects in the Nylsvley Nature Reserve: A Synthesis Report. M V Gandar. October 1982. 39 pp.

64. Terrestrial ecology in South Africa - project abstracts for 1980-1981. December 1982. 148 pp.

65. *Alien invasive vascular plants in South African natural and semi-natural environments: bibliography from 1830. V C Moran and P M Moran. December 1982. 42 pp.

66. Environmental Research Perspectives in South Africa. December 1982. 39 pp.

67. The Sancor Estuaries Programme 1982-1986. February 1983. 43 pp.

68. The Sancor Programme on Coastal Processes. April 1982 - March 1988. Edited by D H Swart. February 1983. 29 pp.

69. Guidelines for the management of large mammals in African conservation areas. The proceedings of an international workshop held at Olifants Camp, Kruger National Park, South Africa. Edited by A A Ferrar. May 1983. 95 pp.

70. Marine Linefish Programme Priority Species List. Sancor. Edited by J H Wallace and R P van der Elst. May 1983. 113 pp.

71. Mineral nutrients in mediterranean ecosystems. Edited by J A Day. June 1983. 165 pp.

72. South African programme for the SCOPE project on the ecology of biological invasions. A description and research framework produced by The Task Group for Invasive Biota of the National Programme for Environmental Sciences. July 1983. 25 pp.

73. South African Marine Pollution Survey Report 1976-1979. B D Gardner, A D Connell, G A Eagle, A G S Moldan, W D Oliff, M J Orren and R J Watling. September 1983. 105 pp.

74. Ecological notes and annotated checklist of the grasshoppers (Orthoptera: Acridoidea) of the Savanna Ecosystem Project Study Area, Nylsvley. M V Gandar. November 1983. 42 pp.

*Out of print.