

INVERTEBRATE BIODIVERSITY OF THE MKOMAZI GAME RESERVE, TANZANIA

Final Technical Report for the Darwin Initiative Funded Project

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Introduction

The contribution of tropical savannas to global biodiversity may be considerably greater than previously thought, not least because they occupy some 40% of the land surface in the tropics (Solbrig, 1996). Furthermore, the relative importance of the various arthropod groups differs greatly between tropical savanna and forest habitats, with the consequence that savanna areas often support different and characteristic taxa, thus significantly increasing the overall diversity of a region. Many of these groups play a significant trophic role (Gillon, 1983). Perhaps the most abundant of these are the termites and the dung beetles, both of which are fundamental to savanna ecology, as primary consumers and agents of nutrient transfer. Among the secondary consumers the dominant ecological role is probably played by the ants and spiders, though this may under-estimate the importance of other groups, such as the scorpions, solifuges, centipedes and, as illustrated in this study, the ground beetles and tiger beetles.

A number of ecological factors influence savanna biodiversity, but in Africa the presence of large numbers of herbivorous mammals is a particular force, generating considerable vegetational patchiness within the savanna habitat (Braithwaite, 1996), an attribute which has been shown to correlate positively with increased species diversity of both plants and animals (Samways, 1994; Braithwaite, 1996). This may partially explain why African savannas are more diverse than temperate grasslands (not least in terms of dung beetles, which thrive on the mammals' droppings), and why they are almost as rich in plant species as African rain forests (Menaut, 1983), although this may be more a reflection of the relative species poverty of the latter. Fire also has a significant impact on savanna biodiversity, by further increasing habitat diversity through the creation of a mosaic of successional stages based on burning. Although such increases in habitat diversity are likely to enhance invertebrate diversity, the experimental manipulation of fire to increase the biodiversity of savannas is rare (Braithwaite, 1996).

This project is a component of the *Mkomazi Ecological Research Programme*, a three-year programme undertaken jointly by the Royal Geographic Society and Oxford University at the request of the Government of Tanzania's Department of Wildlife. The chief aim of the Mkomazi Ecological Research Programme (MERP) is to identify and map key elements of the biodiversity of Mkomazi, in order to facilitate the effective conservation management of the Reserve in the context of local human development. To achieve this it is important to select, and then sample, a representative sub-set of the plants and animals present.

The aims of the invertebrate diversity project were to:

1. To conduct a baseline inventory of selected terrestrial invertebrate groups for the MGR by making representative taxonomic collections and identifying these where possible to genus and/or species.
2. To provide quantitative measures of the species numbers and diversity of key invertebrate groups for the major habitat types within the MGR, including calculation of appropriate indices of diversity.
3. To measure the degree of change in species diversity (β) and faunal similarity between major habitat types within the MGR.
4. To determine the effects of burning and grazing on species richness and diversity in different habitat types.
5. To develop secure, well-documented savanna invertebrate biodiversity collections at the TPRI, Arusha, Tanzania.

6. To provide training for Tanzanian personnel in:
 - collection and preparation of biological material for diversity studies,
 - maintenance of biodiversity reference collections,
 - taxonomy of appropriate invertebrate groups, and
 - measurement and interpretation of ecological parameters including diversity indices.

This report covers the scientific finding of the project (objectives 1 - 4 above). Aspects of the project concerned with training and institution building (objectives 5 and 6) are covered in the formal report to the Darwin Initiative.

Methods

Pitfall trapping

Activity of ground-living invertebrates was studied with pitfall traps constructed from plastic coffee beakers each 7 cm in diameter and 10 cm deep. Traps were spaced at a minimum of 2 metres apart and filled to a quarter of their depth with water to which a trace of household detergent was added. To reduce disturbance resulting from daily emptying, two plastic cups were placed one inside the other and only the inside cup was removed from the ground. Catches were sorted to order in the field and transferred to 70% ethanol for return to the UK.

During August 1993, a total of 30 traps were placed in burnt and unburnt *Acacia/Commiphora* bushland on the hillside immediately behind the Ibaya Camp over a 6 day period. In the footslope grassland below Ibaya Camp 50 traps were placed in burnt and unburnt grassland and operated over the same period. More extensive pitfall trapping was carried out in six different habitat types over a period of three weeks in November, 1994. Comparison was made: (i) between an area of hillside that had been burnt approximately 3 months previously, and an equivalent habitat where burning had not taken place (i.e. burnt and unburnt hillside, respectively), and (ii) between an area of grassland plain that had been burnt 3 months previously, and a corresponding area that had last been burnt at least 18 months previously (burnt and unburnt grassland, respectively). 30 traps were serviced for six days at the beginning of the trip, followed by a further three days at the end of the trip. The second spell of sampling, to study beetle emergence, was carried out in response to the first major rain of the season which fell on November 24th (there was a smaller burst on the 15th). In each of the two other sites, *Acacia senegal* woodland and an *Acacia drepanolobium* vlei, located near to Ndea hill, 60 traps were serviced for three days. Systematic monthly sampling of burnt and unburned hillside bushland and valley grassland at Ibaya camp was initiated in April 1995 and continued until March 1996. On each sampling occasion 30 traps were placed in each site over a 6 day period to give a total of 180 trap days. Total trapping effort over the two years of field sampling amounts to 12,370 trap/days or 33.9 trap/years from 15 separate sites. This almost certainly is the largest single sampling programme for surface-active invertebrates ever undertaken in East Africa, and perhaps in Africa as a whole.

Canopy sampling

One of us (GMcG) visited the MGR on five separate occasions to collect arthropods from tree canopies using a standard insecticidal knockdown technique. Samples were taken during the periods July 28th 1994 - August 14th 1994, April 4th 1995 - April 21st 1995, December 29th 1995 - January 18th 1996, March 28th 1996 - April 3rd 1996 and January 2nd 1997 - January 13th 1997.

Sampling was carried out using a *Hurricane Minor* petrol-driven, mist blower (Cooper-Pegler Ltd.) fitted with an ultra low volume delivery nozzle and charged with undiluted Pybuthrin 216 (Roussel Uclaf). The advantage of this method over other mass collection techniques such as fogging is the degree to which the mist can be directed accurately into the canopy from ground level. Pybuthrin 216 a pyrethroid formulation synergised with piperonyl butoxide, is ideal for use in the field since it gives rapid knockdown with non-persistence. Sampling was carried out whenever possible in dry, still conditions. Experience showed that best time of day was between dawn and 10.00 hours after which time winds, largely katabatic in origin, made sampling impossible. Foliage above 10m high was not sampled in any case. Arthropods knocked down were collected on purpose built, square, funnel-shaped trays (each 1m²). The trays, which were made

from rip-stop nylon balloon fabric, braced with 16 gauge aluminium tube were tied to wooden stakes by strips of inner tube. For small trees whose foliage was too low or spiny to permit the use of suspended nylon trays, plastic washing up bowls (each 0.16m²) were used instead.

Trees whose canopies were isolated from surrounding trees were selected for sampling and the calculation of canopy cover area assumed a near-circular canopy. Collecting trays or bowls were placed below the tree in positions likely to maximise samples (branches which were bare or did not appear healthy were avoided). Canopy foliage above the collecting trays was sprayed for a minimum of 15 seconds in three five-second bursts from different directions. When trees were in full leaf, the spray time was increased to a maximum of 30 seconds in three bursts to ensure thorough penetration through the canopy. For most trees one hour was used as the standard drop time period as most material was knocked down in the first 15 minutes and nothing was collected after 45 minutes. For some trees, such as those less than 3m high or with a small or low canopy, the sample time was reduced to 30 minutes. Again the vast majority of the total catch was obtained during the first quarter. During the sampling period GPS coordinates and measurements of tree height, canopy cover and tree girth were recorded. The height of trees over 2.5m was estimated, by visual comparison against measured heights. Canopy depth was not estimated. Other factors such as the presence or absence of flowers and seed pods were also recorded. At the end of the sampling period all material and fallen foliage was gently brushed into the collecting jars and pooled. Catches were examined, separated from debris and plant material and transferred to 70% alcohol.

Arthropods were initially sorted to class or subclass. Insects were sorted to the level of order and family and then morphotyped into Recognisable Taxonomic Units (RTUs). The classification used follows that of CSIRO (1991). Larvae have been excluded from the analyses presented here to avoid counting two developmental stages as different RTUs. Five individuals of each RTU were measured to the nearest 0.01mm and the median was then taken to calculate the dry biomass per RTU using the formula given in Moran & Southwood (1982).

Sweep net samples

Sweep net samples were taken in a range of different grassland types in November 1994 and January 1995. At each site, 10 parallel transects, each of 20 sweep strokes, were taken. Spiders were sorted from the catch for each transect and transferred immediately to individual vials of 70% ethanol.

Other samples

Opportunistic collecting of grasshoppers by hand-netting was undertaken in the vicinity of Ibaya Camp and in a range of woodland, bush and grassland habitats in the western third of the Reserve (west of Kisiwani). Fixed-time collecting was not used to compare habitats since ease of access varied due to vegetation structure and time availability in many habitats was dependent on priorities of other team members.

Other methods of sampling included litter sorting and hand-collecting. Hand collecting was carried out in a variety of habitats and in dry montane forest on the summit of Ibaya ridge litter was collected and sorted for spiders at Ibaya camp. In July/August 1994 additional invertebrate sampling was done using a sweep net. Six grass areas (various locations) were swept (50 sweeps) and the invertebrates stored in alcohol. A number of other insect samples were taken on an *ad hoc* basis. For example, three or four species of water bug were collected from a single kettle hole in the rocks by Ngurunga Dam and an ant-attended plataspid (Hemiptera: Plataspidae) species was collected from old termite galleries on the trunk of a species of *Balanites* at Zange Gate. Galls from three branches of an *Acacia seyal* var *fistula* and all the galls present of three small *Acacia drepanolobium* trees were plugged and the contents removed and preserved for examination. Insect samples were taken from lights around the Ibaya camp site after dark.

Data Analysis

a) Diversity measures

Three diversity indices was calculated for the ground-active invertebrates of each habitat type and each individual tree (fogging study), using the Biodiv™ software package. These included: (i) the

Margalef index, a simple measure based on species richness and abundance; (ii) Simpson's dominance index, which gauges the equitability of species abundances in a community; and (iii) Fisher's α index, which incorporates both species richness and evenness/equitability into its calculation.

b) Faunal similarity and community structure

In order to elucidate the relationships between habitat/tree type and the nature of the beetle communities they support, computer-based classification and ordination techniques (TWINSPAN and DECORANA, respectively) were used. These programmes objectively test for similarities between samples based on the number of species shared, and provide a means for determining which habitats/trees are most alike faunistically, and which are notably different (i.e. those which harbour a significant number of species not found in other samples). With TWINSPAN, sites with similar insect assemblages are clustered together in a hierarchy, while DECORANA represents faunal similarities and disparities in terms of separation distances on a two-dimensional graph.

1. The Coleoptera of Mkomazi Game Reserve

Background

Studies of beetle diversity have been rare in savannah habitats, focusing more often on tropical rain forests, and in particular the tree canopies (see, for example, Stork *et al.*, 1996). Yet even cursory investigation of ground-dwelling invertebrates in African savannah reveals an impressive diversity (and also biomass), which is orders of magnitude greater than that of vertebrates (Gillon, 1983). Beetles represent a very significant proportion of this fauna. Indeed, Gillon describes the Tenebrionidae, which is one of the three most abundant families in the savannah ground fauna along with the ground beetles (Carabidae) and dung beetles (Scarabaeidae), as one of the "faunistic markers" of dry savannahs.

The chief aim of the Mkomazi Ecological Research Programme (MERP) is to identify and map key elements of the biodiversity of Mkomazi, in order to facilitate the effective conservation management of the Reserve in the context of local human development. To achieve this it is important to select, and then sample, a representative sub-set of the plants and animals present. Of these, arguably the single most representative group of all is the beetles (order: Coleoptera) with their enormous number and variety of forms, sizes and ecological functions, ranging from fungivores and detritivores to herbivores, scavengers and predators. The ability to exploit such a wide range of food types, which has been one of the main factors in the success of beetles throughout the world, makes the group not only highly significant ecologically, but also probably more analogous with overall biodiversity than any other group of organisms.

The main objectives of this element of the Programme, therefore, were: (i) to compile as comprehensive an inventory as possible of the Coleopteran fauna of the Mkomazi; (ii) to assess beetle diversity in a number of different habitat and tree types throughout the Reserve; (iii) to investigate the effects of savannah fires on beetle diversity and community composition; and (iv) to study seasonal variations in both the diversity and composition of the beetle communities. In order to fulfil objectives one and two, sampling was carried out in as many different habitat types and tree species as the field trips allowed, while repeat sampling of four areas situated close to Ibaya camp was carried out throughout the year in order to achieve objectives three and four.

Methods

Ground-dwelling beetles were sampled in various habitat types throughout Mkomazi by pitfall trapping, while arboreal beetles were sampled using insecticide mist-blowing. Detailed descriptions of these methods, and of the sampling periods and localities, are provided above ("Biodiversity of the Mkomazi arthropod fauna"). In summary, pitfall trapping was carried out: (i) in burnt and unburnt habitats at Ibaya (in order to investigate the effects of fire on invertebrate species diversity and composition); (ii) every month for a whole year at Ibaya (May 1995 to April 1996) by our Tanzanian counterparts (to investigate seasonal differences in the fauna); and (iii) in a variety of different locations throughout the Reserve (both to investigate the effect of habitat type and to contribute to an overall inventory for Mkomazi. Insecticide spraying was carried out on a large number of tree species

throughout the Reserve, both to investigate the effect of tree type on species diversity and composition, and also to compile a comprehensive inventory of arboreal invertebrates.

Owing to the difficulties of processing of insect material from twelve months of pitfall sampling, a full account of seasonal variation in beetle populations was not possible. Instead, the collections made in August 1995 and January 1996 were used, together with those from the November 1994 and April 1995 sampling trips, to provide a relatively even distribution of sampling points throughout the year. Similarly, the arboreal beetle study had to be restricted to the beetles from only a small sub-sample (17) of the total number of trees sampled in the mist-blowing project.

Beetles were pinned, mounted and labelled at the Natural History Museum in London, then sorted to family and (numbered) morphospecies. All specimens are currently being held at the Museum, and a representative reference collection is being prepared for the Tropical Pest Research Institute in Arusha. Although the collections of ground-dwelling and arboreal species were compiled separately, any arboreal species already represented in the pitfall collections were given the same morphospecies number as previously allocated. A separate database was established for both studies, incorporating species' presence and abundance data for each habitat type (pitfall study) or each tree (arboreal study).

The composition of the beetle fauna

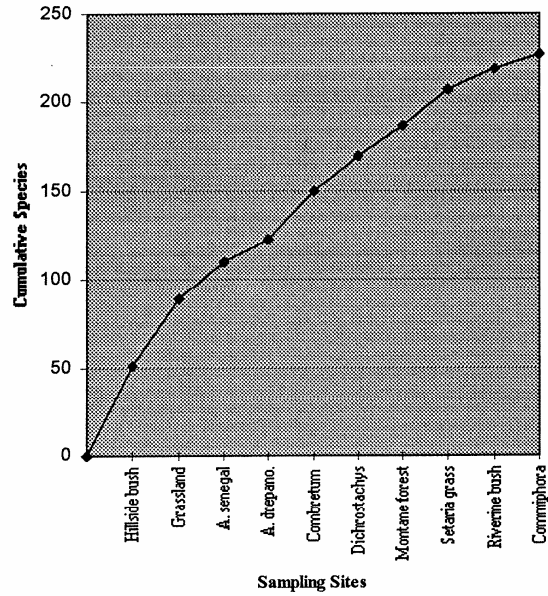
A total of 675 morphospecies, belonging to 47 families, were collected by pitfall trapping, insecticide mist-blowing, and by hand collection. The pitfall sampling resulted in the collection of 5,338 individual beetles belonging to 421 morphospecies, while a total of 1,254 individuals, belonging to 167 morphospecies, were collected from the 17 trees sampled in the insecticide-spraying study.

The species composition of the different beetle families is shown in Table 1. The most species-rich families were the Scarabaeidae (with 13.9% of all species), Chrysomelidae (also with 13.9%), Carabidae (13.2%), Curculionidae (9.6%), Staphylinidae (6.5%), and Tenebrionidae (5.9%). With few similar studies to provide comparative data on beetles, it is difficult to assess quite how rich the beetle fauna of Mkomazi is, relative to other areas of Africa, or how the composition of the families compares with those from other studies. However, the baseline inventory provided by this survey will serve as a standard against which future studies both in Mkomazi and elsewhere may be compared.

It is also, of course, impossible to know exactly what proportion of the total beetle fauna of Mkomazi has been collected during this study. Only a long-term, exhaustive survey of the Reserve could provide an accurate overall figure. A species accumulation curve for the pitfall sampling to date (Figure 1) reveals that the number of species from the Reserve continued to increase significantly as more habitats were surveyed during the study, with no evidence that a limit had been reached. Furthermore, even though approximately 90% of the species so far recorded were collected in one or other of the two wet seasons, sampling at different times of year is also likely to add considerably to the overall species list for Mkomazi.

An accurate inventory of overall beetle species richness for Mkomazi, requires knowledge of the number of unsurveyed habitat types and thorough sampling at different times of year. Large parts of the Reserve were inadequately covered by this study, and they probably include unsampled habitat types.

Figure 1. Cumulative numbers of beetle species from pitfall traps in Mkomazi Game Reserve.



The distribution of beetles across habitats in Mkomazi

Information regarding the distribution of beetle species in different parts of the reserve helps to identify the more diverse habitats and allows for the identification of those areas which contain rare or restricted species. Information on the distribution and diversity of beetles in different parts of Mkomazi are provided both by the pitfall study of habitat types (I) and by the insecticide fogging study of different tree types (II).

Table 1. Species composition of the different beetle families from Mkomazi.

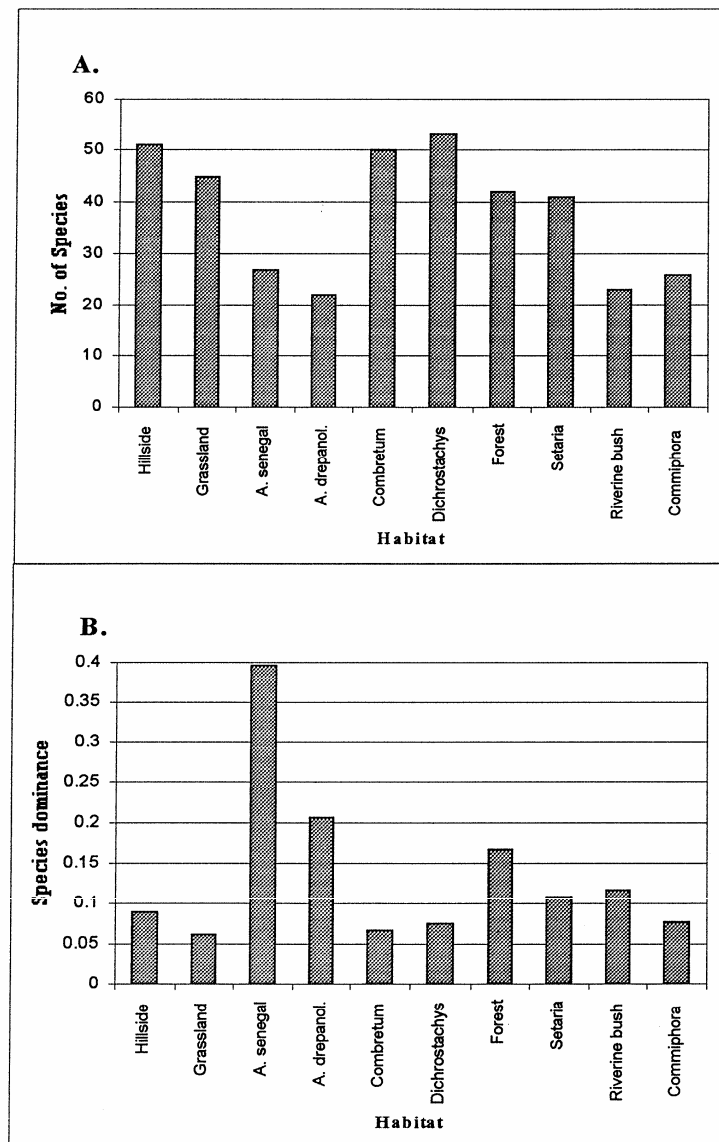
Family	No. of species	Family	No. of species
Carabidae	89	Phalacridae	11
Cicindelidae	8	Erotylidae	1
Staphylinidae	44	Corylophidae	7
Pselaphidae	5	Coccinellidae	17
Leiodidae	4	Endomychidae	1
Scydmaenidae	7	Lathridiidae	4
Scaphidiidae	1	Biphyllidae	1
Histeridae	11	Monommidae	2
Scarabaeidae	94	Colydiidae	3
Limnichidae	1	Tenebrionidae	40
Buprestidae	23	Lagriidae	1
Elateridae	12	Alleculidae	4
Cantharidae	2	Scraptiidae	2
Lycidae	2	Mordellidae	5
Dermestidae	2	Meloidae	24
Anobiidae	8	Anthicidae	13
Bostrichidae	3	Aderidae	1
Peltidae	2	Cerambycidae	14
Trogositidae	1	Chrysomelidae	94
Cleridae	2	Bruchidae	5
Melyridae	14	Anthribidae	1
Nitidulidae	13	Curculionidae	65
Cucujidae	1	Scolytidae	8
Silvanidae	2		

I. Habitat Types

The species richness of the ground-dwelling beetle faunas from ten different habitat types throughout Mkomazi is shown in Figure 2A. The clearest feature is the high species richness in the two Dindira habitats (*Combretum* bush and *Dichrostachys* bush), the two Ibaya Hill habitats (*Spirostachys* forest "forest"; *Setaria* grassland - "Setaria"), and the two Ibaya Camp habitats (hillside *Acacia/Commiphora* bush - "hillside"; footslope grassland - "grassland"). This suggests that these sites, all of which are situated in the west of the Reserve, may be highly significant for beetle diversity in Mkomazi. In contrast, the dry habitats around the Umba River (Riverine bush and *Commiphora* woodland) and Ndea Hill (*Acacia senegal* woodland and *Acacia drepanolobium* vlei - "A.drepanoi") produced much lower numbers of species.

Species dominance in the two Ndea Hill sites, though, was very high (Figure 2B), indicating that a small number of species here were occurring in large numbers. In the dry and sandy *A. senegal* woodland the dominant species was a zophosine tenebrionid beetle, or "sand-swimmer". Perhaps the ability of these beetles to bury themselves rapidly under the surface in avoidance of predators gives them a competitive advantage in the bare, sandy soil. This species was completely absent from the nearby vlei, but dominance was nevertheless also high here, with two meloid species, *Coryna arussina* and *Ceroctis rufimembris*, particularly prevalent. The hydrophilic carabid *Styphromerus 4-maculatus* was also present in significant numbers, an indication that the vlei, despite being parched at the time of sampling, becomes waterlogged in the wet season. The beetle communities of the two Umba River habitats were also dominated by meloids and tenebrionids (including the same sand-swimmer as above), with very few species belonging to other beetle families.

Figure 2. Diversity and dominance of beetle faunas of ten habitats in Mkomazi Game Reserve



Although the wetter habitats had a greater diversity of beetles than the drier areas, a large proportion of their species seem to be relatively common throughout Mkomazi. In contrast, despite yielding relatively few species, the drier habitats tend to contain species not found elsewhere in the Reserve, and may thus contribute significantly to beta diversity (i.e. the overall species complement of the

region). For example, although a total of 75 beetle species were collected in the two Dindira habitats in comparison with only 43 from the two *Acacia* habitats at Ndea, it was the latter, drier site which had a greater number of species unique to those habitats (22 from Ndea (51% of the total) compared with 19 (25% of the total) from Dindira).

Further analysis reveals that the faunas of habitats from the same location (e.g. the *Combretum* and *Dichrostachys* scrub, which were adjacent habitats near Dindira Dam) were more similar to each other than to habitats from other parts of the Reserve. Also, the beetle samples from the drier habitats around the Reserve (including the Ibaya habitats during the dry season, and in particular the burnt sites) showed a high degree of similarity with each other, suggesting that similar communities of arid-land species may exist throughout Mkomazi when conditions become hot and dry. The most prominent of these xerophilic specialists are the tenebrionids, particularly zophosines, which are abundant in extensive areas of bare sandy soil, such as occur in burnt or arid habitats.

Tenebrionids are very effective indicators of restricted water availability. In Mkomazi they are most abundant and species-rich in the dry, eastern habitats of riverine bush (7 species, 23 individuals) and *Commiphora* woodland (8, 35) near the Uмба River, and in the bare sandy soil of the *Acacia senegal* woodland (10, 190). Even on the top of Ibaya Hill where the two habitats sampled are within 50m of one another, the open and drier *Setaria* grassland produced four species and 37 individuals, compared to none at all in the forest.

Analysis of community composition in the two Ibaya Hill habitats shows that they support a high beetle species richness and harbour a very distinct, and localised, fauna. Of the 42 species collected in the forest, 31 (74%) were unique to this habitat, while in the *Setaria* grassland 41 species were collected, of which 17 (42%) were only found here. Clearly, the forest, and to a lesser extent the *Setaria* grassland, are the most distinct and diverse beetle habitats sampled in this study. This small patch of forest, a rare feature in the Mkomazi landscape, is thus of particular importance for the biodiversity of the Reserve.

Identifying further habitats which make a significant contribution to the biodiversity of Mkomazi, either in terms of the numbers of species they support or the distinctive nature (or rarity) of their faunas, is clearly important for the long-term management of the Reserve. Further surveys, particularly in the rarer habitats of Mkomazi, are likely to produce many more beetle records for the Reserve, and also help in any future identification of priority habitats for protection.

II. Trees

Sampling of the 17 trees analysed in this study was carried out between July 28th and August 5th, 1994. Details of the trees are given in Table 2.

Species richness and dominance varied considerably between tree species (Figure 3). The greatest number of species (46) was collected from the *Acacia mellifera*, which was a small tree with a limited canopy. Five other trees, the two *Lannea stuhlmannii*, the *Terminalia* sp., the *Acacia reficiens* and the *Acacia tortilis*, which varied in height from five to ten metres, produced similar numbers of species (from 32 to 37), while each of the other trees had fewer than 15 species. The smaller number of species from the three *Acacia drepanolobium* bushes (which produced a total of only eight species and 11 individuals between them), and to a lesser extent the four *Acacia zanzibarica* trees, are probably related to the small size of the trees and the limited canopy area from which insects were fogged. However, *Melia volkensii*, *Acacia anthelmintica* and the two *Acacia senegal* also exhibited low species diversity despite their relatively large heights, canopy areas and collecting areas.

Table 2 Details of trees sampled for arboreal beetles by insecticide mist-blowing.

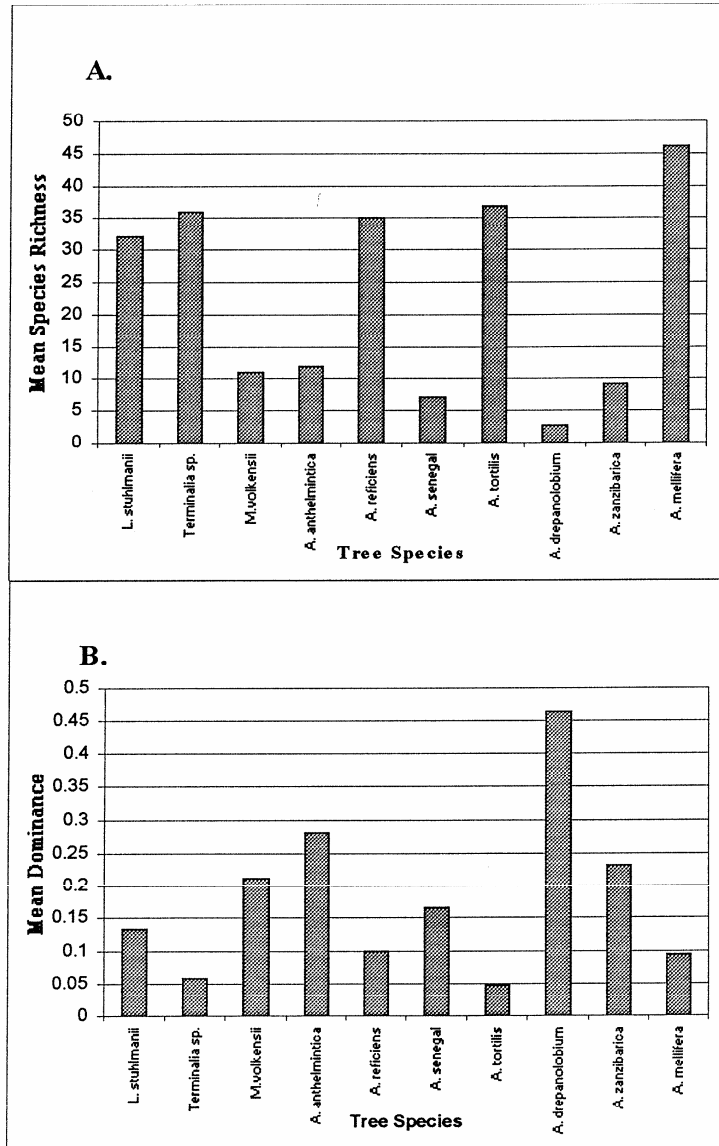
Tree species	Tree code	Location	Height (m)	Collection area (m ²)
<i>Lannea stuhlmanii</i>	LSTL28	Ibaya Camp	6	4
<i>Lannea stuhlmanii</i>	LSTL29	Ibaya Camp	5	2
<i>Terminalia sp.</i>	TERM29	Ibaya Camp	10	2
<i>Melia volkensii</i>	MVOL29	Ibaya Camp	7	2
<i>Albizia anthelmintica</i>	AANT30	3.5 km north of Zange Gate	8	4
<i>Acacia reficiens</i>	AREF30	3.5 km north of Zange Gate	7	2
<i>Acacia senegal</i>	ASEN1A	1 km north of Zange Gate	8	2
<i>Acacia senegal</i>	ASEN1B	1 km north of Zange Gate	8	2
<i>Acacia tortilis</i>	ATORT1	1 km north of Zange Gate	10	2
<i>Acacia drepanolobium</i>	ADRP3A	Vitawine ridge	2	0.32
<i>Acacia drepanolobium</i>	ADRP3B	Vitawine ridge	2	0.32
<i>Acacia drepanolobium</i>	ADRP3C	Vitawine ridge	2	0.32
<i>Acacia zanzibarica</i>	AZAN4A	East of Ibaya Camp	3	0.64
<i>Acacia zanzibarica</i>	AZAN4B	East of Ibaya Camp	4	0.64
<i>Acacia zanzibarica</i>	AZAN4C	East of Ibaya Camp	7	0.64
<i>Acacia zanzibarica</i>	AZAN4D	East of Ibaya Camp	5	0.64
<i>Acacia mellifera</i>	AMELL5	3 km north of Zange Gate	4	2

Unsurprisingly, therefore, analysis of the relationship between species richness and the various measures of tree and/or sample size revealed no significant correlations, suggesting that taxonomic differences between the trees may be the main cause of the variability in the beetle faunas. This is supported by faunal similarity analysis, which revealed that trees from the same species shared more beetles than those from different species. The faunas of the four *Acacia zanzibarica* trees, for example, had a number of beetle species in common. Two species (a chrysomelid and a curculionid) were common to all four trees, while a further three were found on three of the trees (one corylophid, a nitidulid and another curculionid). A similar pattern is revealed by the two *Lannea stuhlmanii* trees, which shared 16 (exactly 50%) of their species.

There was very little similarity between the faunas of different tree species. The one exception was the *Acacia mellifera* and the *Terminalia sp.* which, perhaps surprisingly for species from different genera, shared 14 species of beetles. However, 13 of these were also found in other trees around the Reserve, suggesting that they were "tourists" (that is, not host-specific). The fauna of *Acacia tortilis*, as well as being rich in species, was also quite distinct from those found on the other trees in the study, suggesting that this species (similar to the *Spirostachys* forest in the habitat section above), might be of particular importance to the overall beta diversity of Mkomazi.

Species dominance also varied between tree species, with the species-poor trees generally having much higher dominance (Figure 3B). In *Acacia anthelmintica*, for example, two beetle species were particularly common (an anthicid with 30 individuals and a melyrid with 48 individuals), thus decreasing the equitability of the tree's beetle fauna. Similarly, dominance was also high (and species richness low) in the three *Acacia drepanolobium* trees. This may be because only a limited number of species are able to share the bushes with the species of ant which guards this species from insect attack. Conversely, none of the 37 species collected from the *Acacia tortilis* were represented by more than eight individuals, with the result that the dominance score was very low.

Figure 3. Species richness and dominance of beetles from the canopies of ten tree species in Mkomazi Game Reserve.



The low similarity between the faunas of the different tree species in this study indicates that the sampling of further trees will continue to augment the beetle species list for the Reserve, particularly since the ten species sampled here represent only a small fraction of the total number of species recorded for the Reserve. The arboreal beetles, therefore, clearly constitute a very significant

proportion of the total beetle fauna of Mkomazi. The limited time available for analysing the beetle material from the mist-blowing study has greatly restricted the scope of the investigation. An assessment of the other taxa collected by mist-blowing, including an estimate of the total number of arboreal insect species in Mkomazi, is given elsewhere in this volume (see McGavin, Part II).

The effect of burning on beetle diversity at Ibaya

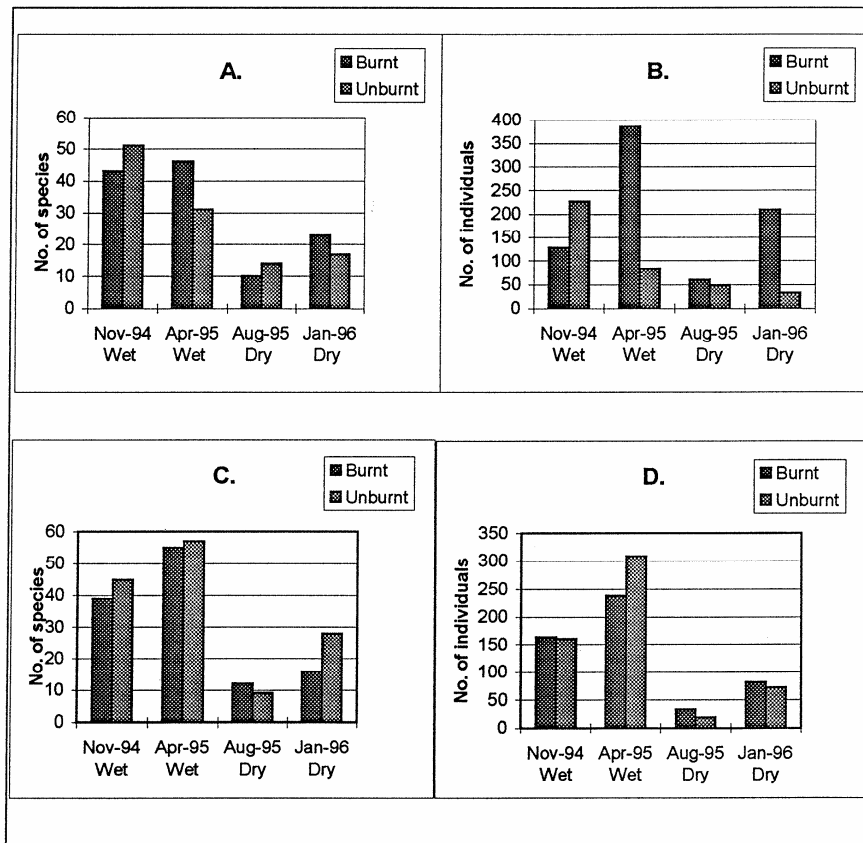
Beetle species richness and abundance for burnt and unburnt habitats at Ibaya, as recorded at four different times of year, are illustrated in Figure 4. None of the differences in species richness (Figures 4A and 4C) between burnt (shaded) and unburnt (unshaded) habitats were found to be statistically significant, but there were significant differences in terms of the number of individuals caught. In the hillside *Acacia/Commiphora* bushland sites (Figure 4B), beetle abundance in November 1994 was significantly higher in the unburnt area, while in April 1995 and January 1996 it was higher in the burnt area. This suggests that although burning initially has a detrimental effect on beetle populations, in the longer term it results in significantly higher beetle abundance and activity. This may be due to the removal of the large biomass of dead grass (which is likely to physically impede beetle movement over the substrate), and/or through the rejuvenation of the site owing to the release of recycled nutrients to the soil.

By contrast, in the footslope grassland sites (Figure 4D) the only major difference between burnt and unburnt habitats was in April 1995, when beetle abundance/activity was significantly higher in the unburnt patch. This means that in April 1995 beetle abundance on the hillside is significantly higher in the burnt area while in the grassland it is higher in the unburnt area. This disparity perhaps relates to the recent history of burning events in the two sites. While there was no recent record of fire in the unburnt hillside, the 'unburnt' grassland had in fact experienced burning 18 months previously. Thus, the higher abundance in the unburnt grassland relative to the unburnt hillside may, as above, be due to its lower biomass of dead grass and higher nutrient status, resulting from the earlier fire.

Burning therefore can play a positive ecological role in the savannah by removing excess ground vegetation. However, the sparse and patchy vegetation left after fire will also reduce beetle numbers and diversity, owing to the increased vulnerability to predation; hence the lower diversity in the burnt habitats in November 1994 (only three months after the fire) relative to April 1995 (eight months after the fire). An optimum environment is likely to exist some months after a burn, particularly if the subsequent wet season brings about a recovery in the vegetation. Regeneration of the grass layer is more than likely to have taken place in the burnt habitats between August 1995 and January 1996, following the November rains, which may explain the consistent increases in beetle diversity between these two dates (Figure 4). Indeed, the only habitat in which significant increases in diversity did not occur was the unburnt hillside, the one habitat that was already heavily overgrown, and in which further growth of the grass layer was unlikely to benefit the fauna.

The clearest, and statistically most significant, difference in Figure 4 is between the high abundance and diversity in November 1994 and April 1995 (i.e. 3 and 8 months after the fire, respectively) and the low values observed in the August 1995 and January 1996 samples (i.e. 12-17 months after the fire). Although this might be interpreted as an effect of time elapsed since fire, it is more likely to result from seasonal rainfall in November and April. This highlights the difficulties associated with attempting to isolate fire-induced population changes from background seasonal variation. In an attempt to control for this, sampling in this study was carried out not only in burnt and unburnt areas but also at four different times of year. However, in order to take proper account of seasonal variation it would probably be necessary to monitor population changes monthly for several years. Such shortcomings must always be borne in mind when investigating the impacts of fire on insect population dynamics.

Figure 4. Effects of burning on the abundance and species richness of ground-active beetles in flosslope grassland (A & B) and hillside bushland (C&D) in mkomazi Game reserve



Whelan (1995), in a review of studies on responses of ground-dwelling invertebrates to fire, found that in some cases invertebrate abundance was reported to increase after fire, while in others there was a decrease. There are similar discrepancies in the recorded effects of fire on vegetational diversity, with, in one case, two authors in the same volume giving contradictory evidence; one suggests that protection from fire leads to an increase in plant diversity (Braithwaite, 1996), while the other reports that the elimination of fire produces an accumulation of plant biomass, which reduces diversity (Bulla, 1996). Potential causes of these contradictory results may be: (i) variations in fire intensity from study to study; (ii) differential responses by the various constituent taxa (i.e. some groups will suffer great losses while others benefit from the burn); and (iii) differences introduced by the use of a wide variety of sampling protocols (Whelan 1995).

The use of pitfall sampling for monitoring population dynamics following a fire has problems associated with it. Capture rates in pitfall traps are more an indication of beetle activity than true population size (Whelan 1995) and increased catches may simply reflect increased activity of a reduced population. Such increases in activity are particularly likely after a fire, for three reasons: firstly, exposed and vulnerable invertebrates will increase active searching for holes to avoid predation; secondly, the distance and duration of foraging will need to increase in order to maintain adequate food input in an impoverished environment; and thirdly, the shift in complexity of the habitat from

three-dimensional to two-dimensional (and the ensuing reduction in niche diversity) is likely to result in an increased pitfall catch of those species normally associated with the tree and shrub layer. Therefore, increases in the number of beetles caught directly after fire are as likely to be due to sampling effects as to real increases in population size.

Seasonal variations in the beetle fauna of Ibaya

The pitfall study at the Ibaya Camp sampling sites (Figure 4), showed that beetle species richness and abundance was significantly higher in the two wet season sampling periods than in the dry season for all four Ibaya habitats. This suggests that a large proportion of the beetles of Mkomazi time adult emergence to coincide with the rains in order to profit from increased food availability.

Savannah invertebrates generally tend to be more abundant during the wet season, though different taxonomic groups respond in different ways. Gillon (1983), working in an area of relatively high annual rainfall (over 1200mm), identified four patterns of seasonal abundance exhibited by savannah arthropods: (i) peak abundance during the rainy season itself (e.g. cockroaches, acridids, reduviids and carabids); (ii) an increase leading up to a peak at the beginning of the next dry season (e.g. tettigoniid grasshoppers and caterpillars); (iii) peak abundance coinciding with the beginning of the annual grass fires (e.g. most Homoptera); and (iv) a multimodal pattern with two or more peaks (e.g. mantids and ruteline beetles). Some groups show no discernible variation in abundance at all (e.g. some spiders). The beetles in this study would appear to exhibit two peaks of abundance and diversity, associated with the two wet seasons of November and April, though a more long-term study would be required to confirm.

The equitability of the beetle populations also varied seasonally, with dominance significantly higher in the two dry season sampling periods than in the two wet seasons, a pattern that was particularly pronounced in the burnt hillside and burnt grassland. These habitats were dominated in the dry season by large numbers of the same species of zophosine tenebrionid (in both January and August), as well as by the meloid *Coryna chevrolati*, an anthicid, and two histerids. This suggests that stressful conditions (i.e. those that are very hot and dry) tend to favour a few species that are specifically adapted to thrive in them.

Most other savannah insects have evolved adaptive mechanisms to avoid the worst effects of the dry season. The most common of these "escape strategies" is diapause, during which development is arrested. Many species thus spend periods of drought underground, burrowing into the relatively loose soil towards the end of the rainy season, with the hard soil of the dry season serving to protect them both from predators and from savannah fires. This explains the low numbers of beetle species and individuals trapped during the dry season months.

Finally, seasonal variations of climate tend to be far less marked and much more predictable in wetter savannahs than in the drier savannahs (Gillon, 1983). If a similar pattern were to exist between the wetter and drier parts of Mkomazi (from wetter in the west, to drier in the east), a study of seasonality in the eastern end of the reserve, similar to that carried out at Ibaya, may be expected to produce even greater differences in beetle species richness between wet and dry seasons.

Discussion: implications for the management of Mkomazi

This investigation into the distribution and extent of the beetle fauna of Mkomazi, and the ecological factors influencing it, provides information for the long-term management of the Reserve. In particular, it serves to identify those areas of the MGR which are likely to be of particular significance for biodiversity, and which are thus most worthy of conservation and/or sympathetic management.

It also supports the thesis that biodiversity conservation would be best served through the maintenance of a mosaic of different habitat types, each contributing an optimal number of unique species to the overall list for the Reserve. In particular, areas such as the small patches of *Spirostachys* forest and *Setaria* grassland, on the top of Ibaya Hill, are of great importance owing to the richness and rarity and limited distribution of the beetle communities they contain. Nearly three-quarters of the beetle species collected in the forest were found nowhere else in the study, suggesting that if this restricted

habitat were to be lost (and there are already signs of tree stem removal) there may be a significant negative impact on the beta diversity of the region.

The climate gradient in the Reserve, from relatively wet in the West to hot and dry in the East, also seems to have a marked influence on the distribution and diversity of beetles. Although the habitats in the West tend to support a greater diversity of beetle species, those in the East sustain important populations of arid-land specialists not found in the wetter areas, emphasising that those areas with low species richness are by no means lacking in value.

Two of the most fundamental ecological factors in the savannah, fire and rainfall, have a profound effect on beetle diversity, both directly and indirectly. The direct effects of both are usually catastrophic, with high beetle mortality often associated with burning and, less significantly, flooding events. Indirectly, though, the effects can often be more beneficial. Both fire and rainfall have key roles to play in plant productivity, the former through the removal of dead material and the recycling of nutrients, and the latter through the provision of plant available moisture. The resultant higher plant productivity is strongly related to vegetational diversity (Bulla, 1995), which is, in turn, likely to have a major influence on the productivity and diversity of both primary and secondary consumers. However, the correlation between productivity and diversity is not linear, with maximum species richness at intermediate levels of productivity, as suggested by the increased diversity of beetles in areas around Ibaya which had burnt but in which the vegetation had recovered following subsequent rains (for example, the burnt hillside and burnt grassland in April; Figure 4).

Reductions in diversity seem to be associated with stress and limited resources at the lower end of productivity, and with competition at the higher end; the most productive species tend to out-compete, and eventually eliminate, less competitive species, thus reducing diversity as well as equitability. At the lower end of productivity, this would seem to explain, firstly, the low levels of beetle diversity recorded in the recently-burnt habitats in November 1994 relative to the same areas five months later (suggesting that the vegetation in April 1995 had developed to a high, but not inhibiting level), and secondly, the very low figures for the dry season. At the higher end of productivity, it explains the relatively low diversity, throughout all four seasons, recorded in the only heavily overgrown habitat (i.e. the unburnt hillside).

It therefore seems likely that controlled burning of patches of savannah, or at least a policy of non-intervention towards natural fires, may help to maintain the overall species richness of the Reserve. In particular, early (low-intensity) dry season fires will remove dead grass without being too destructive. Such fires typically impact minimally on the canopies of trees, while higher intensity fires, which are usually the result of a much greater accumulation of dead plant biomass, can scorch high into the canopy and cause significant mortality in arboreal insects (Braithwaite, 1996). According to Tainton & Mentis (1984), however, burnt tropical savannahs may, in the long term, support only about 30% of the invertebrate fauna of unburnt savannahs, as the more hydrophilic arthropod groups tend to be excluded. This only serves to re-emphasise the importance of maintaining a mosaic of habitats, including those that are both burnt and unburnt.

As indicated by species accumulation curves, much of the beetle fauna of Mkomazi remains to be recorded. More extensive sampling, and particularly in locations not visited in the current study, will greatly enhance the overall assessment of the extent and distribution of beetle diversity throughout the Reserve, thus facilitating the effective conservation of its biodiversity as a whole.

2. The spider fauna of Mkomazi Game Reserve

Diversity of Mkomazi spiders compared to other sites in Africa.

While some effort has been devoted to inventory of spider diversity in tropical forests (reviewed by Russell-Smith & Stork, 1994), very much less is known about the composition of the arachnid communities of savanna ecosystems. In Africa, previous inventories of savanna arachnids have either been undertaken for purposes other than biodiversity assessment (e.g. Blandin *et al.* 1981, Russell-Smith, 1981) or have been conducted over a limited time span or in a limited area (Russell-Smith *et al.* 1981, Van der Merwe *et al.*, 1996). Most previous studies have also used a very restricted range of sampling methods which are likely to have provided a biased sample of the arachnid fauna as a whole.

The importance of using as wide a range of sampling techniques as possible in invertebrate diversity surveys has been stressed by Hammond (1990) who convincingly shows that only a combination of different techniques adequately sampled the extraordinary beetle diversity of tropical rain forest canopies. Although savannas are possibly less complex structurally than rain forests, the behavioural diversity of savanna invertebrates is such that similar considerations apply. In the baseline survey, we routinely used four different methods of sampling for arachnids; pitfall traps, sweep-net samples, canopy fogging of trees and hand collecting. Table 3 provides an estimate of the sampling effort and number of habitats in the reserve sampled by each technique.

Table 3. Estimated sampling effort and total number of habitats sampled using different techniques in Mkomazi Game Reserve, Tanzania. 1993 - 1997.

Sampling method	Sampling effort	No. of habitat types sampled
Pitfall traps	12,370 trap/days	12
Sweep net samples	n samples of 10 x 20 sweeps	13
Tree canopy fogging	183 trees, 29 species.	N/A
Hand collection	31 samples of 1-2 hrs	16

Although this represents a major sampling effort, probably the largest so far attempted for any single area in Africa, it is biased in two ways. Significantly more effort was spent on sampling with pitfall traps and canopy fogging than on any other technique and the sampling was heavily concentrated in the western and central parts of the reserve. Further sampling with other techniques, particularly in the dry eastern part of the reserve, would undoubtedly extend the species list considerably.

The composition of the Mkomazi arachnid fauna.

Sorting and identification of the samples from Mkomazi is an on-going process. While the majority of material from pitfall traps, sweep net samples and hand collecting have now been sorted to morphotypes, sorting material from tree canopies has only just started. Identification and, in some families, description of the spiders has been initiated but will take several years to complete. Despite this, we now have a sufficiently large sample of the spider fauna to provide a reasonable assessment of the diversity and composition of the arachnid fauna as a whole.

Table 4 shows the composition of the spider fauna as a whole. The most immediately evident feature of the spider fauna of the reserve is the very high family diversity. The 46 recorded from Mkomazi represent nearly half of all currently recognized spider families (total 105). The maximum number of families previously recorded from any other savanna site in Africa is 33 from Ngome State Forest (Natal) by Van der Merwe and colleagues (1996). The estimate for the number of genera (column 2) will undoubtedly be amended once poorly studied families have been revised. This estimate is considered a compromise between excessive "splitting" and "lumping".

The family composition of the fauna is shown graphically in Figure 5. Among the 427 morphotypes recognized so far, the two most species rich families are the jumping spiders (Salticidae) with 55 species (13 % of all species) and the ground spiders (Gnaphosidae) with 51 species (12 % of all species). Salticidae are the largest of all spider families and were found in all vegetation strata, although a majority only occurred on

the ground surface. Gnaphosidae are almost confined to the ground layer (a single species of the genus *Aphantaulax* was swept from grass) and are a characteristic family of semi-arid areas. Both salticids and gnaphosids actively hunt their prey, the former during the day and the latter at night. Web building spiders belonging to the families Araneidae and Theridiidae, represented by 36 species each, were abundant in the field, shrub and tree strata where they build a variety of different types of prey catching webs. Crab spiders (Thomisidae), with 32 species, are particularly abundant in the field layer but also occur on trees and, very occasionally, the ground surface. These five families included just under half of all spider species from the reserve. Wolf spiders (Lycosidae) and lynx spiders (Oxyopidae), both represented by 22 species, are long-legged active hunters, the former almost entirely ground-active and the latter mainly in the field layer. Wolf spiders are diverse in most areas studied but Mkomazi has an exceptionally high proportion of oxyopids in the fauna. Zodariidae (19 species) are characteristic ground active nocturnal hunters of semi-arid habitats in Africa, possibly specializing in ants and termites as prey. They are abundant in both grassland and bushland in Mkomazi, which has the largest recorded fauna of any African site. Corinnidae (formerly included in the sac spiders - Clubionidae) were represented by 18 species, the majority of which are apparent mimics of ants or, occasionally, velvet ants (Mutillidae). The two other families with more than 10 species were the Oonopidae, minute hunting spiders (length < 2.5 mm) which capture small insects in the litter layer, and Linyphiidae which spin small hammock webs in litter and grass.

Figure 5. The family composition of all spiders recorded from Mkomazi Game Reserve. 1993 - 1996.

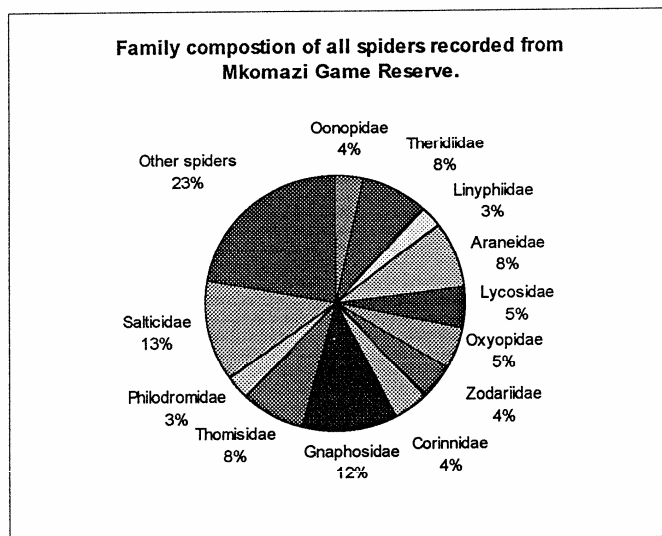


Table 4. Total numbers of families, genera and species of spiders recorded from Mkomazi Game Reserve. 1993 - 1996.

Family	Genera	Species	% of total
Cyrtoucheniidae	1	6	
Idiopidae	1	6	
Dipluridae	1	1	
Atypidae	1	1	
Migidae	1	1	
Barychelidae	2	2	
Theraphosidae	3	3	
Scytodidae	1	4	
Loxoscelidae	1	1	
Caponiidae	1	2	
Tetrablemmidae	2	2	
Pholcidae	2	3	
Ochyroceratidae	2	2	
Leptonetidae	1	1	
Segestridae	1	2	
Oonopidae	5	15	4%
Palpimanidae	5	7	
Mimetidae	2	3	
Eresidae	2	2	
Oecobiidae	1	1	
Hersiliidae	1	2	
Uloboridae	2	4	
Cyatholipidae	1	1	
Theridiidae	13	36	8%
Theridiosomatidae	1	1	
Symphytognathidae	1	1	
Linyphiidae	9	12	3%
Tetragnathidae	5	6	
Araneidae	20	36	8%
Lycosidae	11	22	5%
Pisauridae	3	7	
Dolomedidae	3	6	
Agelenidae	2	4	
Hahniidae	1	1	
Dictynidae	2	2	
Amaurobiidae	2	3	
Oxyopidae	4	22	5%
Liocranidae	1	1	
Zodariidae	12	19	4%
Clubionidae	2	5	
Corinnidae	9	18	4%
Trochanteridae	1	1	
Gnaphosidae	25	51	12%
Thomisidae	15	34	8%
Philodromidae	2	12	3%
Salticidae	35	55	13%
Totals	219	427	

Comparison of the Mkomazi arachnid fauna with that from other areas of Africa.

As mentioned previously, many of the earlier inventories of spiders in Africa suffered from inadequate or inappropriate sampling procedures. For example, the work of Blandin and colleagues in the humid savanna at Lamto (Côte d'Ivoire), one of the largest studies carried out in the region, relied on collection of spiders from large cages of 4, 10 and 25 m² surface area. While this is an effective method for large species and has the advantage of providing estimates of absolute population densities, many small species will have been completely overlooked. This technique is also not well adapted for assessment of diversity because the results provide a "snapshot" of the spider populations at a particular season and time of day. In particular, nocturnally active species are likely to be inadequately censused.

Recently however, a major survey of ground-active arachnids in Etosha National Park, Namibia has been carried out (Griffin, Pers. comm.). The park is considerably larger than Mkomazi Game Reserve (220,000 km² compared to 3,600 km²) and is also more arid, with rainfall ranging from 450 mm per annum in the West to 250 mm in the East. Pitfall trapping was undertaken in 12 different habitats using 8 traps over 150 days in each site, giving a total trapping effort of 14,400 trap/days. This is about 15 % greater than the total trapping effort to date in Mkomazi but for the purposes of estimating total spider species richness is approximately equivalent.

Table 5. shows summary statistics for spiders from pitfall traps in the two areas. Mkomazi is richer in both spider species and spider families than Etosha National Park. This may be attributable to the lower rainfall in Etosha which is also not as well distributed as in Mkomazi (unimodal as opposed to bimodal rainfall distribution). However, historical and geographical factors may also play a role in maintaining the high diversity in Mkomazi. The proximity to the East Pare and Usambara mountain massifs may contribute in this respect, as the eastern arc mountains are known to be centers of diversity for some groups of spiders (Scharff, 1992). The family composition of the spider fauna of the two areas also differs. In the more arid Etosha National Park, gnaphosids account for almost a quarter of all spider species whereas here salticids only represent 3% of the species, as opposed to 19% in Mkomazi. Lycosids, oxyopids, clubionids and oonopids were all proportionately better represented in Mkomazi while, conversely, araneids and theridiids were proportionately better represented in Etosha (Table 3). As with overall diversity, it is not possible at this stage to say to what extent these differences are to be attributed to climatic differences between the two areas or to historical and biogeographical factors.

Table 5. Family composition of spiders from pitfall traps in Mkomazi Game Reserve and Etosha National Park (Namibia).

Mkomazi Game Reserve. Tanzania			Etosha National Park. Namibia.		
Group	No	%	Group	No	%
Salticids	45	19%	Salticids	5	3%
Gnaphosids	33	14%	Gnaphosids	41	23%
Zodariids	18	8%	Zodariids	14	8%
Lycosids	15	6%	Lycosids	6	3%
Oxyopids	9		Oxyopids	6	
Clubionids	14	6%	Clubionids	7	4%
Thomisids	17	7%	Thomisids	13	7%
Philodromids	5		Philodromids	7	
Oonopids	10	4%	Oonopids	2	
Araneids	5	2%	Araneids	8	5%
Theridiids	8	3%	Theridiids	12	7%
Others	61		Others	54	
Total	240		Total	175	
No. of families	45		No. of families	31	

Geographical distribution of Mkomazi spiders.

Relatively few spider families in Africa are sufficiently well known that the distribution of their species can be mapped with any reliability. However, for two of the larger families from Mkomazi, Salticidae and Araneidae, some estimate has been made of the distribution of species on the basis of data provided by Dr W. Weslowska (Salticidae) and Dr M. Grasshoff (Araneidae) (Table 6). In both families a relatively high proportion (43 - 63%) of all species have a poorly known distribution as they have been either recorded only from the type locality or from very few sites. Of the remainder, the araneids have a larger proportion (40 %) of species with a very wide distribution (i.e. in columns 2 - 4 of Table 6) than the salticids (20 %). Amongst araneids, 17% appear to be restricted to East & central Africa and amongst salticids a similar proportion are restricted to East and southern Africa. What proportion of the poorly known species have relatively restricted distributions remains unclear. In both families a fairly high proportion (31 - 44%) appear to be currently undescribed species. If the average proportion of undescribed species for these two families (38%) were applied to all families from Mkomazi, the fauna would include 168 new species. However, given the high level of synonymy known to exist in African spiders, a more conservative proportion of 25% is probably more realistic, giving a total of 110 undescribed species.

Table 6. Geographical ranges of species of Salticidae and Araneidae from Mkomazi G.R.

Family	Cosmop.	O.W. Tropics	Trop. Africa	E. & C. Africa	E. & S. Africa	Unknown	New spp.	Total spp.
Araneidae	1	2	11	6	0	15	11 ?	35
	3%	6%	31%	17%	0	43%	31%	
Salticidae	0	0	11	0	10	35	25	56
	0	0	20%	0	18%	63%	45%	

Spider diversity in contrasting habitats of Mkomazi Game Reserve.

Ground layer spiders.

Pitfall traps were operated in 10 habitats in the reserve, ranging from closed montane forest to open mixed grassland. The family composition of the spider communities varied with both habitat and season. The closed montane forest on Ibaya hill had the most distinctive composition (Fig. 7) in that Salticidae were completely absent from the ground layer and their place taken by Linyphiidae. The average proportion of Salticidae in woodland, bushland and grassland habitats was relatively constant. The proportion of both Zodariidae and Gnaphosidae increased twofold and threefold respectively between grassland and woodland and these families were clearly most abundant in shaded habitats. By contrast, wolf spiders (Lycosidae) were on average twice as abundant in grassland habitats as in the closed montane forest (Fig. 7). These active hunters are normally most abundant in open habitats than in wooded ones (Fig. 7).

There were very clear seasonal effects on the composition of the spider communities in different habitats, illustrated here by family composition in two adjacent bushland communities, *Dichrostachys cinerea* and *Combretum* scrub (Figure 6). In the wet month of April 1995, lycosids (principally a species of *Pardosa* which breeds during the rains) were abundant in both habitats. In the much drier period of January 1996, lycosids were less abundant while both zodariids and gnaphosids, characteristic of dry environments, were correspondingly more abundant in both habitats.

Figure 6. Family composition of spider communities in *Dichrostachys cinerea* communities. Mkomazi Game Reserve, April 1995 and January 1996.

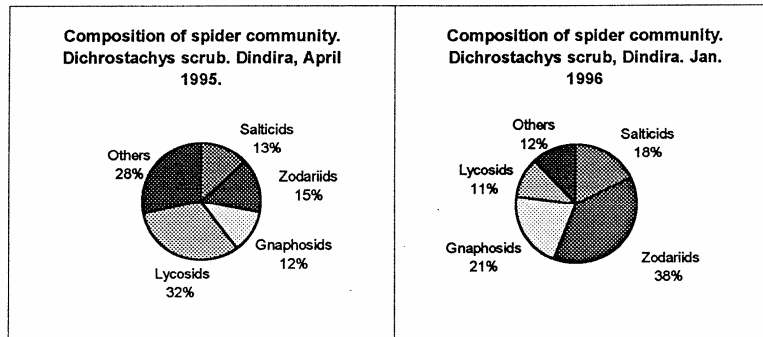
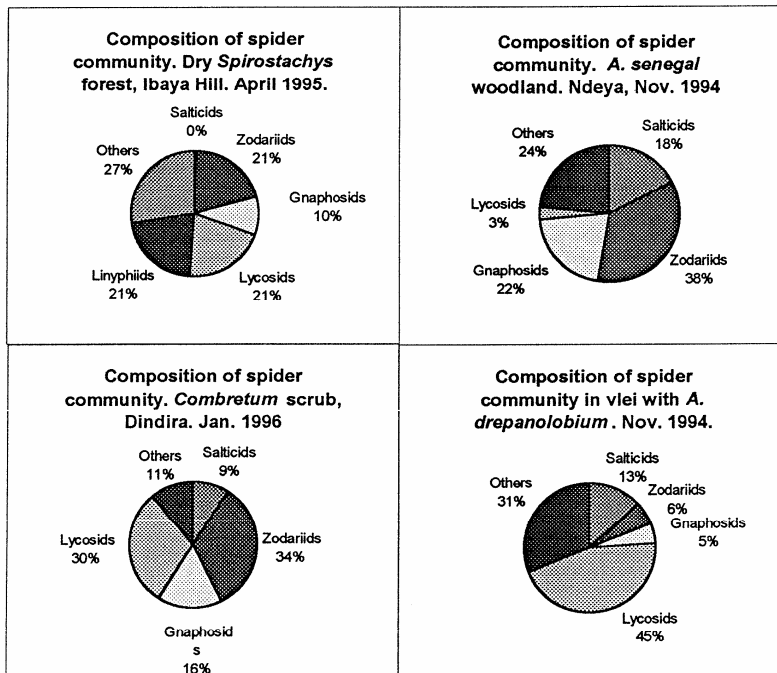


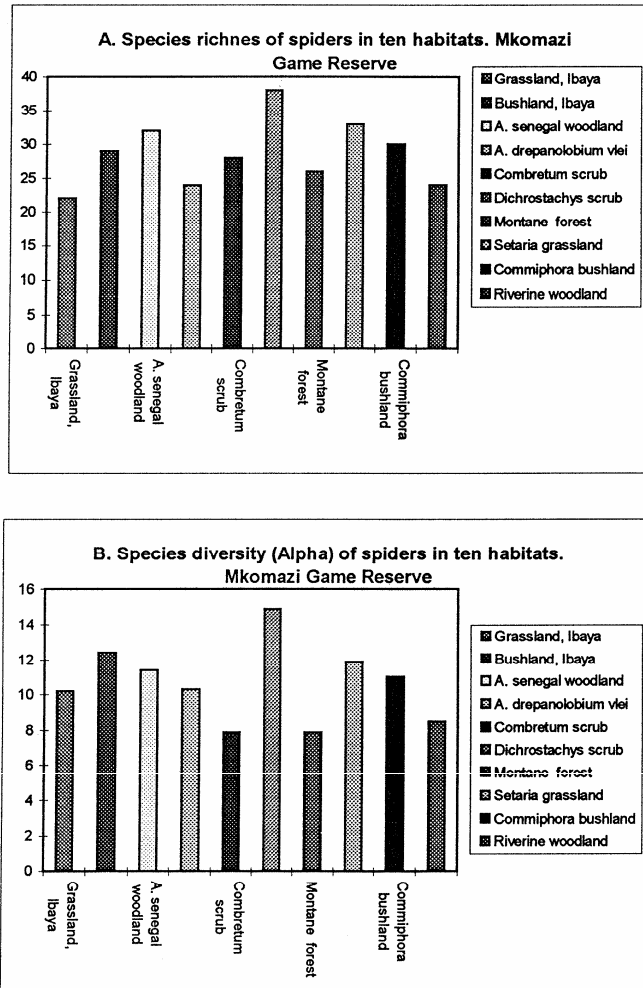
Figure 7. Composition of spider communities in montane forest, Acacia woodland, Combretum bushland and seasonally wet grassland. Mkomazi Game Reserve



Species richness was greatest in closed *Dichrostachys cinerea* scrub near Dindira Dam (38 spp.) (Fig 8) and was also high in well developed but open *Acacia senegal* woodland near Ndeya (32 sp.) and in montane grassland on Ibaya hill (33 spp.). Relatively low species richness was found in unburned foot-slope grassland at Ibaya (22 spp.), vlei grassland with scattered *Acacia drepanolobium* near

Ndeya (24 spp.) and in riverine scrub on the Umba River (24 spp.). As can be seen in Fig 8a and b, species diversity as measured by α was closely related to species richness and, across all 10 habitats, there was a significant correlation between the two measures of diversity ($r = 0.7508, P < 0.02$).

Figure 8. Species richness (A) and species diversity (B) of spiders in 10 habitats. Mkomazi Game Reserve, Nov. 1994 and April 1995.



Field layer spiders.

The dominant spider families in sweep net samples from 11 grassland sites in January 1996 were Thomisidae (mean 38%) and Araneidae (mean 22%) (Table 7). Other well represented families included Philodromidae (12%), Salticidae (12%) and Oxyopidae (5%). Proportions of all families were very variable between different grassland sites and there were no obvious correlations between the proportion of a particular family present and environmental variables except in the case of crab spiders (Thomisidae). Representatives of this family were always most abundant in open, unshaded grasslands and least abundant in shaded grassland in woodland or bush (Fig. 9). When the proportion of crab spiders was correlated with an estimate of % tree or bush cover for each site, a significant negative correlation was obtained ($r = -0.6642$, $P < 0.05$).

Table 7. Composition of spider communities sampled by sweep netting in 11 grassland sites in Mkomazi Game Reserve, January 1996.

Grassland type	Location	Thomisids	Philodromids	Salticids	Arananeids	Oxyopids	Others
Footslope (Unburned)	Ibaya	21%	7%	16%	34%	1%	20%
Footslope (Burnt)	Ibaya	55%	0%	10%	30%	0%	5%
<i>A. senegal</i> woodland	Ndeya	28%	10%	10%	14%	7%	31%
<i>Acacia/Commiphora</i>	Ibaya/Simba	44%	3%	21%	21%	3%	9%
Vlei grassland	Ndeya etc.	44%	9%	8%	22%	10%	7%
<i>Themeda</i> grassland	Ndeya road	49%	21%	2%	21%	6%	1%
<i>P. mezianum</i>	Nyati Plot	43%	22%	13%	17%	0%	4%
Grassland	Ubani track	46%	21%	27%	2%	0%	4%
<i>Cynodon</i> grassland	Kisima Plot	48%	4%	26%	9%	9%	4%
Thick dead grass	Kikolo Plot	11%	22%	16%	32%	11%	10%
Sparse dead grass	Cadaba Plot	29%	11%	7%	36%	6%	89%
	Average	38%	12%	14%	22%	5%	17%

Species richness of spiders was highest in *Acacia senegal* woodland near Ndeya hill and lowest in open grassland in the Nyati and Simba experimental plots. Species richness was positively and significantly correlated with estimated percentage tree or bush cover for each site ($r = 0.7417$, $P < 0.01$). Species diversity (α of the log series) was also greatest in *Acacia senegal* woodland but was lowest in *Cynodon* grassland below Kisima experimental plot and in *Themeda triandra* dominated grassland near Ndeya hill (Table 8). Species diversity was even more closely correlated with estimated tree or bush cover for each site than species richness ($r = 0.8711$, $P < 0.001$).

Figure 9. Family composition of spider communities in the field layer of shaded (A,B) and unshaded (C,D) grasslands. Mkomazi Game Reserve, January 1996.

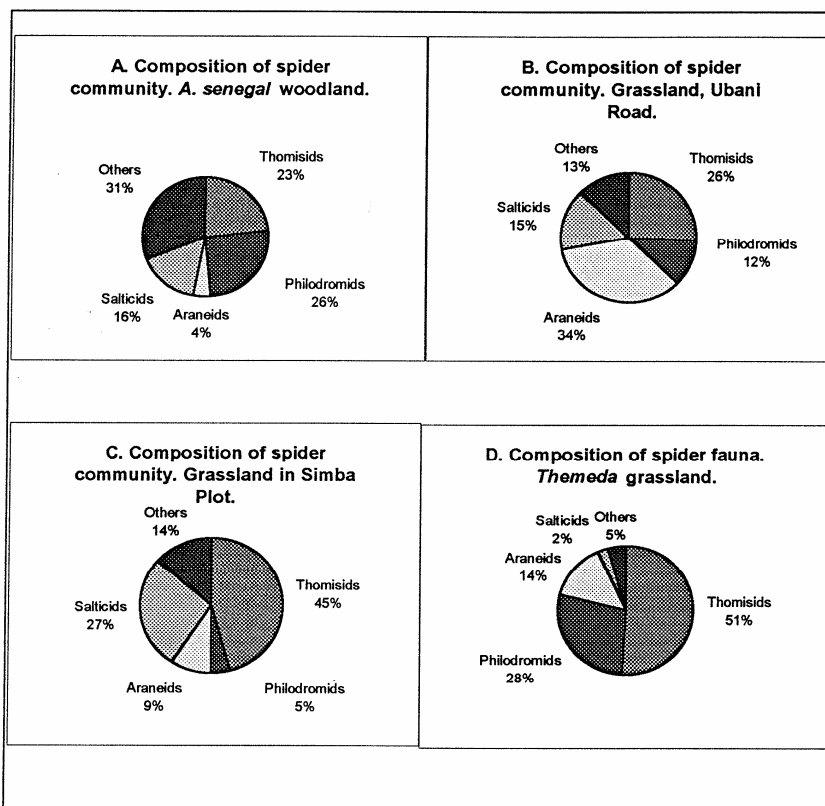


Table 8. Diversity indices for grassland spiders swept from 11 sites, Mkomazi Game Reserve January 1996.

Site	1	2	3	4	5	6	7	8	9	10	11
Species numbers	35	10	9	21	10	16	9	9	16	26	13
Margalef diversity	7.19	3.00	2.77	5.04	3.06	4.85	2.55	2.63	3.07	5.61	3.19
Simpson's dominance	0.063	0.150	0.222	0.080	0.136	0.083	0.217	0.188	0.172	0.070	0.124
Alpha of the log series	17.40	7.96	7.16	12.90	8.54	4.82	5.44	5.97	4.77	12.70	6.33
Estimated tree cover (%)	60	0	40	40	10	0	0	10	0	50	0

Key to sites:

1	<i>Acacia senegal</i> woodland	7	Nyati plot
2	Burnt Grassland, Ibaya	8	Simba plot
3	Cadaba plot sample 1	9	<i>Themeda</i> grassland
4	Cadaba plot sample 2	10	Ubani road
5	Kikolo plot	11	Vlei near Simba plot
6	<i>Cynodon</i> below Kisima plot		

Discussion

The family composition of spider communities in the 10 different habitats studied in Mkomazi confirms results from other African semi-arid savanna ecosystems. Russell-Smith (1981) found that Gnaphosids and Zodariids were more abundant in Mopane woodland than in floodplain grassland in the Okavango Delta of Botswana. *Acacia/Commiphora* bushland sampled in the dry season in Kora National Reserve, Kenya, had a family composition similar to that in unburned *Acacia/Commiphora* bushland at Ibaya sampled in August (Russell-Smith *et. al.* 1987). In both cases Salticidae, Gnaphosidae and Zodariidae were the dominant families. However, this is the first published data that covers a large range of different savanna habitats and demonstrates a systematic variation in family composition between woodland, bushland and grassland habitats.

The factors controlling species richness and species diversity of spiders in the ground layer of the 10 habitats studied are not at all clear. When averaged for each habitat type (forest, woodland, bushland or grassland) the range of values for these indices was quite small, 26 to 31 for species richness and 8 to 11.5 for species diversity, and they showed no particular trend across the different habitat types. Although the intensity of trapping was relatively high (180 trap-days in each site) it is possible that was insufficient to discriminate other than very large differences in species richness or diversity. This view is possibly supported by comparison of the diversity indices from these 10 habitats with those obtained from monthly sampling of *Acacia/Commiphora* bushland a foot-slope grassland at Ibaya. All the values for species richness and diversity (α) for the 10 separate habitats lay within the same range as those for the 10 monthly samples from bushland and grassland at Ibaya. At Ibaya the maximal species richness measured in any given month represented about 46% of all species obtained over the whole 10 month period. This suggests that the sampling in the 10 individual habitats probably covered too short a time period (normally 6 days) to recover a sufficiently large proportion of total species richness to allow adequate representation of differences between habitats. From a conservation viewpoint, it is clear that woodland and some bushland habitats have particularly diverse spider communities and management should be aimed at conserving such components of the overall habitat mosaic of the reserve.

There are virtually no published data on either the composition or the diversity of spider communities in the field layer of savanna habitats from Africa. Earlier work from the humid savannas of Lamto (Côte d'Ivoire) used large cages to sample spiders, the results from which do not discriminate between activity of ground and field layer components of the fauna (Blandin, 1971, 1972; Blandin & Celerier, 1981). The studies described here have limitations resulting from the use of sweep nets which only sample a part of the grass layer (the proportion depending on the stage of growth of the grasses) and which also present only a "snapshot" of the community at one particular point in time. Despite this, the studies have demonstrated very clear differences between communities in different types of grassland with Thomisids dominating open grasslands and other families more important in shaded grasslands within woodland or tall bushlands. The fact that both species richness and species diversity increase with the degree of tree cover within the grassland also underscores the importance of wooded and bushed grasslands for the conservation of arachnid diversity.

The effects of burning on activity and diversity of spiders in bushland and grassland.

Pitfall trapping at Ibaya was undertaken over 12 months from April 1995 until March 1996 but results are currently only available for the first 9 months.

Activity of spiders in burnt and unburnt bushland and grassland.

Figure 10a and 10b shows the activity of spiders in each month in each habitat. In the hillside bushland active numbers in the burnt habitat were nearly double those in the unburnt in all months except December. By contrast, in the foot-slope grassland, although activity was somewhat higher in the burnt habitat in 5 out of 9 months, differences in activity between the two habitats were very much smaller. In both the bushland and grassland, activity was greatest in the wetter months of April, May and November.

Figure 10. Activity of all spiders in A) unburnt and burnt hillside and B) unburnt and burnt grassland. Ibaya camp, Mkomazi Reserve, 1995

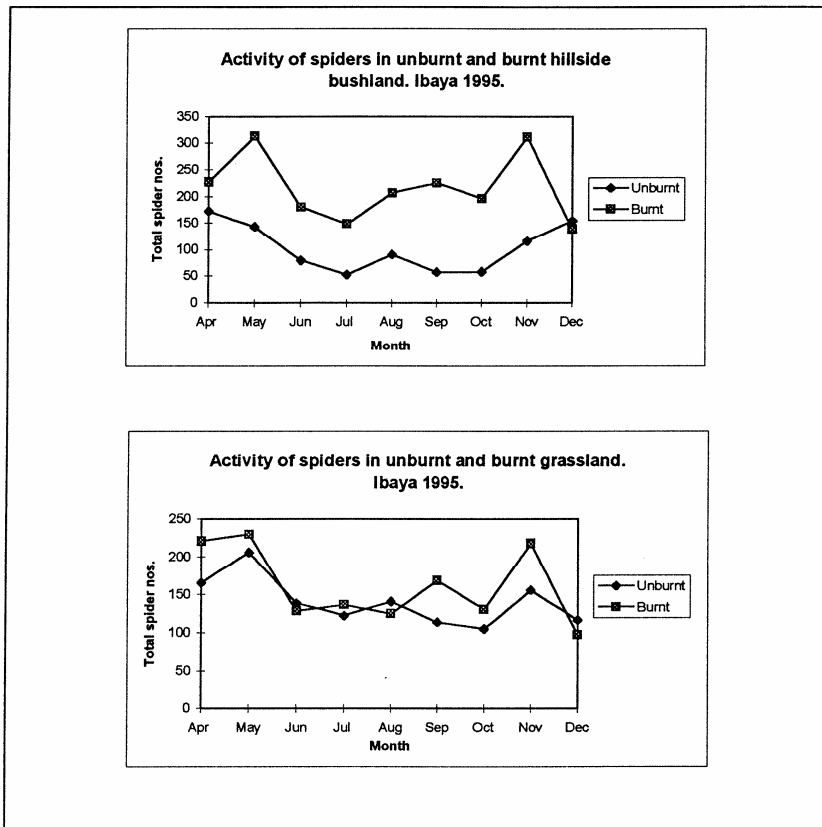


Figure 11 shows seasonal activity of the four most species rich spider families in these two habitats. As with the spider community as a whole, most families were greatly more active in burnt than unburnt hillside bushland, while levels of activity in the burnt and unburnt grassland were more similar. The exception were the Lycosidae (wolf spiders) which were also more active in the burnt grassland than the unburnt grassland. In general, numbers of spiders trapped in the burnt hillside were approximately double those in the burnt grassland but the differences between numbers trapped in unburnt bushland and grassland were less consistent.

Although activity of all spiders in the bushland was higher in the burnt than in the unburnt site, individual species showed a range of different behaviour patterns (Fig. 12). *Stenaelurillus* sp. A (Salticidae), was clearly much more active in the burnt than in the unburnt bushland. By contrast, the zodariid *Mallinella* sp. A was more active in unburnt than burnt bushland, although the differences were relatively small other than in May. *Stenaelurillus* sp. was more active in burnt than unburnt grassland until September, after which activity was greater in the unburnt site until December. As in the bushland, activity of *Mallinella* sp. A was greater in unburnt than burnt areas but in this case substantially so through much of the sampling period.

The very much greater numbers of many species trapped in the burnt habitats was not expected. Burnt ground is hotter, drier and subject to greater extremes in temperature than corresponding better vegetated sites and, in principle, spiders in such areas would also be more susceptible to predation. To some extent, high temperatures and visual predators can be avoided by nocturnally active species. While most of the gnaphosid and perhaps zodariid species active in burnt areas are night hunters, salticid and most lycosid species are diurnally active.

Interpretation of spider activity data from pitfall trapping is notoriously difficult. Factors that influence trapping of spiders include species, sex, season and vegetation type. For example, peaks in activity of hunting species are often the result of males seeking out females in the breeding season. This is likely to have accounted for the peak of activity of *Akyttara akagera* in May in the burnt hillside, where the sex ratio was 4 males to each female. Vegetation density can also influence numbers of a particular species trapped. For active ground hunters, a much larger proportion of the population is vulnerable to trapping in open ground than in densely vegetated areas. Although this may have influenced results in this study, it cannot be the only factor involved since species such as *Mallinella* sp. A were trapped in much greater numbers in unburnt than in burnt habitats. In addition, the fact that many species were trapped in large numbers in burnt areas suggests that bare ground plays an important role in their biology. Certainly species of Gnaphosidae and Zodariidae are particularly abundant in arid areas and it is possible that burnt areas provide the physical conditions they require in an otherwise more mesic environment in which other species are better able to compete.

Species richness and diversity of spiders in unburnt and burnt habitats.

Species richness of spiders was slightly higher in unburnt than in burnt bushland in April, May and December but in the intervening months the burnt bushland site always had more species than the unburnt bushland (Fig. 13). Species numbers were greater in the wet months of April, May, November and December than in the intervening dry months in both unburnt and burnt bushland. During the dry months there were often significantly more species in burnt hillside, with a maximal difference of 42% more species in the burnt site in October 1995. In the grassland by contrast, the unburnt site had more spider species in six out of nine months but the differences in numbers of species between burnt and unburnt were rarely very great, with a maximal difference of 18% more species in the unburnt grassland than burnt grassland in April 1995 (Fig. 13).

Species diversity of spiders in bushland, as measured by α of the log series, was always considerably higher in the burnt area than in the unburnt except in July and October when it was virtually identical in burnt and unburnt bushland (Fig. 13). The greatest difference was in the wet month of April when the index in the burnt area was double that in the unburnt area. Species diversity in the grassland was much higher in the unburnt site in April and May but was closely similar to that in the burnt site during the remainder of the study period. As in the bushland, diversity was highest during the wet months of the year.

Fig. 11. Activity of the most abundant spider families in unburnt and burnt hillside bushland and footslope grassland at Ibaya Camp, Mkomazi Reserve, April - December 1995.

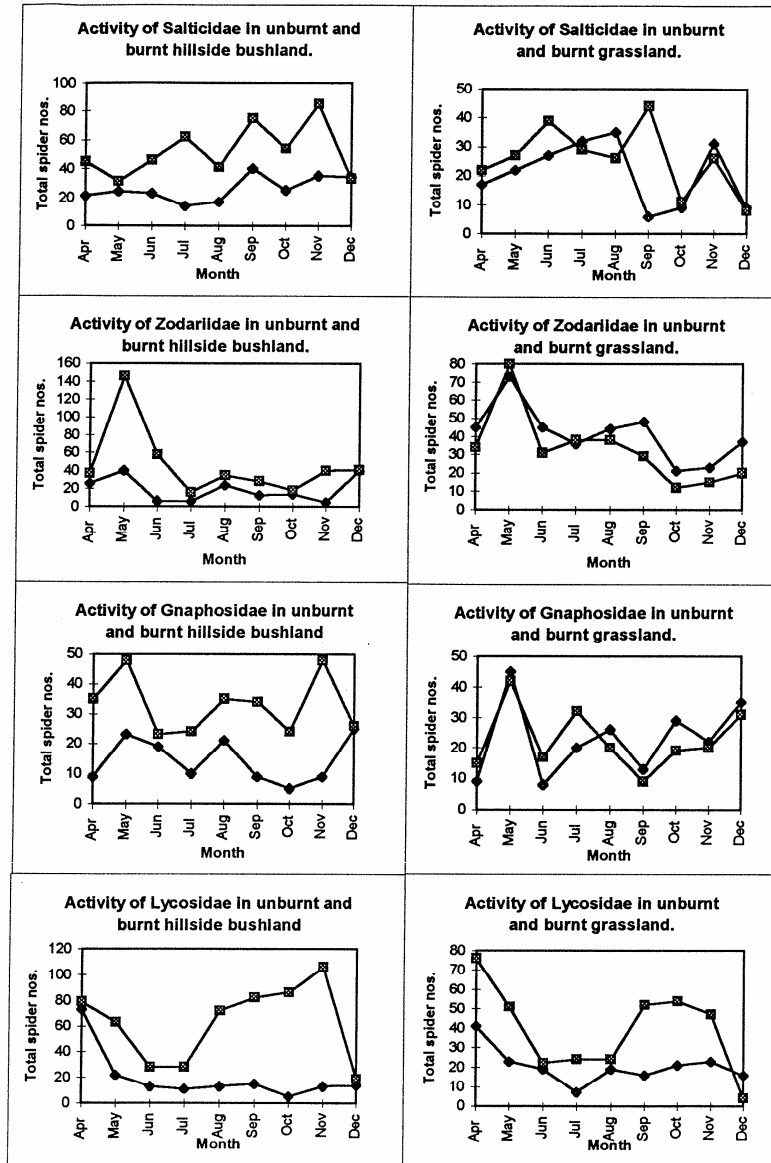


Figure 12. Activity of two common spider species in burnt and unburnt hillside bushland and grassland, Ibaya Camp, Mkomazi Reserve. April - December 1995.

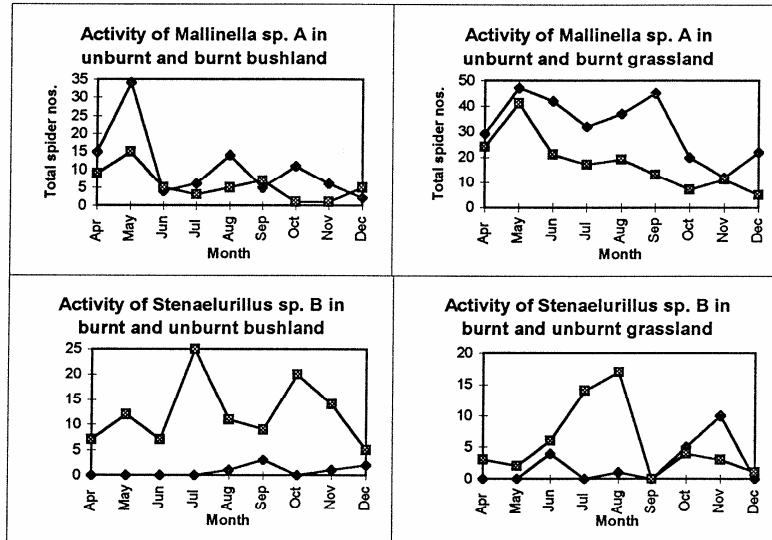


Fig. 14 shows species richness and diversity in the burnt and unburnt bushland and grassland sites over the nine month period as a whole. Total species richness was hardly affected by burning, with just one or two species less in the burnt habitats. However, the index of species diversity was 26% lower in the burnt hillside bushland than in the unburnt. The index of diversity for the burnt grassland was only slightly lower than that for unburnt grassland.

Figure 13. Species richness and diversity of spiders in unburnt and burnt hillside bushland and unburnt and burnt grassland. Ibaya Camp, Mkomazi Reserve. 1995.

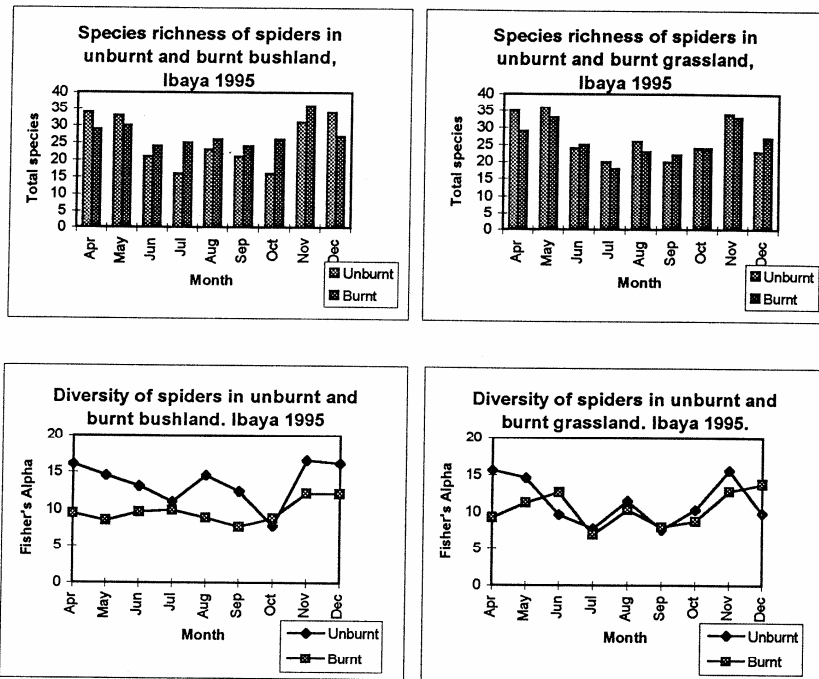
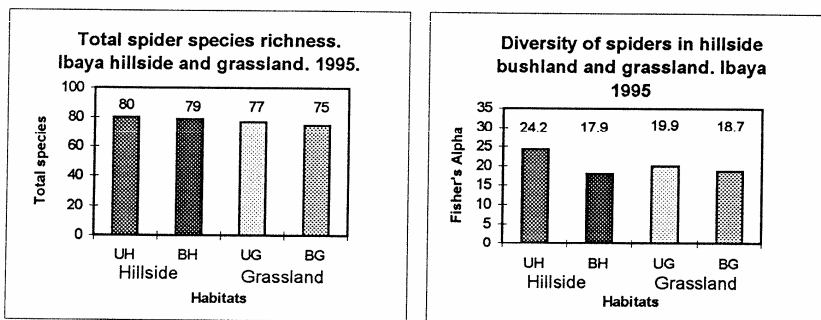


Figure 14. Species richness and diversity of spiders in unburnt and burnt hillside bushland and grassland over the whole period April to December 1995.



Discussion

Both species richness and diversity of spiders were clearly much more influenced by burning in the hillside bushland than in the grassland below. Although monthly species richness was higher in burnt bushland than unburnt in six out of nine months, principally during the dry season, there was little difference between the two habitats over the whole period of study. Species diversity, however, was clearly reduced in the burnt habitat in most months and over the whole nine month period was 26 % lower in burnt than unburnt bushland. In the grassland differences in species richness or diversity between the burnt and unburnt sites were quite small and unlikely to be particularly significant.

At present, the reasons for the differences in the effect of burning between grassland and hillside bushland are a matter for speculation. The burnt hillside was quite badly eroded with a thin layer of soil between exposed stones. It is possible that the productivity of this habitat was much more severely affected by burning than the grassland below and that this was reflected in the diversity of predators in this environment. However, given the apparently elevated activity of certain species in the burnt bushland, it is more likely that habitat structure or physical constraints permitted only a limited number of species to compete in this relatively harsh environment. In the grassland, although burning left the soil surface exposed, rapid regrowth of a dense sward was evident following rains and this may have permitted re-invasion of a diverse fauna from adjacent unburnt grassland.

A synoptic study such as the present one has obvious limitations in studying the longer term effects of burning on invertebrate diversity. Without information on the frequency and intensity of previous fires in a given area, it is not possible to be sure that unburnt "controls" have not themselves been subject to some level burning. Only carefully controlled burning experiments, in which the previous fire history of both burnt and unburnt areas is well documented, could determine long term changes in diversity resulting from fire. Unfortunately, this was well beyond the resources of the present project. However, this study does suggest that greatest spider diversity would be maintained by a mosaic of burnt and unburnt patches. What we were unable to determine was the optimal frequency and intensity of burning or the optimal size of burnt areas in different habitats.

3. The Arthropod Communities of Tree Canopies

Background

During the last 15 years a number of large scale studies have provided a better understanding of insect communities in tropical forest tree canopies (Erwin, 1982, 1983; Moran & Southwood, 1982; Adis *et al.*, 1984; Stork, 1987a, b; Morse *et al.*, 1988; Basset & Kitching, 1991; Stork, 1991; Basset 1996). A review of these and other major studies of arthropod diversity in tropical forest canopies is given by Erwin (1995). Despite the fact that savannas cover over 40 % of the surface area of the tropics (Cole, 1986; Solbrig, 1996), insect communities of tropical savanna tree canopies are still virtually unknown and there are practically no estimates of insect diversity in savannas in general (Lewinsohn & Price, 1996). With the exception of the studies of West (1986) on arthropods from *Acacia* and *Commiphora* canopies in Kora National Reserve, Kenya and Wagner (1997) on beetles sampled from the canopies of three tree species in forests in Rwanda and East Zaire, there have been no large scale studies conducted in the African continent.

Increasing human populations and associated habitat destruction (fire and over grazing) are reducing the time for an assessment of the insect fauna of savannas. Ecological inventories are an essential tool for environmental management and the assessment of habitats for conservation (Campbell, 1993). As insects have a much greater impact on terrestrial habitats than all other animal groups put together and are a major component of diversity, they are an essential component of any such inventory. Studying arthropod communities in savanna habitats is difficult because of a lack of clear habitat boundaries (Lewinsohn & Price, 1996) but savanna trees provide an exception, because they can be considered a discrete ecological unit (Southwood & Kennedy, 1983). Trees also show considerable niche diversification because of their structural complexity (Lawton, 1978; Lawton & Price, 1979; Lawton, 1986), are a stable resource (Southwood, 1978) and their inhabitants are all more or less trophically interlinked (Moran & Southwood, 1982). As Moran & Southwood (1982) conclude, 'in almost all respects it is easier to sample arboreal communities more completely, more widely and more accurately, [...], than it is to sample other very complex communities.' This is especially true for savanna tree canopies where there is often no contact with neighbouring trees.

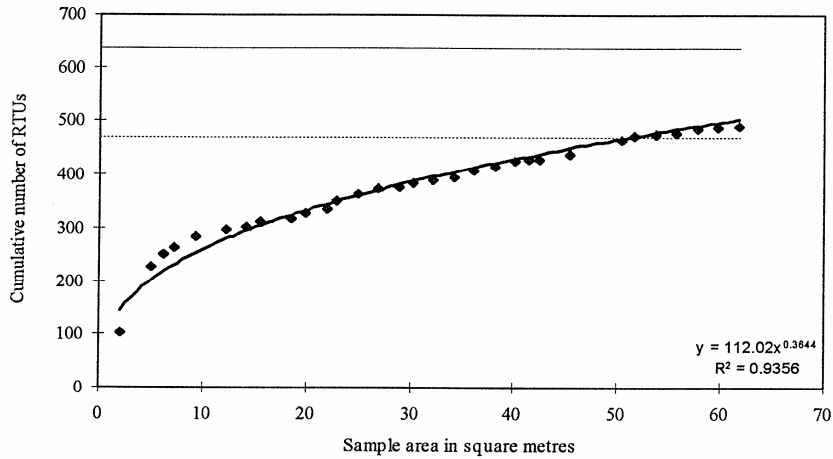
Composition of the canopy fauna

Material sampled between December 30th 1995 and 18th January 1996 from 31 trees belonging to six species of *Acacia* has been analysed. A total of 41,099 insect specimens, belonging to 14 orders, 133 families and 492 RTUs were recognised from the 61.28m² area sampled. The average insect density was 666 per m² (if larvae are included this figure rises to 800-900 per m²) and the mean number of RTUs per tree was 93. The variation in terms of the number of RTUs between individual trees covers a five range fold, and a fourteen range fold with regard to the number of individuals (Table 8). A graph of cumulative area / RTU relationship for the entire fauna sampled shows that, according to the two true richness estimators, between 77 and 100 % of the insect fauna is represented in the samples. Similar percentages were found for Hemiptera, Coleoptera and Hymenoptera (between 80 and 100 %) with the exception of Diptera, where the one estimator indicated that only 53 % of the total was represented (Figure 15).

Table 8. Summary statistics of the 31 trees analysed to date.

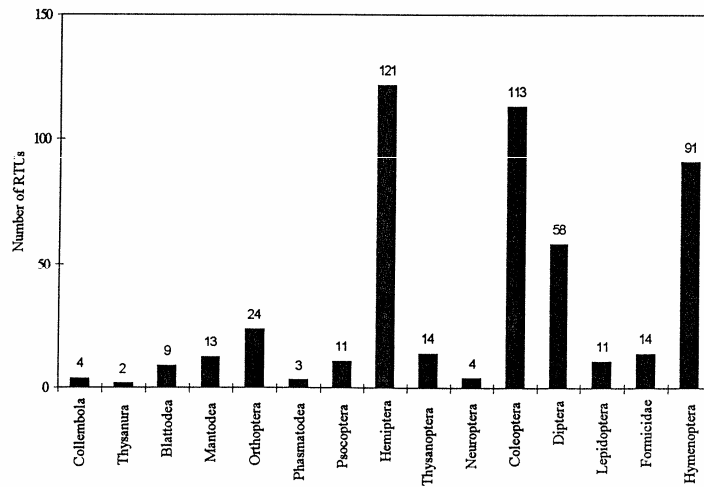
Species	No. sampled	Area sampled (m ²)	Mean no. RTUs	Min	Max	Mean no. ind.	Min	Max
<i>A. etbaica</i>	1	3.00	58	-	-	652	-	-
<i>A. mellifera</i>	4	6.28	62	35	79	386	210	592
<i>A. nilotica</i>	12	23.72	98	65	188	1445	400	2998
<i>A. reficiens</i>	4	8.28	86	65	103	1099	814	1485
<i>A. senegal</i>	8	16.00	107	78	145	1786	1497	2716
<i>A. tortilis</i>	2	4.00	105	84	125	872	439	1304
Total	31	61.28	93	35	188	1326	210	2998

Figure 15. Cumulative area / RTU curve for the entire insect fauna. The two horizontal lines are asymptotes of two true richness estimators, the dashed line from a negative exponential regression (Holdridge et al., 1971) and the continuous line from a non-parametric approach (Chao, 1984).



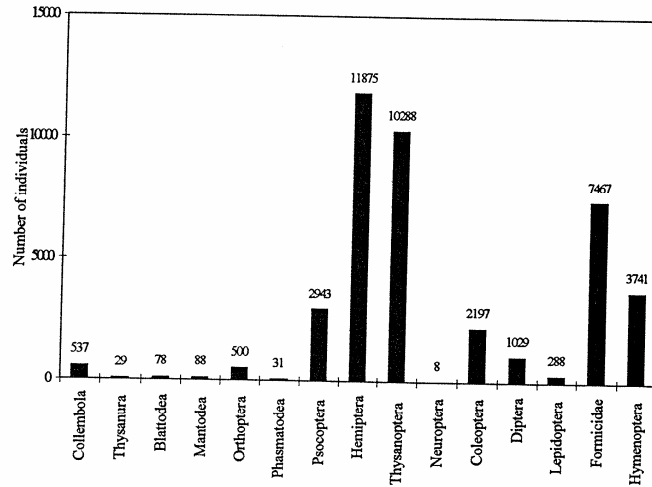
The RTU richness was highest for the Hemiptera, followed by the Coleoptera, Hymenoptera and Diptera (Figure 16). The most diverse families were the Cicadellidae, Chrysomelidae, Miridae and Formicidae with 7.9, 5.5, 4.1 and 2.9% of the total RTU richness respectively.

Figure 16. Distribution of RTU richness among the 14 orders represented. The Formicidae is separated from the rest of the Hymenoptera.



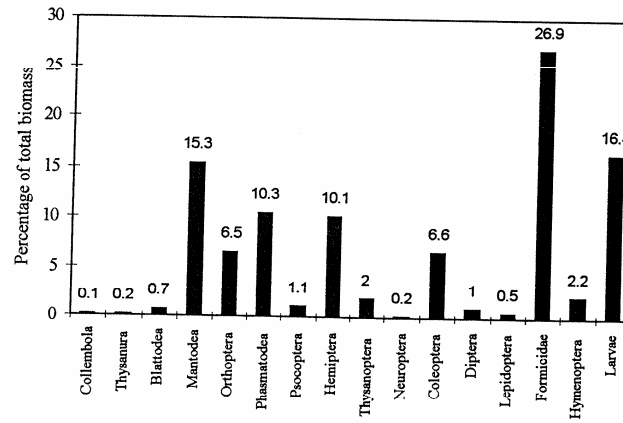
In terms of abundance, thrips (Thysanoptera) and ants (Formicidae) become much more important than Coleoptera but the Hemiptera had the highest abundance (Figure 17). The families with the highest abundances were the Thripidae, Formicidae, Cicadellidae and Miridae with 19.2, 18.2, 12.3 and 12.1% of the total abundance respectively.

Figure 17. Distribution of numbers of individuals among the 14 orders represented. The Formicidae is separated from the rest of the Hymenoptera.



The picture changes again if the distribution of biomass is examined (Figure 18). The highest biomass share is held by the ants followed by larvae and praying mantids (Mantodea). Although the Mantodea had a small share of the RTU richness and abundance they were among the biggest insects collected.

Figure 18. Distribution of percentage biomass share among the 14 orders represented. The Formicidae is separated from the rest of the Hymenoptera



Abundance distribution.

For the entire insect fauna (Figure 19), the observed abundance distribution is best described by a log normal model ($R^2 = 0.908$, d.f. = 12, $P < 0.001$), followed by the log series ($R^2 = 0.710$, d.f. = 12, $P < 0.05$) and the broken stick ($R^2 = 0.007$, d.f. = 12, $P \gg 0.05$). There was no significant deviation between observed abundance distribution and the log normal model ($\chi^2_{12} = 20.99$, $P > 0.05$) but a highly significant deviation from the two other models. Since no mode is visible, a rank abundance graph was also plotted (Fig. 20) and the negative power regression provides a good fit ($R^2 = 0.957$, d.f. = 490, $P < 0.0001$). For the four main orders, the results were similar. The broken stick model never simulated the observed abundance distribution well, and the log normal did in all cases with the exception of Diptera, where only the log series provided a good fit. That a log normal distribution fits the data best makes this system similar to most other communities studied. The broken stick model has been proposed for early successional communities and the ecological implication of the log series model is that there is a single major factor affecting the abundance pattern. *Acacia* canopies are likely to be quite a complex system where the interaction of a number of factors at random creates the observed log normal distribution.

Figure 19. Comparison between the observed abundance distribution and three models, log normal, log series and broken stick. The equation for the log normal is $y = 85.973 * e^{(-0.173^2 x^2)}$, $\alpha = 78.773$ and $x = 0.998087$ for the log series and the equation for the broken stick is $y = \left(492 * \frac{491}{41099}\right) * \left(\frac{1-x}{41099}\right)^{490}$.

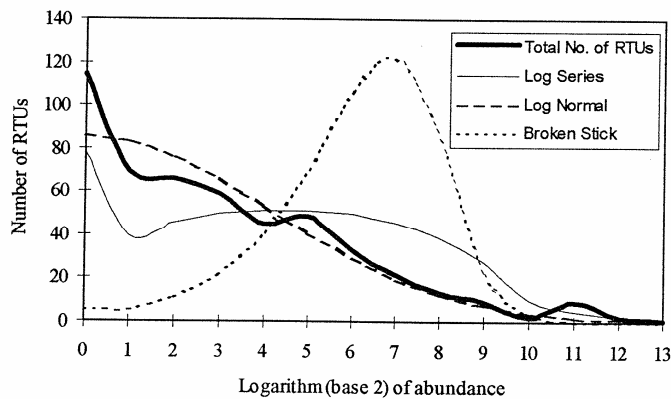
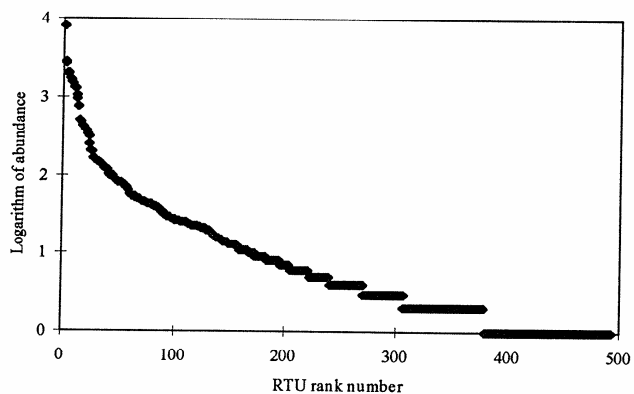


Figure 20. Rank abundance graph of the entire fauna, the relation being best fitted by $y = 7715.7 + x^{-0.9841}$ (note that y-axis on graph is displayed on a log scale for convenience).



Comparing the Mkomazi data analysed so far, with other studies, it can be seen that species richness is lower than in tropical rain forest tree canopies but insect density is higher than in rain forests or temperate tree canopies (Table 9).

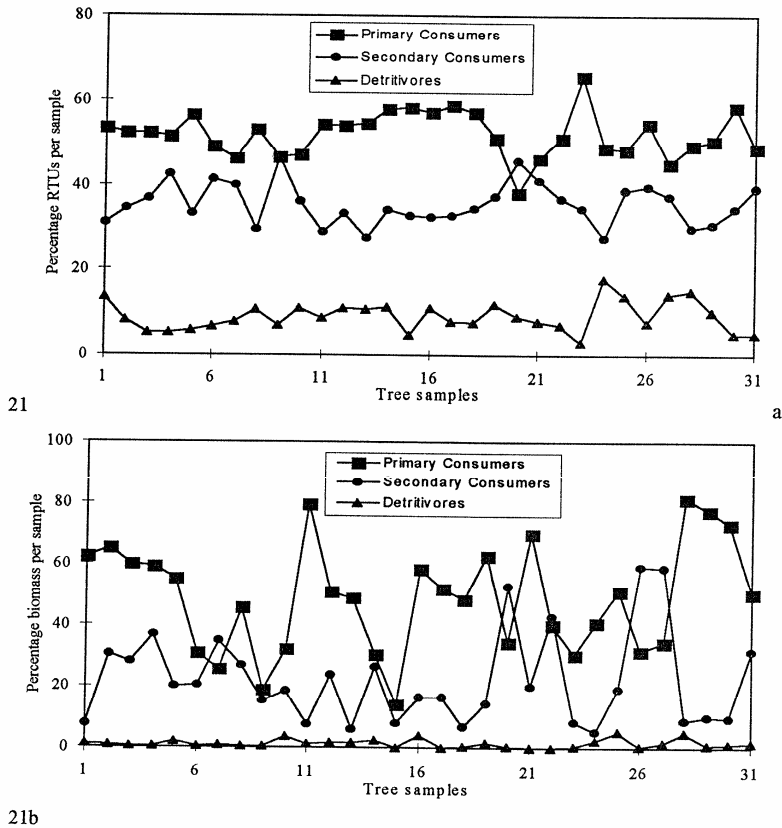
Table 9. Comparison of the Mkomazi study to other studies in tropical and temperate regions. The 4th, 5th and 6th columns give the insect density per m^2 , the species richness per tree and the individual to species ratio, respectively.

Source	Country	Habitat	Ind. / m^2	Spp / tree	Ind. : Species
This study	Tanzania	Savanna	666.3	35-188	41099 : 492
West (1986)	Kenya	Savanna	51.1	-	-
Adis <i>et al.</i> (1984)	Brazil	Rain forest	32-161	-	-
Basset (1991b)	Australia	Subtrop. Forest	19-46	-	-
Southwood <i>et al.</i> (1982)	South Africa	Subtrop. Forest	76	-	-
Southwood <i>et al.</i> (1982)	Britain	Forest	389	330-445	-
Watanabe & Ruaysoongnern (1989)	Thailand	Rain forest	123-256	-	-
Stork (1991)	Bornco	Rain forest	51-218	$\bar{x} = 617$	-
Basset (1991a)	Australia	Subtrop. Forest	-	759	51600 : 759

Guild Structure:

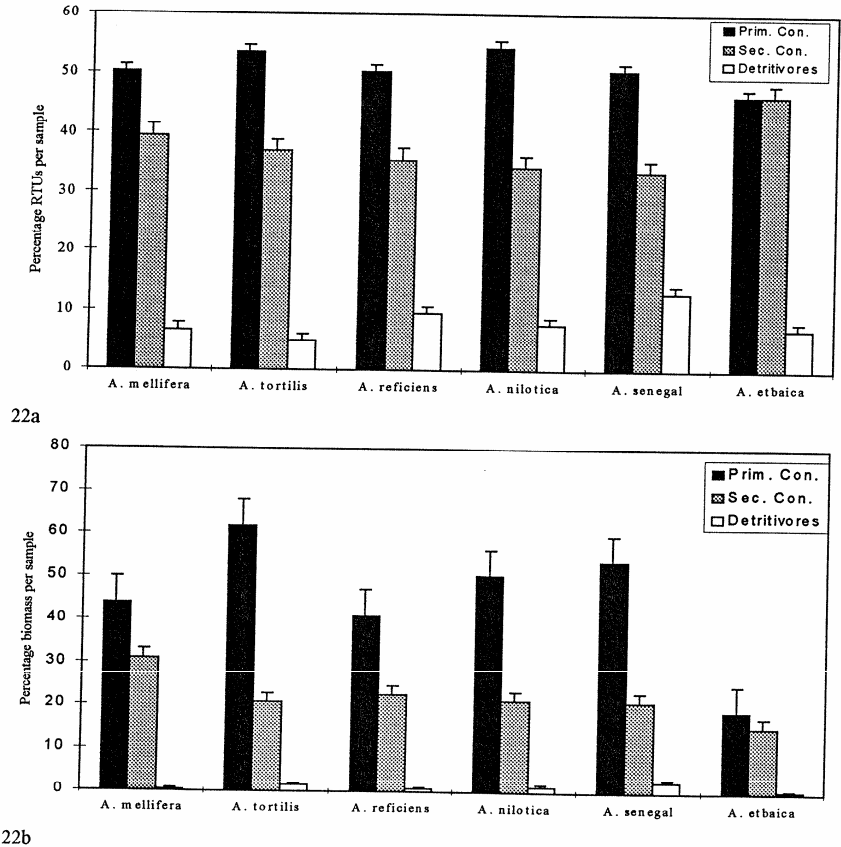
Insects were assigned to nine major ecological guilds and the distribution of species diversity and biomass was analysed. The data cover a 1,000,000-fold body weight range. Between tree variation in the proportion of RTUs and biomass in most guilds is large and covers a 2.5-fold range. RTU diversity was highest in the phytophagous sapsucker guild (*ps*: mainly Hemiptera and some Diptera), followed by the parasitoid (*pa*: Hymenoptera) and phytophagous chewer (*pc*: Orthoptera, Phasmatodea and some Coleoptera) guilds. Biomass share was highest in the ant guild, followed by the *pc* and the *ps* guilds. This structure is consistent with the expectations of energy flow in communities, since the biomass share of predators (*p*), parasitoids and scavengers (*s*) was much lower than that of herbivores. To extract general patterns of variation between trees, guilds were grouped into primary consumers, secondary consumers and detritivores and, while the level of between tree variation decreases greatly in the RTU composition (Fig. 21 a), it is still apparent for the biomass shares (Fig. 21 b).

Fig. 21. A. Between tree variation in the percentage RTU of three trophic levels (primary consumers = phytophagous chewers (*pc*), phytophagous sapsuckers (*ps*), phytophagous nectarivores (*pn*), epiphyte grazers (*e*); secondary consumers = predators (*p*), parasitoids (*pa*); detritivores = scavengers (*s*)). B. Between tree variation in the percentage biomass for the trophic levels.



A comparison between the six *Acacia* species with regard to RTU composition reveals no significant difference for primary and secondary consumers (Fig. 22a, ANOVA, $F_{5,25} = 1.022$, $P = 0.426$ and $F_{5,25} = 2.381$, $P = 0.067$ respectively), while there is a significant difference for the detritivores (ANOVA, $F_{5,25} = 6.994$, $P < 0.0001$). This consistency also holds true for the biomass percentage of primary and secondary consumers and detritivores (Fig. 22 b, ANOVA, $F_{5,25} = 1.136$, $P = 0.367$, $F_{5,25} = 0.291$, $P = 0.913$ and $F_{5,25} = 2.536$, $P = 0.055$ respectively).

Fig. 22 a. Mean percentage RTUs in the three trophic levels for each of the six *Acacia* species. b. Mean percentage biomass in the three trophic levels for the six *Acacia* species



Summary:

Quantitative arthropod samples have been obtained from the canopies of 266 trees representing 30 species). The total canopy area sampled for all tree species is a little over 480m². Details of the samples are given in appendix 1. This work represents the biggest single study of savanna tree canopies ever undertaken.

Only 31 of the 266 tree samples taken has been fully sorted, analysed and identified, comprising 11.6% of the estimated 0.5 million specimens. Species richness and abundance is very much greater than previously recorded in the only similar savanna study of 6 species of *Acacia*, 5 species of *Commiphora* and one species of *Lannea* carried out in the Kora National Reserve, Kenya (West, 1986). In this study, conducted from early November 1983 to late January 1984, 6,742 specimens, assigned to 496 morphotypes, were collected from 49 tree samples each of 4m² (a total of 196m²). The mean density of arthropods in the Kora study was 34.4 /m² as compared with a mean density of 666 /m² (excluding larvae) in the present study. The huge difference in the relative numbers of specimens collected must be largely due to the superior sampling efficiency of a motorised mistblower over a manually-operated backpack sprayer.

Publications

Published papers:

Stone, G., Wilmer, P. & Nee, S. (1996). Daily partitioning of pollinators in an African *Acacia* community. *Proceedings of the Royal Society of London. B*, 263, 1389-1393.

Summary

Many studies have shown sympatric plants with similar floral structures to have flowering periods separated in time, and this is usually interpreted as a selective response to competition for pollination. In highly seasonal habitats, however, the time available for flowering may be highly constrained, and many species often flower together. Under such conditions, one alternative to temporal partitioning on a seasonal scale is for species to flower simultaneously, but with pollen release (dehiscence) structured on a diurnal timescale. Here we provide evidence for such diurnal partitioning of both floral resources and pollinator visitation in an African *Acacia* community. Temporal separation is enhanced by differences in the rewards offered by *Acacia* species to their pollinators: species producing nectar as well as pollen receive flower visits from insect groups absent from acacias offering only pollen. In contrast to competition for pollination, this situation may promote mutualistic maintenance of shared pollinators by the *Acacia* species.

Papers submitted:

Kröger, O. and McGavin, G.C. Insect diversity and abundance in relation to body weight. *Nature*

The entire fauna and four major orders (Hemiptera, Coleoptera, Diptera and Hymenoptera) showed bell-shaped curves with maxima of RTU richness and abundance at intermediate body weights. These findings support recent evidence that the peak in species richness might occur at intermediate body weights. In addition, we demonstrate that an energetic model recently developed (Brown *et al.*, 1993) simulates the distribution of RTUs among body weight classes very well. We also found a relationship between abundance (*I*) and species richness (*S*) which supports both the recent suggestion that $S = I^{0.5}$ but for other orders the alternative that this relationship may follow the pattern of the species area curve with $S = I^{0.2-0.35}$ (Siemann *et al.*, 1996).

Kröger, O. and McGavin, G.C. The influence of ants on the guild structure of *Acacia* insect communities in Mkomazi Game Reserve, north-east Tanzania. *Journal of Animal Ecology*.

The percentage biomass of ants was correlated positively with the diversity share of sapsuckers and negatively with the diversity share of tourists. Negative correlations were found with the biomass share of predators, phytophagous chewers and parasitoids. Diversity and abundance share was much higher in egg and coccoid parasitoids compared to larval parasitoids, probably due to predation by ants on larval parasitoids. Their low diversity supports the hypothesis of a decline towards the equator in ichneumonid diversity.

Krüger, O. and McGavin, G.C. Stability of insect guild composition through ecological space. *Nature*.

Although between sample variation in species composition and biomass share of most guilds was large, at most trophic levels and even at guild level there was no significant difference in both species composition and biomass share of these guilds between six *Acacia* species and nine tree localities. This previously unreported consistency in biomass guild structure suggests that there may be a general ecological rule governing resource partitioning in insect communities.

Krüger, O. and McGavin, G.C. Insect biodiversity of *Acacia* canopies in Mkomazi Game Reserve, north-east Tanzania. *Oikos*.

In most cases, there were significant differences between trees between and within tree species with regard to their insect community. After we performed a standardisation procedure because of unequal sample size, cluster analysis showed that most tree species formed more or less distinct clusters, indicating a moderate level of insect host specificity. Considered by tree localities, clear clusters were visible only if one tree species was sampled. This finding suggests that there is no significant overlap in the insect communities between tree species at a local basis. We carried out a multivariate analysis of biodiversity using four different biodiversity measurements. Results differed depending on the measurement used and no significant association of tree characteristics with insect biodiversity was detectable. Instead, time of the day and ant biomass share seem to be of greater importance. These results emphasise the importance of using different biodiversity measurements to evaluate habitats with regard to their conservation value.

Krüger, O. and McGavin, G.C. The insect fauna of *Acacia* species in Mkomazi Game Reserve, north-east Tanzania. *Ecological Entomology*

The insect density and species richness varied significantly between tree species. The cumulative area RTU relationship provided evidence that most RTUs were represented in the samples. The shape of the curves are similar between the entire fauna and four main orders, except for Coleoptera, where the exponent indicates a high diversity. The faunal composition was partly similar to temperate regions (high diversity and abundance of chewers) and partly similar to tropical regions (high abundance of ants). Cicadellidae and Chrysomelidae had the highest diversity shares, Thripidae and Formicidae the highest abundance shares. The abundance pattern follows a log normal model in most cases, Diptera followed a log series model, the broken stick failed to simulate any abundance distributions. The species richness was lower compared to rain forest canopies while the insect density was higher than in rain forest and temperate tree canopies.

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