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Insect communities in Southern Kalahari, Botswana

—abundance and diversity in relation to land management



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Abstract

The effect of different land management on insect communities in Southern Kalahari, Botswana was investigated between July and September 2002. The study compares communal grazing areas, wildlife management areas, fenced cattle ranches and national parks which differ in grazing pressure and livestock and wildlife densities. The sampling was carried out during the dry period using un-baited and dung-baited pit fall traps, with 370 traps and a total sample amount of 42008 arthropods. The possible importance of pans on insect distribution was examined with the traps set along transects starting at pans following a nutrient resource and disturbance gradient from the pans. Variation in insect abundance was measured at several spatial scales. Various environmental parameters were measured for analysis of importance to trap catch. The catch was dominated by Formicidae (ants), Diptera (mostly flies) and Tenebrionid beetles both in terms of abundance and diversity. Patterns of abundance and diversity to body size were also examined for these taxa. The results of the study show significant differences in species richness between all management types. Total species richness varied between the management types accordingly: commercial cattle ranches > wildlife management areas > communal grazing areas > national parks. Total insect abundance differed among the different management types in the same manner with the exception of wildlife management areas and communal grazing areas not being significantly different in this aspect. Insect distribution between management types was not uniform for all taxa. Regression analysis showed no correlation of insect abundance or diversity with any of the measured environmental variables. Neither was distance to pan found to have any clear effect on insect communities. Patterns of abundance to body size and species richness to body size suggest unimodal relationships.

Foreword

This paper is the result of a “Minor Field Study” sponsored by the Swedish International Development Cooperation Agency (SIDA) distributed through the Committee of Tropical Ecology at Uppsala University. The study is a part of the EU-project “Management and policy options for the sustainable development of communal rangelands and their communities in southern Africa, MAPOSDA”. Project No. ICA4-CT-2001-10050.

Table of contents

1. Introduction	5
2. Aim	7
3. Study area	7
History	8
Land management	8
Pans	10
Map of study area	11
4. Methods	12
Sample areas	12
Design of transects	12
Sample plots, design of small and large traps	13
Sampling and identification.....	14
Data analysis.....	15
5. Results	16
Summary of catches	16
Comparison of trap types.....	18
Comparison of management types	20
Comparison of transects	23
Species richness	24
Environmental factors	25
Spatial scales and gradients	25
Abundance and species richness in relation to body size	26
Relevant sample sizes	28
6. Discussion	28
Abundance and species richness	28
Comparisons between land use types.....	30
Spatial scales	31
Resource and disturbance gradients	32
Abundance and species richness vs. body size.....	32
Conclusion.....	33
Future questions	33
Acknowledgements	34
References:	34

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1. Introduction

Large portions of Africa host savannah type ecosystems, constituting major habitats for humans, as well as wildlife. The savannah environment is often the result of a delicate interaction between physical preconditions, intricate food webs and disturbance. One of the prerequisites for a healthy and resilient savannah is diversity, at several ecological levels, often including large animal populations. Open savannahs are generally maintained by a complex mix of nutrient and water stress, seasonally heavy grazing and fire (Skarpe 1992). It is also the result of millennia of adaptation by the flora and fauna to specific conditions, making it vulnerable to outside influence novel to the environment.

Humans affect the savannah ecosystem in a number of ways; traditionally and in a sustainable way as hunter/gatherers and small scale agro pastoralists and more recently as large scale farmers, cattle rearers and hunters with often less sustainable practices (Kellman and Tackaberry 1997). Although the individual contribution may seem negligible in these cases, the cumulative sum of human activity often has severe environmental effects on the savannah ecosystem such as “desertification” and loss of biodiversity.

Such problems are widespread in the dry savannas of Kalahari in southern Africa. Past studies of the fauna of southern Kalahari and its relation to human settlements has mostly focused on large mammals. Specific knowledge in this field is still limited, but recent studies show patterns in animal distribution that can be explained by various human activities, mainly village settlements and cattle rearing, with different intensities in land use forming a disturbance gradient (Wallgren 2001, Granlund 2001, Viio 2003). These studies indicate that, in general, human and cattle presence have a negative effect on wild mammals in the Kalahari, and local coexistence of cattle and wild ungulates is scarce. A considerable decline in wildlife populations during the last decades correlates with an increased human presence and activity in the area, affecting both local conditions and migratory patterns (Thomas and Shaw 1991, Williamson and Williamson 1984).

On another level, it has also been shown that pans, if not severely impacted by humans, act as congregating points for a large number of mammals (Wallgren 2001, Viio 2003). The distribution patterns of large herbivores around pans are at least partially explained by a gradient in nutrients from the mineral rich pans into the surrounding savannas. It is clear that the geological formations known as pans play an important role in the life of large herbivores, and subsequently the associated predators and symbionts.

Whether these distribution patterns in relation to pans and to human activities apply to insects is little known. In particular, the possible influence on insect communities by livestock grazing in the area is to my knowledge still unexamined. Bestelmeyer and Wiens (2001) have investigated effects of livestock grazing on ant abundance and diversity in North American grasslands and has found little correlation. Studies from Argentinean grasslands suggest a negative correlation between grazing intensity and insect abundance and diversity (Cagnolo et al. 2002). Similar relationships are found by Kreuss and Tschardtke (2001) in German grasslands. Two competing general mechanisms could possibly govern insect occurrence in the current study area. The first is the idea that a pristine untouched savannah promotes the fauna adapted to the characteristics of the region. The other is the potential increase in resources that livestock grazing and borehole drilling might create for insects. Insect abundance has been found to be positively correlated with nitrogen loading in grasslands

(Haddad et al. 2000) which could be analogous to the higher production rates and dung collection at locations where cattle aggregate.

Relationships between productivity and diversity have been subjected to investigation for several decades. Generally, productivity measured as either growth rate or rate of conversion of resources to biomass has been recognized as affecting diversity in one way or the other (Waide et al. 1999). The type of relationship and the underlying mechanisms have however been a matter of some controversy and are yet to be resolved (Abrams 1995). Although researchers have suggested both negative and positive correlations, linear and non-linear, the most common view has been that diversity relates to productivity in a unimodal (hump-shaped) way, or a positive monotonic (linear) way (Tilman and Pacala 1993, Abrams 1995 respectively). The theory behind the unimodal patterns is based on the assumption that diversity is favoured in productive environments but lowered in highly productive systems as a result of various mechanisms of competition, or by lower heterogeneity in very resource rich localities (Tilman and Pacala 1993, Waide et al. 1999). On the other hand, advocates of monotonic patterns invoke other competitive mechanisms in their explanatory models (Abrams 1995). Further, reviews of studies on the subject suggest that the relationships are highly scale dependent (Waide et al. 1999). Thus, there exists no single forecast of how insect species richness should vary along the resource gradient surrounding a pan in southern Kalahari, rather a number of possibilities.

Animal body size in relation to community structure has received quite a lot of attention from ecologists during the last decades. According to the energetic equivalence rule, body size and population density are negatively correlated (Lawton 1991). The mechanism behind this relationship is that smaller organisms consume less energy than larger ones, thus facilitating larger population numbers given limited resources. This theory assumes that there are no other factors influencing body size, e.g. predation risk, and that similar amounts of energy flow through the different size classes. Although the assumption of equal energy flow has been challenged from different positions (Brown and Maurer 1986, Peters and Wassenberg 1983), the negative relationship between body size and abundance is widely recognized (Ricklefs and Shluter 1993). One simple explanation would be that large species tend to eat smaller ones and generally require eating more than one to complete its life cycle. There are also mechanisms that support smaller organisms, both in terms of species richness and abundance, which operate purely through geometry. From a fractal viewpoint the world can be seen as supplying different amounts of life space or niches at different spatial scales (Morse et al. 1986, May 1986). As an ant would give a different account for the length of England's coast than an elephant would, merely because of the differences in pacing, so would an ant find a larger amount of suitable habitats during its hike. The exact mathematical expressions of these fractal effects may be debated as they differ according to how one, two or three-dimensional an ant makes use of the world, but the general effect is the same; an organism's "room for life" should increase with its decrease in size due to the increased heterogeneity at smaller scales. At the other end of the spectrum, organisms cannot become infinitely small. A certain amount of physical size is required to function in a complex way and perform various interactions with its surroundings.

Alternatively to a monotonic decrease in abundance and diversity with increasing body sizes, recent studies have supported the unimodal pattern of species richness in relation to body size classes (Siemann et al. 1999). Theories that assert this size distribution have referred to a tentative diversification from a common ancestor of a certain body size, or alternatively, a divergence around an optimal body size. Such an optimal body size is hypothesized to be the

result of several simultaneous factors, e.g. metabolic efficiency versus reproductive rate (Siemann et al. 1999). It is also plausible that a unimodal pattern could emerge out of one factor alone, e.g. mobility. Mobility could possibly peak around an intermediate body size, at least mobility in relation to body size, regulating the amount of interactions with the environment for a given species. Although the questions concerning body size and community structure have received considerable attention the recent years the results is ambiguous and sometimes open to different interpretations (Lawton 1991). One practical use of the body size to species richness relationship is estimations of species numbers at a global scale. As the smaller species still are the least chartered, estimates of the relationship between body size and species richness is a cornerstone in estimating the world's total number of species. A linear negative correlation results in higher estimates, a hump-shaped unimodal pattern results in lower estimates (May 1986).

2. Aim

This study aims at describing the general occurrence of insects in the south-western Kalahari in the dry period with focus on the possible differences between areas of different land management. The four investigated land use types can be seen as representing a gradient of disturbance. The pans, key habitat to many Kalahari species, form an interruption in the nutrient poor savannah and produce a gradient in resources. The possible importance of this gradient on insect distribution was investigated. Insect community structure, density, species richness and body size were investigated at several spatial scales. Correlations between insect occurrence and vegetation and other environmental factors were also investigated. Lastly, relations of species richness and abundance to body size were examined.

Summary of the aims of the study:

1. Describe insect fauna
2. Examine possible differences in insect fauna between areas of different land use
3. Investigate insect fauna in relation to distance to pan
4. Examine the effect of local vegetation characteristics on insect fauna
5. Explore relations of diversity and abundance to body size

3. Study area

The study was conducted in the south-western Kalahari around the Matsheng-villages (24°00'S, 21°80'E), of which Hukuntsi is the largest with approximately 3800 inhabitants (CSO 2003). The landscape consists of an arid to semi-arid, sparsely populated bush savannah. The true Kalahari, of which this is a part, is situated on a sand plateau at approximately 1000m above sea-level (Thomas and Shaw 1991) covering most of Botswana, the eastern parts of Namibia and the northern parts of South Africa. The plateau is a subsection of the vast Kalahari sand sheet (covering 2.5 million km², ranging from Congo-Brazzaville to South Africa), and has hosted vast numbers of wildlife for millennia (Thomas and Shaw 1991). The soil of the south-western Kalahari consists of sand with generally poor nutrient quality and water holding abilities (Bergström and Skarpe 1985). Annual rainfall is approximately 300mm and for the farthest south-western parts less than 200mm (Parris 197?) almost all of which falls in thundershowers during the rainy season from October to April. The yearly rainfall also varies greatly; coefficient of variation is about 50% to 80 %, with long dry spells as a result (Pike 1972). Summers are hot with temperatures often exceeding 37.8°C (100°F) and winters have warm days and cold nights with temperatures often dropping below 0°C (Parris 197?). The vegetation and animal life is thus highly adapted to a harsh environment

and long periods of drought with e.g. some antelopes being able to use vegetation as their only source of water. Standing or lying dead wood is common throughout the savannah, but increasingly scarce near human settlements.

History

Human activity has been present in central Kalahari in the form of stone age hunter gatherers of San/Basarwa origin for as long as the area has had its present appearance. Although the San people have occasionally kept livestock as pastoralists from as far back as the birth of Christ, the practise of cattle rearing has only been common in the dryer south-western parts since the middle of the 19th century (Thomas and Shaw 1991). Due to the immense development of boreholes and other infrastructure during the last 50 years, human presence and use of the savannah as rangelands has grown rapidly (Perkins 1991). The extensive development of cattle posts and allocation of areas for cattle grazing is also a result of regional politics and heavy EEC subsidies for beef export. Another consequence of these subsidies was widespread veterinary fences for the fear of foot and mouth disease. The veterinary fences are a constraint on migratory movements, essential for many herbivores. Mass death of e.g. blue wildebeest at fences has been recorded during times of drought (Owens and Owens 1980, Williamson and Williamson 1984). During the last decades, a general decline in wildlife has been shown in the study area around the Matsheng-villages (Crowe, in Legett 1995, Granlund 2001).

Land management

Human influence in south-western Botswana occurs in various kinds and intensities and the landscape includes four types of management areas namely, Community Grazing Areas (CGA), Wildlife Management Areas (WMA), Commercial Cattle Ranches (CCR) and protected areas of which the National Parks (NP) is the main constituent. This division is partly a result of the Tribal Land Grazing Policy (TGLP) from 1975 although present management have far older ancestry.

Community grazing areas

The CGAs is frequently used for livestock, grazing freely, including cattle, goats, sheep and donkeys. The CGAs are un-fenced and centred around villages with different shapes and sizes. Livestock tend to keep within a 20-25 km radius from the villages. In practice, the same distance more or less serves as a boundary for wildlife as well, the wildlife showing little interest in mixing with the livestock (Wallgren 2001, Viio 2003). Livestock within the Matsheng area totals some 45 000 animals (Arntzen et al. 1998), most of them wandering freely with increasing densities towards the villages. However, significant numbers are kraaled during nights. In general, livestock densities tend to be highest around water sources such as boreholes or villages, declining with distance to the watersource. Livestock is thus distributed not evenly throughout the CGAs, but rather along piospheres (Perkins 1991). These are localised patterns of disturbance around a resource patch, characterised in the study area by decreasing vegetation cover as well as fodder quality and quantity, with decreasing distance to the village or watering point. Furthermore, since faunal densities vary with distance to pans and villages also for reasons other than water availability (Wallgren 2001), the actual distribution patterns might be too complex to be described easily. It is clear however, that the vegetation of the CGAs show clear signs of heavy grazing. The boundary to where cattle reach from their watering points can readily be spotted when driving towards a village. Lower grass cover, occasional bush encroachment, less dead wood, cow dung and

trampled ground make the CGAs a potentially very different habitat for insects, compared to the surrounding areas.

Wildlife Management Areas

Outside the CGAs the Wildlife Management Areas begin, with wildlife utilization as the main purpose. Here, if they are present at all, livestock is sparse and their distribution is subject to large variations (Viio 2003). WMAs comprise the bulk of land in the south western Kalahari with 22% of Botswana's total area (Broekhuis 1997) and acts as a buffer zone surrounding the National Parks. Its effectiveness as a buffer is open for debate as hunting, both legal and illegal, is widespread throughout WMAs (Legett 1995). Many small and remote villages can be found in the WMAs, relying partly on subsistence hunting and/or selling hunting rights to recreational hunters.

Commercial cattle ranches

The cattle ranches are fenced and generally 8 by 8 km in size, placed in remote areas bordering WMAs. The idea of these ranches is to keep large densities of cattle on a rotational system of grazing, maximizing beef offtake. Whether rotational grazing was practised in the studied ranches is unknown. The exact production of these ranches is difficult to ascertain since the offtake of livestock is not reported centrally (Perkins 1991). However, livestock density was clearly highest in this management type (personal obs., Viio 2003). Since the ranches have permanent water sources in the form of boreholes, cattle aggregate around these points and distribution can be described on a local scale as following piospheres rather than producing homogenous distributions within ranches. The studied ranches had noticeably more dead lying wood than other areas. This is possibly an effect of clearing to increase grass cover and could have effects on insect occurrence. The studied ranches were in the Ncojane ranch block area, constructed in the mid 1970s and have a documented history of overgrazing (Thomas and Shaw 1991).

National Parks

National parks cover large areas of Botswana and do not allow any livestock or hunting within their unfenced borders. These areas have been protected since the independence of Botswana and have consequently not been subjected to any significant direct disturbance from man. Acknowledging the fact that the ecology of the national parks is influenced also by circumstances outside their borders, the herds of large herbivores has lately diminished due to constraints (veterinary fences) on their migratory movements. The little impact of humans that nonetheless occur within NPs comes almost exclusively from wildlife tourists. In contrast to some other African nations, Botswana's wildlife tourist strategy is one of high cost / low numbers of tourists rather than low cost / large numbers. The national park sampled in this study is the Kgalagadi Transfrontier Park, formerly known as the Gemsbok National Park, located at the very south western corner of Botswana and adjacent areas of South Africa. During the time of the study, safari facilities were still being constructed and tourist densities were low. At some of the pans in the park, water holes are artificially kept filled throughout the year to lessen the need for long migratory movements of herbivores. This was the case with the Mpaathlutwa pan, sampled in the study. Information from 1997 states that there are 88 boreholes on the Botswana side of the KTP with possible more to come (NPB and DWNP 1997).

Recently, studies have investigated the correlation between wildlife occurrence, management areas and various environmental factors. For larger wild mammals it has been shown that

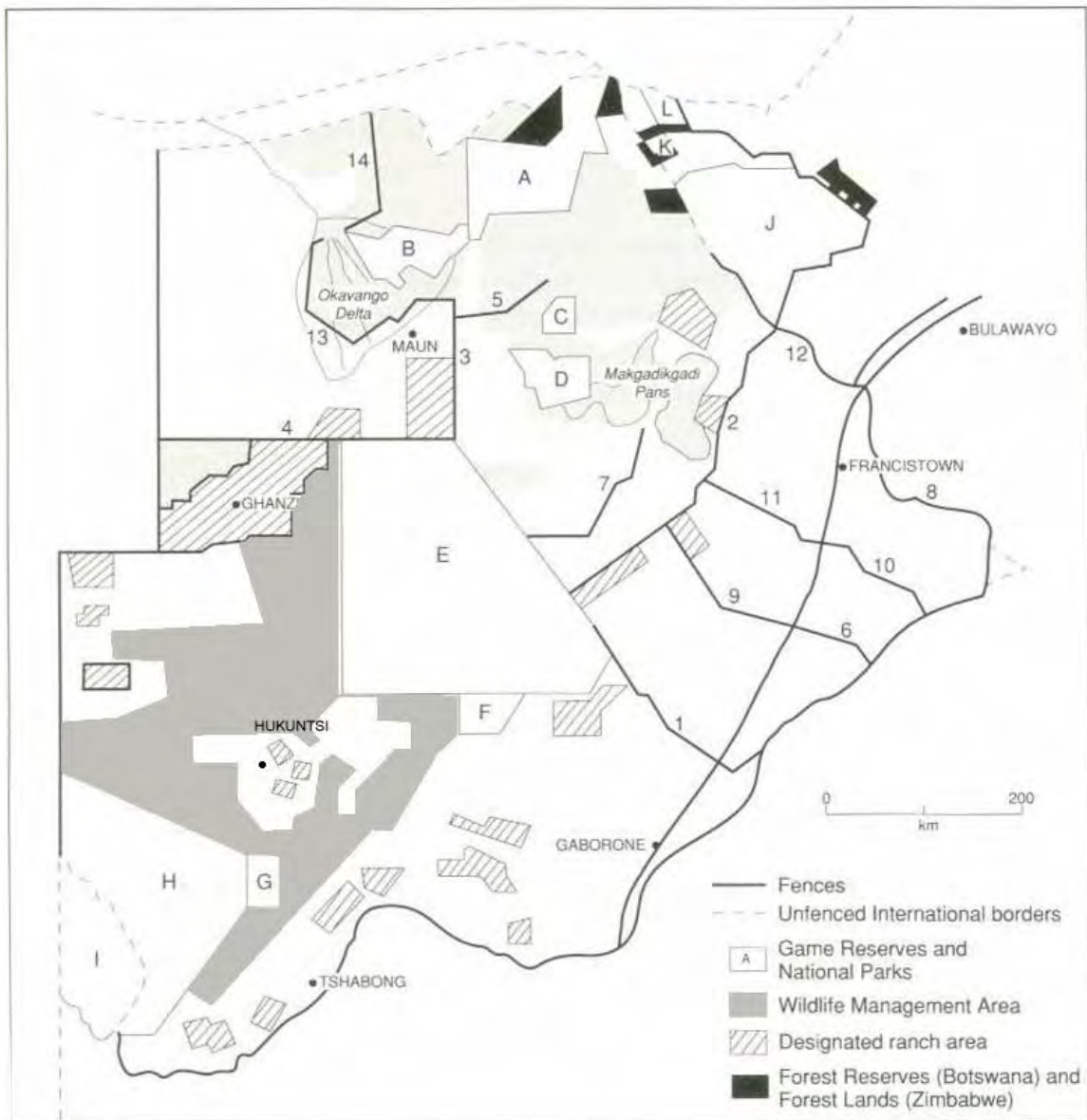
national parks have the highest densities followed by WMAs, CGAs and CCRs, respectively (Viio 2003). Similarly, Bergström A. (2003) has showed that rodent densities are highest in National Parks, followed by WMAs, CGAs, and lastly CCRs.

Pans

A conspicuous feature of the otherwise so homogenous bush savannah, typical to the area, is the geological formations known as pans. They are roughly circular, shallow depressions in the ground. Their origin is a matter of some debate but is most likely a combination of aeolian mechanisms and weathering forces induced by localised groundwater flows (Thomas and Shaw 1991). The pan soil is generally calcareous and more clayey than the surrounding sandveld soil and often holds a much higher mineral content. In the dry season the pan floor is usually bare and hard. Significant amounts of the fine pan soil may be carried away by the wind and deposited close to the pan, often constructing significant sand dunes (Parris 197?). With the winds of the dry period being mainly north to northwest, the location of these sand dunes are typically at the south to southeast end of the pan, often acting as the only landmarks in the area. In the rainy season, the lower parts of the pans are sometimes filled by rain water, making them hotspots for animals. Apart from the occasional waterhole, pans appeal to animals also by offering mineral rich salt licks, vegetation of high nutrient content and an open terrain, giving them a heads up on possible predators. Animals tend to congregate around and on the pans also in the dry period. Older and recent studies in the area show an inverse correlation between distance to pans and densities for larger mammals, supporting common observations of wildlife's affinity to pans (Parris 197?, Bergström and Skarpe 1999, Wallgren 2001, Granlund 2001). Insects associated with higher fauna are likely to display a similar distribution pattern but the direct importance of pans on insects and their actual distribution around pans is little known.

Although pans at a superficial glance may display discrete borders in vegetation cover, their ecological effect can be described as a gradient ranging from their centre to the completely unaffected savannah. Soil composition, nutrient content, plant species composition, vegetation density, grazing pressure and water availability vary along this gradient (Thomas & Shaw 1991, Parris 197?). Hypothetically, particularly the gradient in resources and usage by large herbivores may covary with insect distribution. Also, insects requiring specific soil properties may show distribution patterns correlated to distance to pans (e.g. termites with complex underground constructions). Further, these tentative variations of insect distribution transecting the pan/savannah gradient may show either discrete borders due to niche differentiation in overlapping sections (in accordance with Gause's exclusion principle, Gause 1934) or more continuous patterns implying a community of generalists.

Map of study area



National Parks and Game Reserves

- A Chobe National Park
- B Moremi Wildlife Reserve
- C Nxai Pan National Park
- D Makgadikgadi Pans Game Reserve
- E Central Kalahari Game Reserve
- F Kutse Game Reserve
- G Mabuasehube Game Reserve
- H Gemsbok National Park
- I Kalahari Gemsbok National Park
- J Hwange National Park
- K Kazuma Pan National Park
- L Zambesi National Park

Veterinary Cordon Fences

- 1 (1954) Dibete Cordon Fence
- 2 (1955) Central Ngwato
- 3 (1955) Ngamiland
- 4 (1958) Kuke
- 5 (1968) Shorobe–Chobe
- 6 (1977) Palapye–Sherwood
- 7 (1979) Orapa
- 8 (1979) Vakaranga–Tuli
- 9 (1981) Makoro–Makoba
- 10 (1981) Serule–Limpopo
- 11 (1982) Serule–Thalamabele
- 12 (1982) Vakaranga–Tomasarka
- 13 (1982) Gomare–Shorobe ('Buffalo Fence')
- 14 (1989) Northern Fence

Figure 3.1 Map of study area showing land use types and veterinary fences. White area surrounding Hukuntsi is CGA. From Thomas and Shaw (1991)

4. Methods

Sample areas

The field work was carried out during three months in the dry period, between July and September, 2002. The collecting of insects was carried out by pit fall traps. With 13 transects, the sample consisted of roughly 370 samples in total, trapped for 3 days each, minus some ruined traps, making the total number of trap nights ca 1770. With an average catch of about 110 insects and 13 species per sample point, the total catch comprises of 42 008 insects.

Each of the management areas where sampled in a fashion as similar to one another as possible. The number of transects sampled per land use type was: CGA 4, WMA 4, CCR 2, NP 3. The transects in the different management types were analysed with some randomisation in time. The pans sampled in each area were chosen both by their ability to represent each area, and practical reasons, e.g. their location near a road and that road's possible connection to other pans. The direction of the transects was either due north (6), east (4), west (2) or south (1). In many cases there would be a village or some other obstacle within 5km of the pan, directing us to another heading. Sometimes the direction of a transect would be chosen to save time and fuel. On each occasion, the location of and direction of the transect was set so as it would represent the pan and its distinct features adequately, and not be influenced by distractions, this being for example villages, roads, sand dunes or bore holes.

Design of transects

The traps were set along 2-dimensional transects, 100 metres wide and 5 km long (see figure 4.1 for transect design). The transects were comprised of 24 sampling points where environmental data was collected and un-baited pit fall traps were set (diameter ca 7cm). The exact location of the sampling points were determined by GPS in reference to the first point, which was set randomly at the pan fringe. Sometimes the fringe was not very distinct, as it is a result of both local geology and grazing pressure. At several pans the vegetation closest to the bare pan floor was very patchy and sparse the first 100 meters. A certain amount of subjectivism was certainly present on those occasions. The ambition was to set the start of the transects at the place showing the most distinct change in vegetation cover, at the same time striving to place the transects consistently to each other. The sampling plots were placed at 12 distances from the pan fringe. These were: 0m, 100m, 200m, 300m, 500m, 600m, 1000m, 1100m, 2000m, 2100m, 5000m and 5100m. Each distance was thus represented by 2 sample plots, placed with 100m between them. The shape of the transect thereby resembled a grid of larger "squares", see figure 4.1. The aim with this design was to enable measurement of variation of catches at different scales. The scales available by this method is: land use areas, transects within the same land use area, distance to pan and finally different places or micro habitats 100 m apart, at roughly the same distance to pan. In addition to the un-baited traps at the sample points, 7 dung-baited pit fall traps (diameter ca 30cm) were set at the centre of each transect. These larger, dung baited traps were placed at distances 50m, 150m, 250m, 550m, 1050m, 2051m and 5050m from the pan fringe. The dung-baited traps were set roughly at the middle of the "larger squares" and not exactly determined by GPS, rather they were placed so as to maximize catches. The dung-baited traps were thus not set in sample plots. The location of the traps were marked by coloured tape in addition to the noted GPS-location.

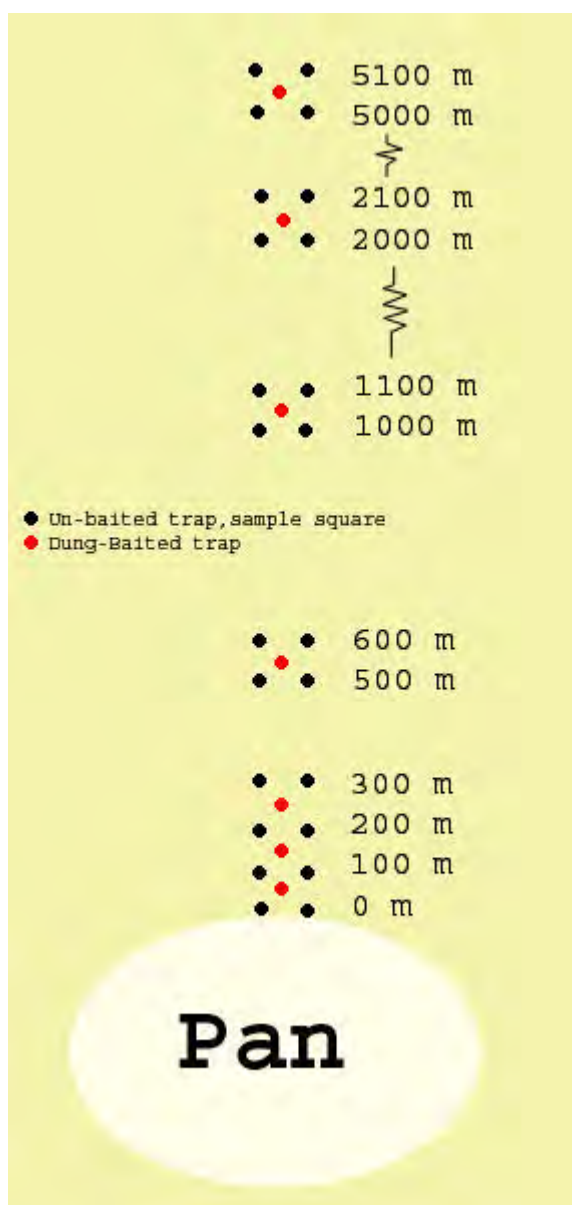


Figure 4.1 Design of transect

Sample plots, design of small and large traps

The 24 sample plots of each transect were quadratic, 1,5m by 1,5m. Within each sample plot, several characteristics were assessed. No environmental data were collected at the baited traps.

Data were collected on:

Soil type: categorised subjectively as pan soil (a clayey loam), sandy pan soil or sand.

Grass cover: Percentage of sample plot covered by standing grass, assessed visually.

Grass height: The average height of grass measured with a ruler to the nearest cm.

Cover of other vegetation: Percentage of sample plot covered by vegetation other than grass. (This category is divided into four height classes, according to at which height the vegetation occurs.) Classes are: 0-0,5m, 0,5-1m, 1-2m and above 2m.

Overall view of vegetation: Rough visual estimate of the density of the vegetation within a ca 100 m radius of the sample plot. Divided into three ordinal classes based on canopy cover and recorded separately for the grass, bush and tree strata.

Litter cover: Percentage of sample plot covered by detached litter except for faeces.

Faeces: Number of faeces droppings. Droppings encompass both large pats from cow and small pellets from e.g. steenbok. Hence animal of origin was also recorded.

Distance from pan: measured by GPS in metres.

At each sample plot, 2 pit fall traps were set which were pooled when collected and henceforth treated as one sample. All traps were set out during one day and checked the following three days. The pit fall traps were filled with about 2cm of water with dish washing liquid for elimination of surface tension and a dash of angostura to make it unappetizing for mammals. Within the same sample plots, 2 Sherman collapsible rodent traps were set as part of a parallel study (Bergström A. 2003). The rodent traps were baited with a mixture of peanut butter, syrup and oatmeal. This paste sometimes attracted ants to the sample area, some of which ended up in the insect traps. Peanut butter loving insects such as ants is therefore probably overrepresented in the catches. This error should be uniform over the whole sampling period since the same amount and type of bait was used every time.

The larger dung-baited traps were buckets of about 10 litres which were dug down in a similar way to the small ones. The soil surface was not connected with the bucket rim as smoothly as was the case with the smaller traps. Although no evidence in support was found, this can have led to an under-representation of smaller insects in the dung-baited traps. The large traps were filled with about 4 cm of the same liquid as the small ones and covered with chicken mesh where fresh cow dung was placed. The mesh had holes large enough for big Scarabaeids to fall through. The cow dung was usually collected fresh the morning of the day the traps were set. Occasionally, when fresh dung could not be obtained due to remoteness of the transect, the dung was kept fresh by adding of water and placing a lid on the storage container. The amount of cow dung used for each trap ranged between 5 dl and 1 litre. When interpreting results from the dung-baited traps, one should keep in mind that there is a possibility that the dung itself contained some insects when it was collected, most notably Staphylinidae. This, combined with the fact that the dung was often not collected at the sample location means that some of the catches may not be representative. Data of Staphylinidae has therefore been omitted from comparisons of transect and management types.

Captured rodents were released at each checking and sometimes caught again. Very few rodents died in the traps and these were removed before any decomposing could begin (checking every day). Any overrepresentation of saproxylic insects in those cases should be insignificant.

The insects were collected on the last day of checking and conserved in 70% ethanol.

Sampling and identification

The samples were processed in a lab where insects from each trap station were ordered into groups of the same morphospecies, with the exception of Isoptera, Arachnids, primitive orders such as Collembola and Thysanoptera, and larvae. For each morphospecies, the taxonomic order was noted. For insects of the order Coleoptera, family name was also noted for the most common families. For Hymenoptera, the family Formicidae was separately noted. Literature used in identification was Holm & Scholtz (1986) and Picker et al. (2002). Each morphospecies was also measured in body size, recorded as length in millimetres from tip of head to end of abdomen, not including antennae, legs, wings or other protruding body parts. When variation in length was observed among one morphospecies within the same sample, length was adopted for statistical analysis as the intermediate value of the extreme lengths.

The respective morphospecies was not uniquely named or treated for every trap since this would have demanded an effort comparable to that of discerning all individuals to unique species. Thus, e.g. morph number 1 of one sample may actually be the same species as morph number 3 in another and so on. Not analysing individuals to species obviously lessen the information and the interpretations possible, but was an unavoidable consequence of the sample size and time available.

Since the traps were checked each day, traps that were ruined during the first or second night could be fixed for the remaining of the sampling time, making the number of trap nights ranging from 0-3. Traps were interfered with by several species including Black backed Jackal, Mongoose, cattle, goats, Spotted Hyena, various birds and sometimes humans. As each sampling point had two traps pooled as one (except for the dung-baited ones), the number of effective trap nights of a sampling point could be e.g. 2.5.

Data analysis

The study covered 13 transects; 4 in CGAs, 4 in WMAs, 3 in NP and 2 in CCRs, named after the pan they started from. Occasionally, traps were ruined or in other ways interfered with by animals and in a few cases humans, so that they could not be included in the study. Of theoretically 403 traps, at the end of the study, 374 (93%) was actually collected and thus available for processing.

Total catch and number of morphospecies for the respective management type were log-transformed and subjected to parametric analysis. GLM ANOVA was used to identify the dependence on these variables on management type. Two-sample t-test were performed to find pairwise differences between the management types in various parameters. Data divided for the respective trap types did not fit the requirements for parametric analysis and were analysed using the non-parametric Kruskal-Wallis method. Trap data were divided into different taxa and differences within taxa between trap types and between management types were analysed using Kruskal-Wallis tests. Correlation of number of morphospecies and number of individuals were tested by Pearson correlation analysis after log-transformation of both variables.

Regression analysis was used to examine the effect of environmental data on trap catch, using the best sub-sets method in Minitab to reveal suitable multiple regression models. Ordinal regression analysis was used to investigate the effect of the environment parameters of “overall view” on trap data. Nominal regression analysis was performed to study the possible effect of soil type on trap data.

In all graphs where confidence intervals are shown, they were computed as $\pm = t_{0,05;n-1} \sqrt{\frac{s^2}{n}}$.

Confidence intervals computed by this formula are inserted in figures 5.8 and 5.10 for comparison with the Kruskal-Wallis tests presented in tables 5.4 and 5.5 although data do not meet the requirements of parametric analysis. Confidence intervals within these figures should be viewed with that in mind.

All values of number of individuals are weighted for differences in number of trap nights unless otherwise is stated. While the number of individuals per trap can be assumed adopting a linear equation with time as the denominator, number of species is more likely to show a logarithmic function over time, eventually reaching the asymptote indicating the total species amount of the area. Since the number of trap nights only varied from 0.5 to 3, no credible

function could be fitted to the data. Adding to this, the slope of the curve of morphospecies vs. sample time was remarkably flat. Numbers of morphospecies are therefore not weighted for difference in trap time.

5. Results

Summary of catches

A presentation of the study's total catch is shown in figure 5.1. The total number of sampled insects was 42008, of which 46% are ants. Other prominent orders are Diptera (21%) and Coleoptera (20%). Among ground dwelling insects, apart from ants, the dominance of beetles is evident. Furthermore, approximately 97% of all Coleoptera in the un-baited traps, and 49% in the dung-baited traps were of the family Tenebrionidae, showing their aptitude for the dry sandveld habitat. Individuals of the order Diptera were almost exclusively flies.

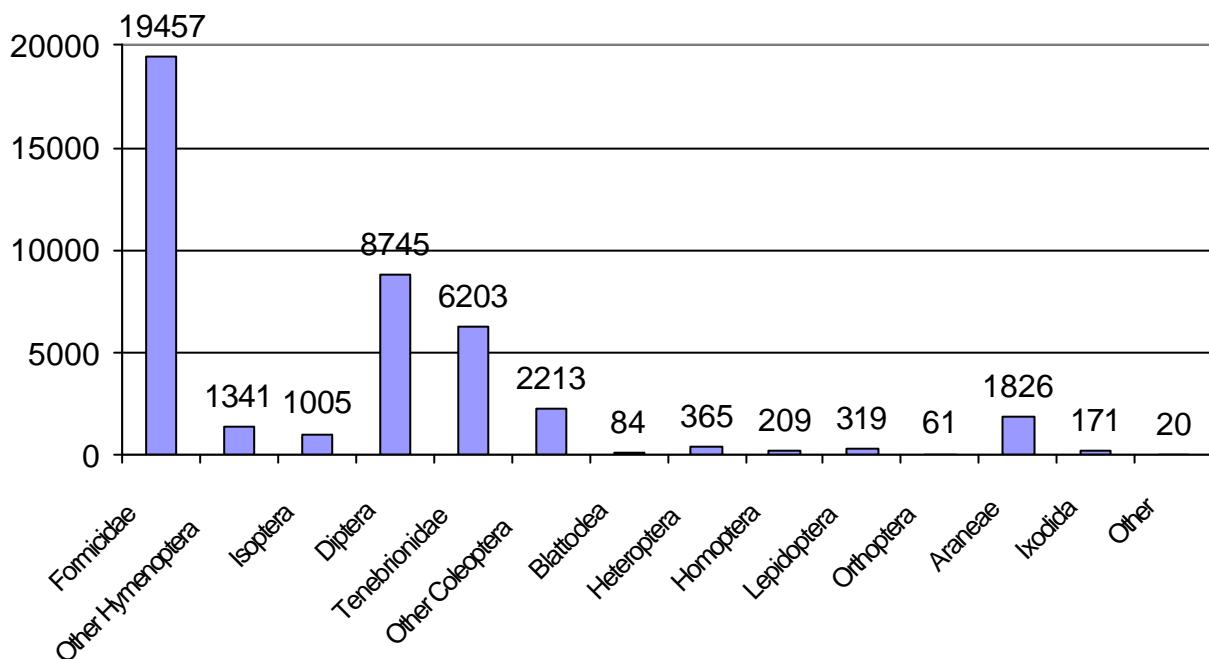


Figure 5.1 Total catch of the study. Numbers not weighted for difference in trap time.

Species richness

The number of individuals caught in every trap strongly correlates with the number of morphospecies found in the same ($p < 0,001$). Pearson correlation coefficient is 0,603, see figure 5.2.

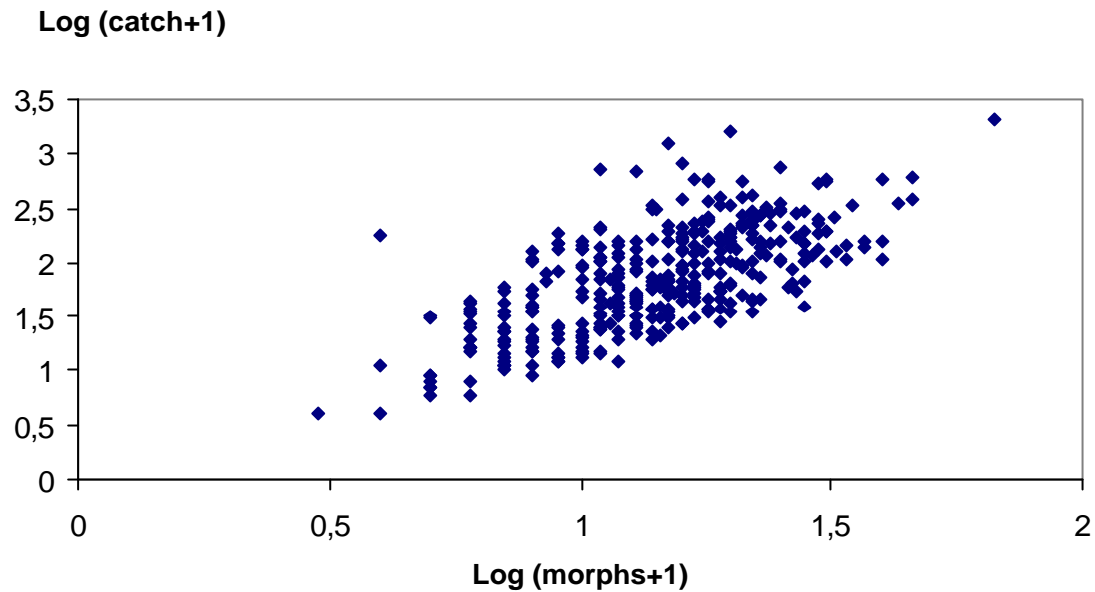


Figure 5.2 Catch versus number of morphospecies. Correlation coefficient 0,603 (Pearson correlation. $P < 0,001$)

The frequency of morphospecies in samples varied between the different taxa. Almost all samples from unbaited traps (95%) had at least one morphospecies of ant, and a few samples (<1%) had as much as 10 morphospecies. Other taxa with high frequency are Tenebrionidae and Diptera, whereas Ixodida, Orthoptera and Blattodea were found in < 15% of the samples (tables 5.1) In the dung baited traps Tenebrionidae, other Coleoptera and Diptera were found in >90 % of the samples (table 5.2). The average number of morphospecies of all traps was 112. Note that apart from baits, the trap types also differed in size

Table 5.1 Percentage of un-baited traps containing at least respective number of morphospecies. N=293 *Not separated into different morphospecies.

Morph number	1	2	3	4	5	6	7	8	9	10	11
~Formicidae	95%	82%	68%	48%	34%	20%	9%	4%	2%	<1%	-
Other Hymenoptera	41%	11%	3%	<1%	<1%	<1%	<1%	-	-	-	-
Isoptera*	21%	-	-	-	-	-	-	-	-	-	-
Diptera	78%	50%	24%	13%	8%	3%	1%	-	-	-	-
~Tenebrionidae	86%	57%	31%	17%	5%	2%	<1%	-	-	-	-
Other Coleoptera	28%	7%	2%	1%	<1%	<1%	-	-	-	-	-
Blattodea	11%	1%	1%	-	-	-	-	-	-	-	-
Heteroptera	38%	12%	4%	2%	1%	<1%	-	-	-	-	-
Homoptera	25%	6%	1%	-	-	-	-	-	-	-	-
Lepidoptera	37%	5%	-	-	-	-	-	-	-	-	-
Orthoptera	12%	1%	-	-	-	-	-	-	-	-	-
Araneae*	79%	-	-	-	-	-	-	-	-	-	-
Ixodida*	15%	-	-	-	-	-	-	-	-	-	-
Other*	2%	-	-	-	-	-	-	-	-	-	-

Table 5.2 Percentage of dung-baited traps containing at least respective number of morphospecies . N=80 *
Not separated into different morphospecies .

Morph number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
~Formicidae	89%	75%	54%	35%	24%	11%	5%	1%	-	-	-	-	-	-	-
Other Hymenoptera	58%	31%	10%	4%	-	-	-	-	-	-	-	-	-	-	-
Diptera	91%	81%	73%	61%	45%	33%	26%	19%	14%	8%	3%	1%	1%	1%	-
Isoptera*	30%	-	-	-	-	-	-	-	-	-	-	-	-	-	-
~Tenebrionidae	99%	78%	43%	21%	10%	5%	3%	1%	1%	-	-	-	-	-	-
Other Coleoptera	94%	79%	61%	45%	33%	25%	18%	14%	9%	1%	-	-	-	-	-
Blattodea	16%	3%	1%	-	-	-	-	-	-	-	-	-	-	-	-
Heteroptera	48%	15%	4%	3%	-	-	-	-	-	-	-	-	-	-	-
Homoptera	48%	13%	9%	3%	-	-	-	-	-	-	-	-	-	-	-
Lepidoptera	43%	10%	3%	1%	1%	-	-	-	-	-	-	-	-	-	-
Orthoptera	20%	3%	-	-	-	-	-	-	-	-	-	-	-	-	-
Araneae*	80%	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ixodida*	18%	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Other*	1%	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Comparison of trap types

The dung-baited traps showed a slight tendency to higher catches than the un-baited ones, see figure 5.3, however the difference was not significant ($P=0,067$). The mean number of morphospecies caught in the respective trap types differed significantly, the dung-baited traps catching more species, see figure 5.4. In terms of the taxonomic origin of the catch, the number of insects and number of morphospecies are distributed over the taxa in a roughly similar way for both trap types, see figure 5.5 and 5.6. The differences in abundance and morphospecies richness between trap types are covered in table 5.3.

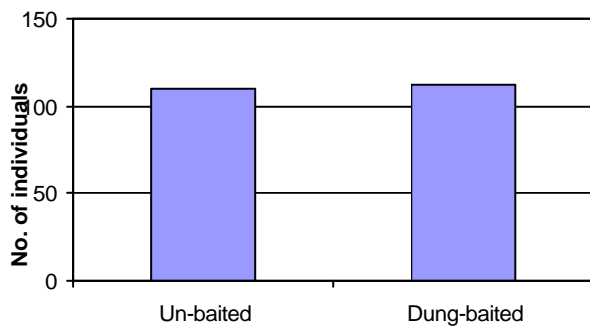


Figure 5.3 Mean catch for the different trap types. No significant difference ($p=0,067$, Kruskal-Wallis). Numbers not weighted for difference in trap time.

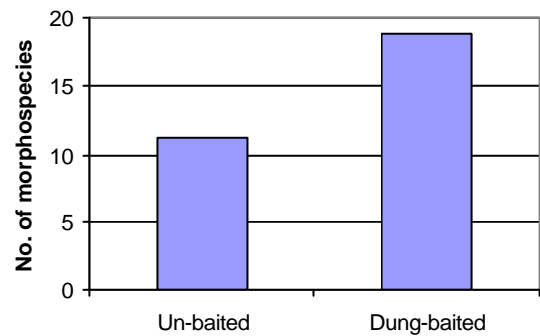


Figure 5.4 Mean numbers of morphospecies per trap for the different traps types. The difference is significant ($p<0,001$ Kruskal-Wallis).

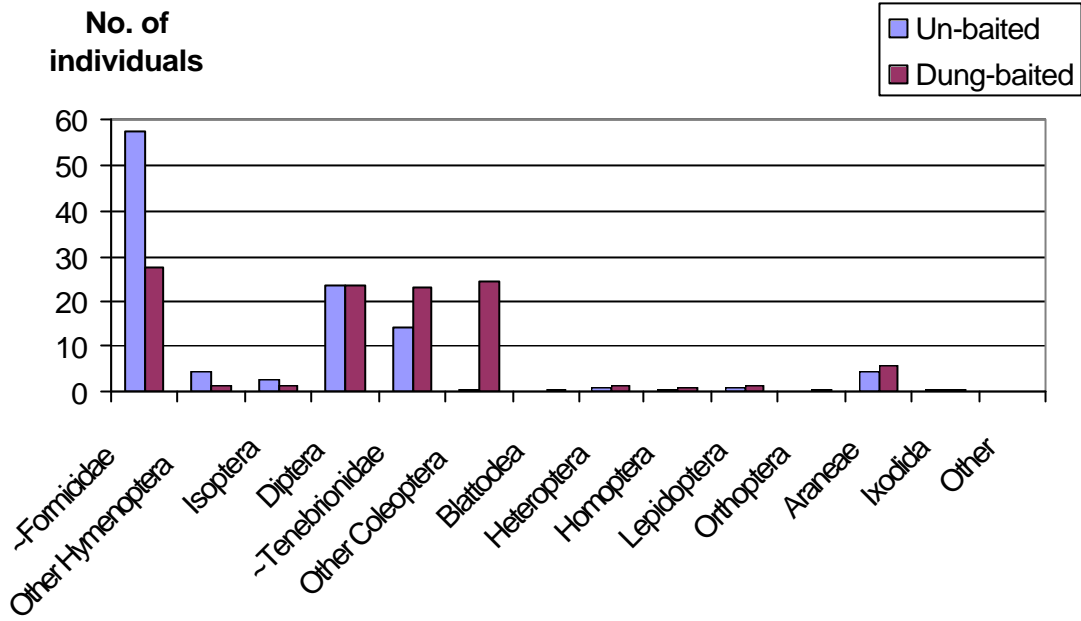


Figure 5.5 Mean numbers of individuals per trap of the different trap types, divided into major taxa. Numbers not weighted for difference in trap time. (Baited traps catch of Diptera slightly higher than un-baited traps)

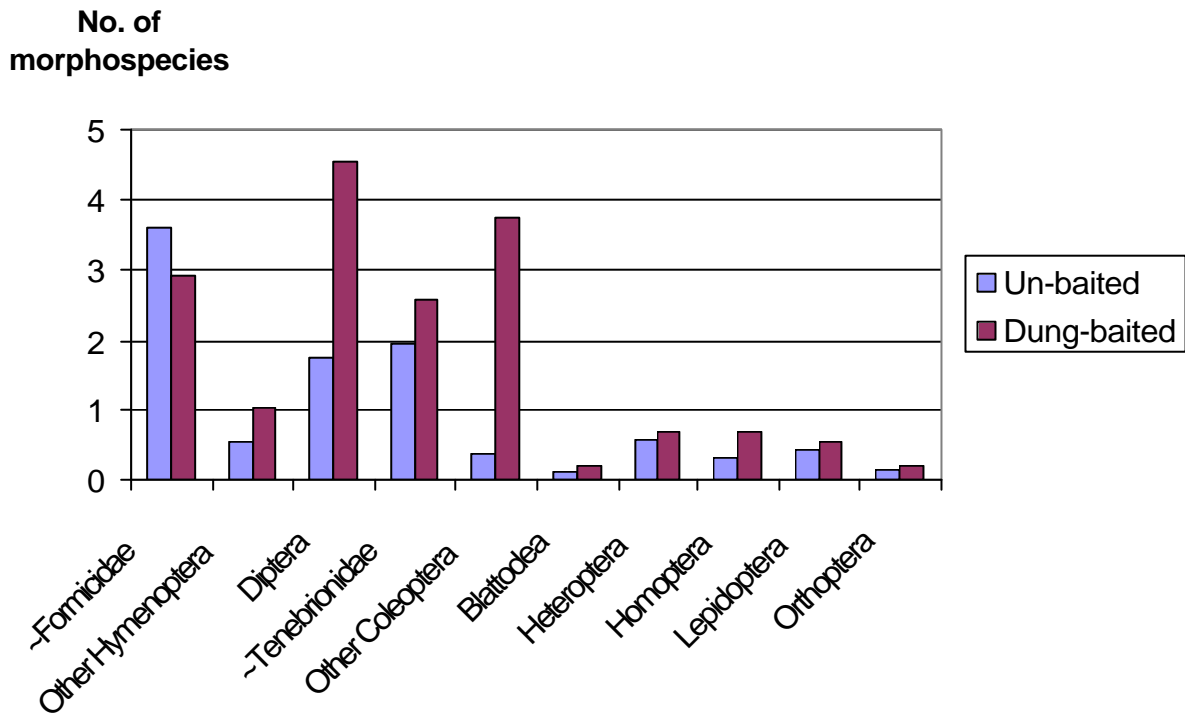


Figure 5.6 Mean number of morphospecies per trap divided into major taxa.

Table 5.3 Differences in mean abundance and mean number of morphospecies between un-baited and dung-baited traps. P-values from Kruskal-Wallis tests. Significant p-values in bold print.

Taxa	Abundance P-value (adjusted for ties)	Morphospecies P-value (adjusted for ties)
~Formicidae	0,030	0,012
Other hymenoptera	<0,001	<0,001
Isoptera	0,147	Not measured
Diptera	0,004	<0,001
~Tenebrionidae	0,001	0,001
Other coleoptera	<0,001	<0,001
Blattodea	0,152	0,085
Heteroptera	0,149	0,155
Homoptera	<0,001	<0,001
Lepidoptera	0,106	0,273
Orthoptera	0,050	0,105
Araneae	0,139	Not measured
Ixodida	0,579	Not measured
Other	0,526	Not measured

Comparison of management types

The size of the catches clearly suggests that there is a difference in insect densities between the different land-use types. Figure 5.7 shows the mean total catch per sample of each land use type. With the exception of CGA to WMA, all land-use types differ significantly from one another. The Commercial Cattle Ranches gave the largest catches by far, with almost 6 times more insects than national parks and almost 3 times more than in community grazing areas and wildlife management areas. The National Parks had roughly half the catches of the Communal Grazing Areas and Wildlife Management Areas.

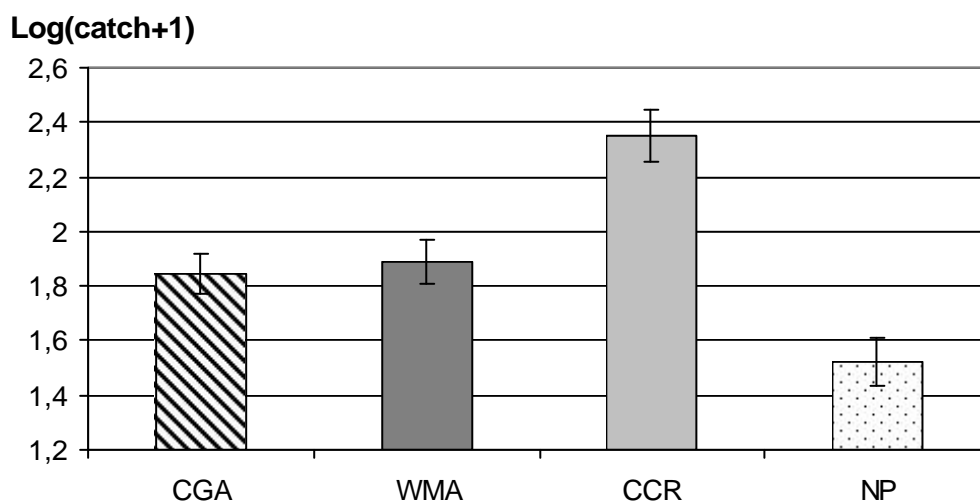


Figure 5.7 Average catch per trap and management area type. 95% confidence intervals inserted. GLM ANOVA show significant differences ($p < 0,001$). Pair wise comparisons by two sample T-tests indicate significant differences ($p < 0,001$) between all management types except CGA vs. WMA ($p = 0,429$).

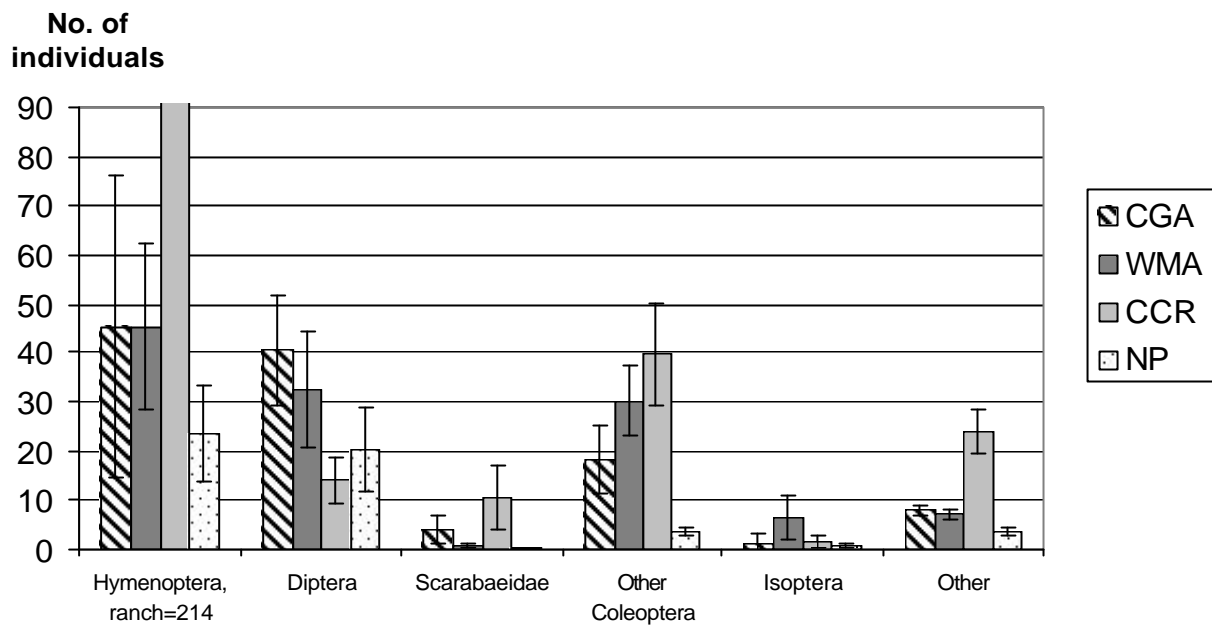


Figure 5.8 Mean abundance per trap of some major taxa and management type. 95% confidence intervals inserted. Note, data not parametric.

Table 5.4 Kruskal-Wallis test for differences in mean abundance of different taxa between different land use types. $P < 0,05 = *$, $p < 0,01 = **$, $p < 0,001 = ***$. All p-values are adjusted for ties.

	CGA-WMA	CGA-CCR	CGA-NP	WMA-CCR	WMA-NP	CCR-NP
Hymenoptera	0,049*	<0,001***	0,547	<0,001***	0,008**	<0,001***
Diptera	<0,001***	0,011*	<0,001***	0,248	0,313	0,037*
Scarabaeidae	0,153	0,547	0,071	0,132	0,588	0,095
Other Coleoptera	<0,001***	<0,001***	<0,001***	0,049*	<0,001***	<0,001***
Isoptera	<0,001***	<0,001***	0,024*	0,788	0,046*	0,132
Other	0,224	<0,001***	<0,001***	<0,001***	<0,001***	<0,001***
Totalt	0,457	<0,001***	<0,001***	<0,001***	<0,001***	<0,001***

The absence of significant differences in scarabaeids is probably a result of the both trap types being pooled in this comparison. Scarabaeidae were almost exclusively caught in the dung-baited traps, resulting in skewed data in this comparison. Since Kruskal-Wallis tests use median values, the similarities between land use types are probably exaggerated in this particular comparison.

Log(catch+1)

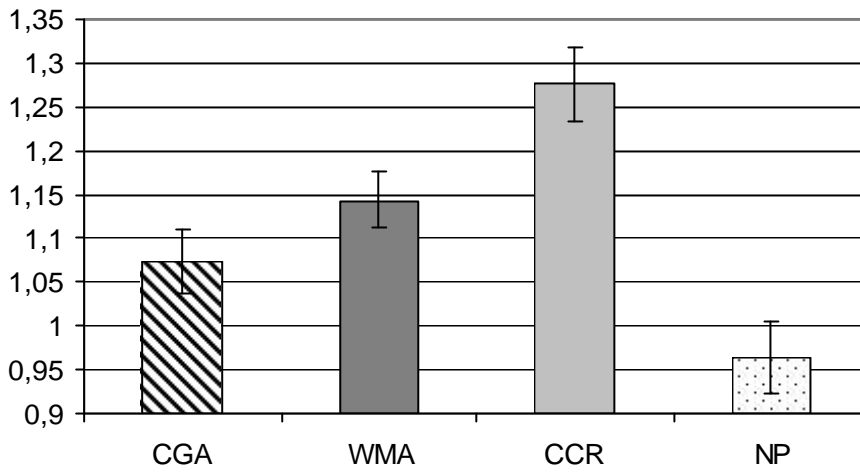


Figure 5.9 Average numbers of morphospecies per sample and management type. 95% confidence intervals inserted. GLM ANOVA show significant differences ($p < 0,001$). Pair wise comparisons by two sample t-tests indicate significant differences between all management types. CGA vs. WMA $p = 0,005$, all other comparisons $p < 0,001$.

No. of individuals

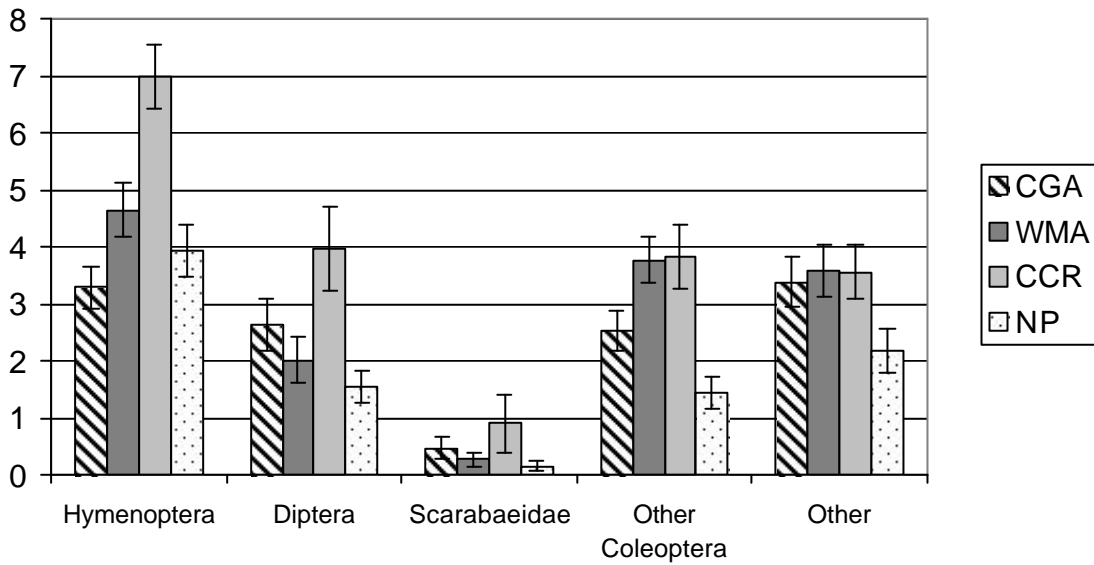


Figure 5.10 Average numbers of morphospecies of major taxa and land use type. 95% confidence intervals inserted. Note, data not parametric.

Table 5.5 Kruskal-Wallis test for differences in mean number of morphospecies between different land use types. $P < 0,05 = *$, $p < 0,01 = **$, $p < 0,001 = ***$. Non significant p-values listed. All p-values are adjusted for ties.

	CGA-WMA	CGA-CCR	CGA-NP	WMA-CCR	WMA-NP	CCR-NP
Hymenoptera	<0,001***	<0,001***	0,043*	<0,001***	0,050*	<0,001***
Diptera	0,025*	<0,001***	0,001**	<0,001***	0,274	<0,001***
Scarabaeidae	0,207	0,582	0,098	0,134	0,651	0,098
Other Coleoptera	<0,001***	<0,001***	<0,001***	0,964	<0,001***	<0,001***
Other	0,489	0,149	<0,001***	0,527	<0,001***	<0,001***

Figure 5.10 shows the average number of morphospecies per sample for major taxonomic groups. 95% confidence intervals are calculated as for parametric values even though data does not technically meet these standards. Table 5.5 shows non-parametric results of comparisons between the same taxonomic groups. Kruskal-Wallis test seems more powerful than parametric tests and results in more comparisons showing significant differences. As in table 5.4, the scarabaeid comparisons should be viewed with a grain of salt.

Comparison of transects

Figure 5.11 gives a summary of mean catches from all transects in the study. Worth mentioning is that the Kwakai and Bohelabhato pans, 17-LJ and Mutton-chop pans and Khiding and Mpaathlutwa pans are located fairly close to one another (ca 12-25km), making their environments relatively similar. Values for these transects seem to be closer positioned than others. Note also that the y-axis is logarithmic and starting at the value 1, giving the graph a truncated shape. Figure 5.12 gives the corresponding summary of average number of morphospecies for all transects.

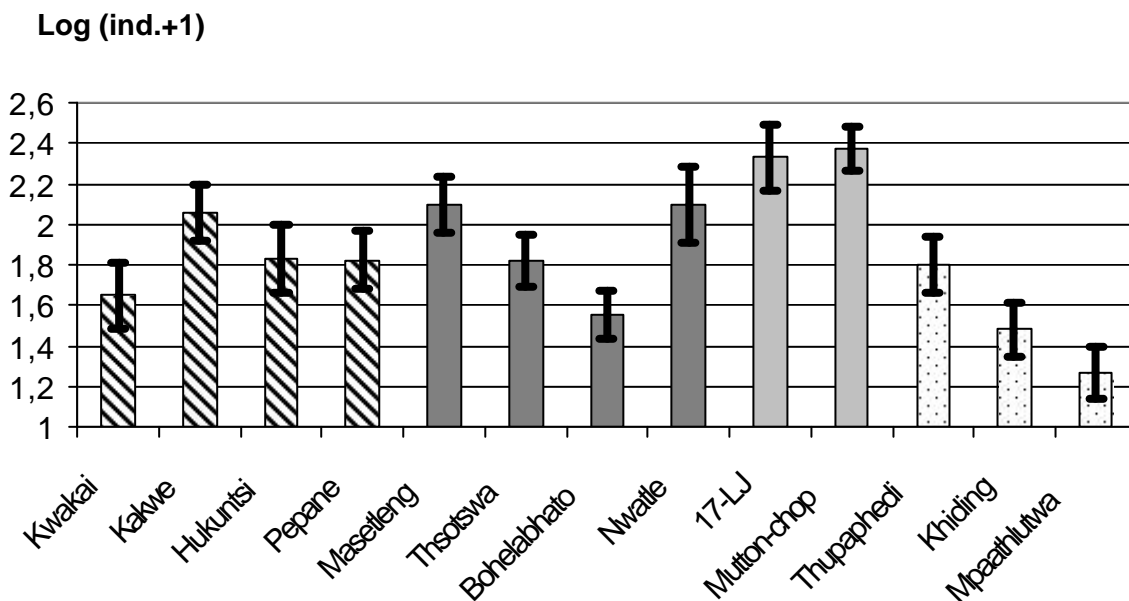


Figure 5.11 Mean catch per trap and transect. 95% confidence intervals inserted. Striped bars are CGAs, dark grey WMAs, light grey CCRs and dotted NPs.

Log (spec. +1)

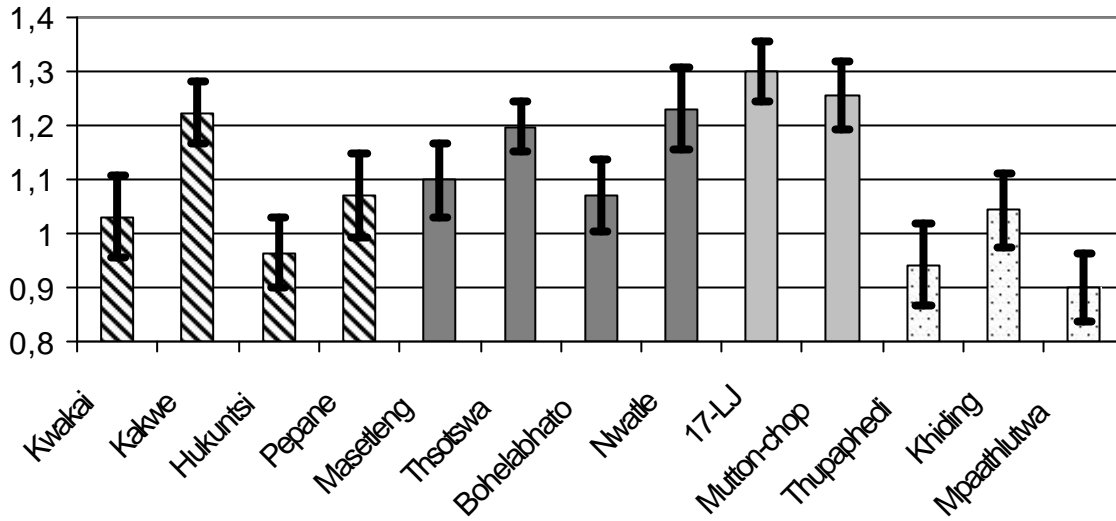


Figure 5.12 Mean numbers of morphospecies per trap. 95% confidence intervals inserted. Striped transects are within CGAs, dark grey WMAs, light grey are CCRs and national parks are dotted.

Species richness

Figure 5.13 show the average number of insects divided by number of morphospecies for the respective management types. The pattern is roughly that the higher abundance of insects, the higher ratio of abundance/number of species. The CGAs showing a slightly higher ratio than the WMAs is consistent with the fact that the WMAs had proportionally more species than CGAs (see figures 5.7 and 5.9). The pattern is clearly visible for transects as well, as shown in figure 5.14 with its close resemblance to figure 5.11.

**Abundance/
No. of species**

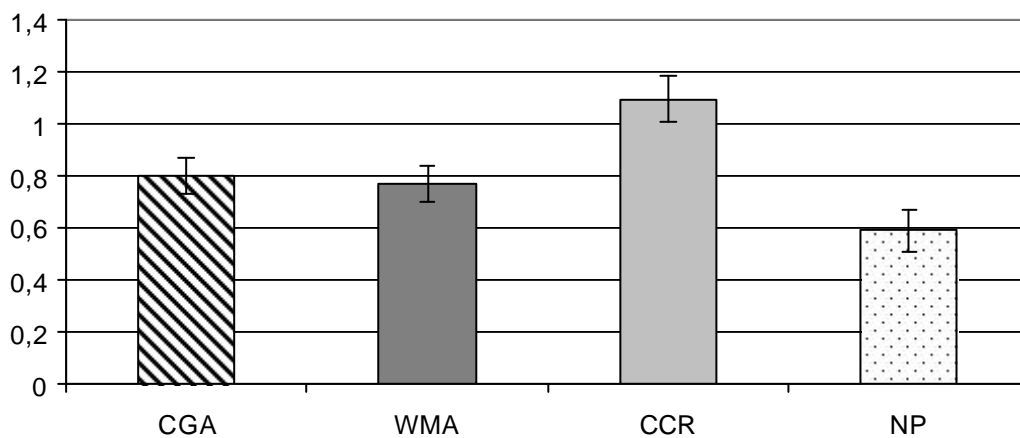


Figure 5.13 Number of insects divided by number of morphospecies, mean values for management types. 95% confidence intervals inserted.

**Abundance/No.
of species**

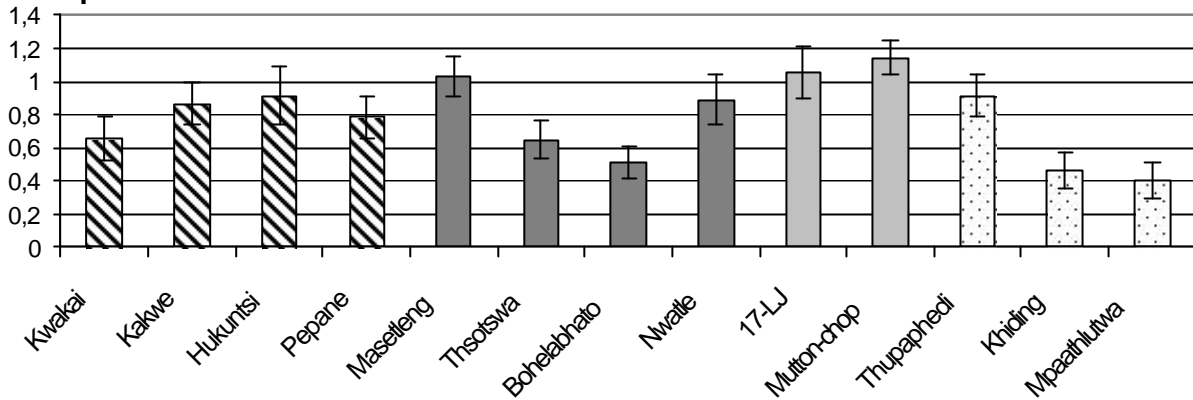


Figure 5.14 Number of insects divided by number of morphospecies, mean values for transects. 95% confidence intervals inserted.

Environmental factors

A total of 13 environmental factors for each sample plot were estimated. These are covered in methods above and include distance to pan, number of faeces pellets, cover of litter, soil type and various vegetation qualities. Trap data were compared to these factors through regression analysis. In addition to that, rodent trap data from the same sample plots (Bergström A., 2003) was compared to insect catches. No clear correlation between any of these factors and insect catch was discovered. Due to the large sample size, p-values were in several cases highly significant but the variation in insect catches was always poorly explained by environmental data. The best predictor for insect catch that was found, is percentage of grass cover, with $R^2=0,037$ (adjusted value). The best combination of environmental factors gave an adjusted R^2 -value of 0,088, which is still very low.

Spatial scales and gradients

As mentioned above, the setup of the study and shape of transects were designed so as to facilitate comparisons on several spatial scales. From small to large; 1) microhabitats approximately 100 metres apart at roughly the same distance to the pan fringe, 2) sites within the same transect with different distances to the pan ranging from 100 m to 5 km, 3) different transects within the same management type with several tens of kilometres between them and 4) larger geographically distinct areas with different types of management. The longest distance between traps in this study was approximately 260 km, between the farthest north in the Ncojane ranches and to the farthest south in the Mabuasehube section of the Kgalagadi Trans frontier Park.

Generally, insect abundance showed large variations on all investigated scales. On the two largest scales - management types and individual transects – significant differences in insect abundance and species richness were found and are presented above. Relating to the two smallest scales, figure 5.15 shows a summary of mean number of insects caught at different distance to the respective pans. Results of regression analysis for the relationships between

catch and distance to pan vary between the different management types and are listed in the graph. When all samples were pooled, regression analysis of total catch vs. distance to pan as well as morphospecies amount vs. distance to pan give non-significant values and adjusted R^2 -values very close to zero. Regression analysis of *mean* number of morphospecies per distance vs. distance to pan is also non-significant with adjusted R^2 -values very close to zero. Regression analysis of *mean* abundance per distance vs. distance to pan is non-significant with adjusted R^2 -values of 0,023.

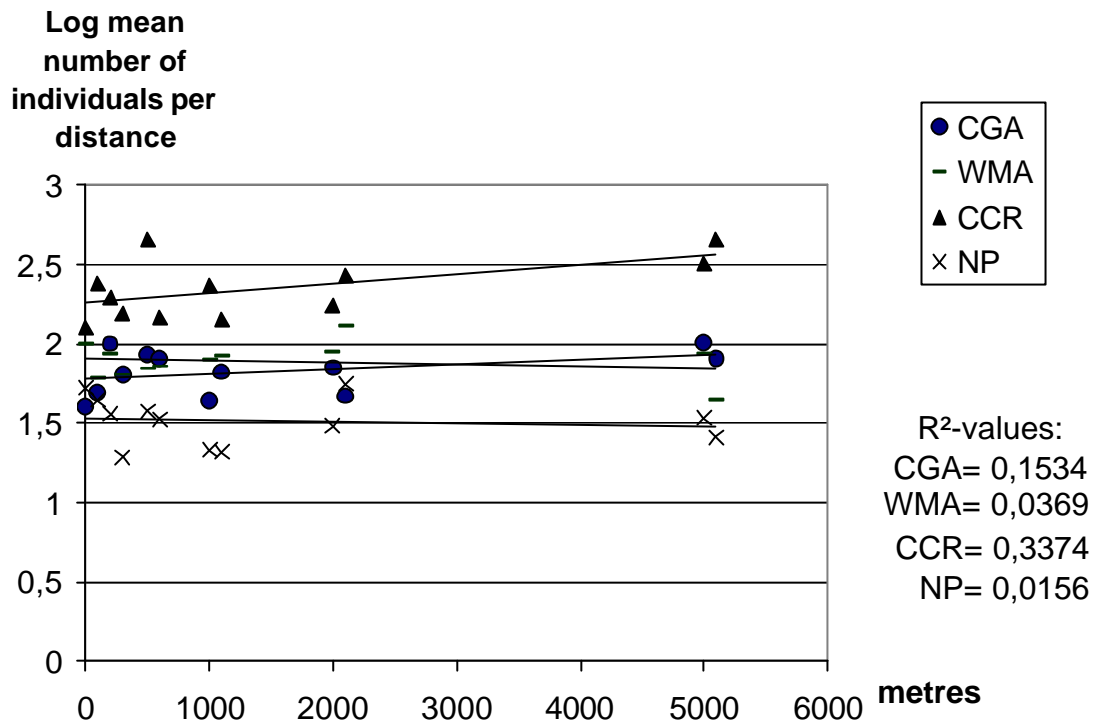
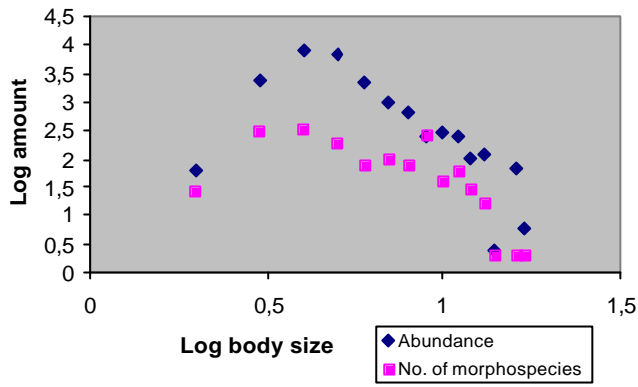


Figure 5.15 Mean numbers of individuals per distance to pan.

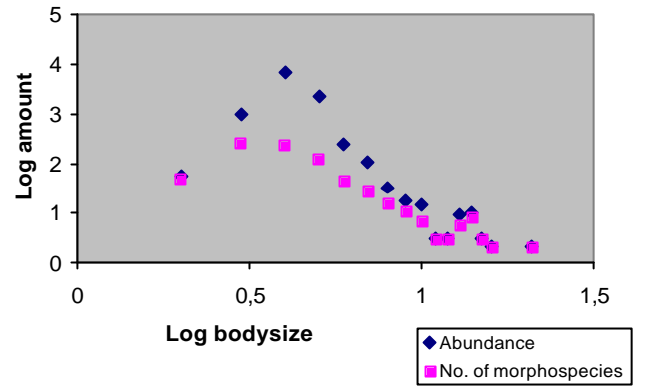
Abundance and species richness in relation to body size

Body sizes were measured for all morphospecies during identification. The measurements were recorded as average length in millimetres. Figure 5.16 show the relationships of abundance and morphospecies richness to body size for the three most abundant taxonomic groups of the study, Formicidae, Diptera and Tenebrionidae. Since morphospecies were not linked between different traps, the same species is very likely to be accounted for several times. Thus, morphospecies richness in figure 5.16 should be viewed only as an approximation of true species richness. The relation between abundance to body size and morphospecies richness to body size resemble a unimodal pattern for all three most abundant taxonomic groups in the study. The different taxa were sampled simultaneously and the apex of their curves are placed slightly apart suggesting that the patterns can not wholly be interpreted as a result of a sampling being biased towards larger individuals. Figure 5.17 shows the relationship between the abundance/morphospecies ratio in relation to body size and is a rough estimate at the mean species density at different body sizes.

a)



b)



c)

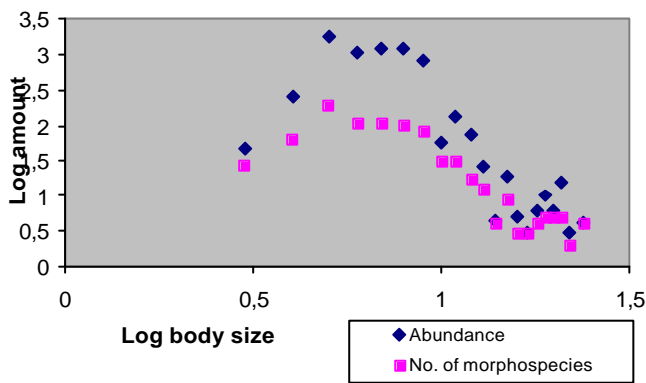


Figure 5.16 Abundance and number of morphospecies vs. body size for a) Formicidae, b) Diptera and c) Tenebrionidae

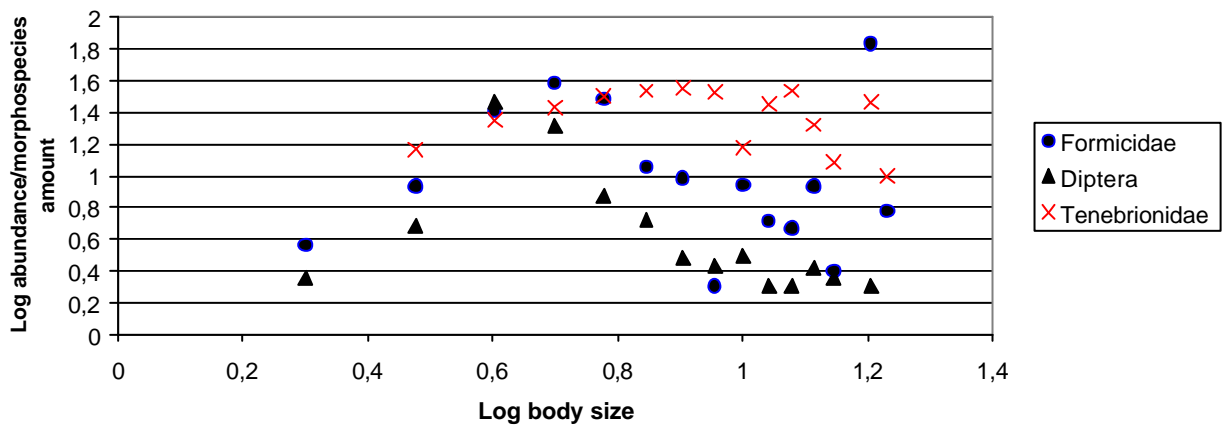


Figure 5.17 Abundance/morphospecies amount ratio vs. body size

Relevant sample sizes

Table 5.6 gives an estimate of the sample sizes required to make assertions about insect abundance in the area. The requirements are based on the assumption that the variances found in this study are accurate and that abundance of insects stay more or less the same. Values are therefore merely a rough guide and future sample sizes ought to be set with ample safety margins.

Table 5.6. Sample sizes of current study. 'Actual N' is the sample size available in this study for comparisons between management types. 'N*' is the sample size required to yield a 95% confidence interval in mean number of insects that is smaller than half of the difference to the management type of nearest value, i.e. an estimation of how large sample size is required to show differences to all other management types in insect abundance. 'N**' is the sample size required to yield 95% confidence intervals in mean number of insects smaller than 5% of the mean insect abundance for the respective management type.

	Sample sizes		
	Actual N	N*	N**
CGA	118	1395	82
WMA	111	1409	79
CCR	51	8	31
NP	88	25	114

6. Discussion

Abundance and species richness

The total catch of this study, with its roughly 370 sampling points, paints an image of the south western Kalahari insect community as dominated by the three insect groups; Formicidae, Diptera and Tenebrionidae. When comparing the proportions of specific taxa one must keep in mind that the sampling was performed exclusively during the dry season, when water and moist vegetation is particularly scarce. Species and groups specialized in extremely dry habitats may not be as dominant in the summer when groups associated with fresh vegetation e.g. Homoptera, Hemiptera and Orthoptera is likely to show a larger presence.

The absence of insects with sucking mouthparts, associated with fresh vegetation, is noticeable in relation to other studies in grassland environments (Cagnolo et al. 2002; Haddad et al. 2000; Kreuss et al. 2002). Compared to studies in less arid environments, the insect community appears "skewed" to groups with special skill for coping with water stress, e.g. low transpiration and ability to cope with dehydration by various osmoregulatory functions (Cloudsley-Thompson 2001). Even so, it is important to keep in mind that pit fall traps, used in this study, are a measurement of activity on the ground surface and not a true measurement of actual occurrence within the whole area. Thus, these results ought not to be directly compared to studies with other sampling techniques. To the comparisons defence, however, it can be said that in the whole area, vegetation was sparse and dry, mostly consisting of dry standing grass, limiting the opportunities for insects dwelling in vegetation and/or reliant on repeated water intake. Visual observations of Hemiptera and Orthoptera were also scarce (significant groups in other studies, e.g. Cagnolo et al. 2002).

Hymenopterans stand for the bulk of species in the un-baited traps, with ants being the dominating constituent, as seen in table 5.1. Morphospecies abundance of Formicidae was practically the same in dung-baited traps, indicating that the dominance in species richness by Formicidae is a fairly good estimate of the true species composition (table 5.2). Second to

Formicidae, Diptera and Tenebrionidae share the place as most diverse taxa of the study. If all Coleoptera species is viewed as one group, they constitute the second most diverse taxon.

As seen in figure 5.2, species richness is clearly correlated with insect abundance. Patterns of insect abundance per management type (figure 5.7) also resembled that of species richness per management type (figure 5.9). This is compatible with the general correlation between sample size and species richness (Ricklefs 1997) as well as with results from other studies of insects in a grassland milieu (Kreuss et al. 2002, Siemann et al. 1999). However, variations of the general relationship between abundance and diversity were revealed when splitting up the results in different categories. First of all, some of the variation can be attributed to the fact that the community structure was not the same for every trap. The relative abundance of different species quite naturally differs slightly among traps. Since the various species have different densities, the overall ratio of individuals/morphospecies per trap varies accordingly. This is simply a matter of natural variation.

Furthermore, dung-baited traps had a higher average species richness than the un-baited traps ($p < 0,001$, figure 5.4), while in the case of average individuals per trap, the trap types did not differ significantly ($p = 0,067$). This could be interpreted as the dung-baited traps generally attracting rarer species than the un-baited ones (with the un-baited traps - at least in theory - representing an un-biased sample). At first glance, Chi-square test of the mean species densities for baited traps in comparison to un-baited traps confirm this, giving significant test values ($p < 0,001$). However, the result of the test is highly dependent on which taxonomic groups are included. For example, if the family Formicidae is omitted from the test, the differences is no longer significant ($p = 0,058$). The reason for why the omission of Formicidae might be prudent in this case is the proximity of the un-baited traps to the rodent traps, containing peanut butter (described in methods). As peanut butter visibly attracted ants to these traps, it is probable that the individuals/morphospecies ratio is misrepresented for this group. Ants typically live in large colonies and tend to aggregate collectively around various resources. Ants found in un-baited traps cannot therefore be seen as representing a natural state. Furthermore, with ants out of the picture, the only insect group with significantly lower individuals/morphospecies ratio in the baited traps compared to un-baited ones are Diptera. This indicates that fresh cow dung has a slight tendency to attract rarer fly species, compared to un-baited (note, water-baited). This could point at different strategies among fly species e.g. that less abundant species (due to poor competitive ability) compensates this disadvantage with wider dispersal patterns. Again, this cannot be said for all taxa or even for insects on average for reasons already mentioned.

The significant differences in Diptera abundance between trap types (table 5.3) should be viewed with the statistical method in mind. The trap types do not differ much in mean values of Diptera abundance while they do differ highly in median values. In the un-baited traps, the distribution of Diptera abundance is highly skewed to the left, with a few very large observations, whereas in the dung-baited ones, the abundance distribution more closely resembles a normal distribution. This explains the similarities in mean numbers (shown in figure 5.5.) despite large differences in median value (used in Kruskal-wallis analysis).

On a less equivocal note, dung-baited traps seem to attract Coleoptera generally and Scarabaeidae and Staphylinidae especially. These groups together dominated the catch of the dung-baited traps both by amount and species richness on a scale they did not in the un-baited ones. Formicidae unconsidered, dung-baited traps had approximately 60% larger total catch than the un-baited ones, while the corresponding figure for all Coleoptera is approximately

220%. On the whole, this highlights the dung-specialized species' strategies as ones of movement and resource preemption (Doubt 1991), in contrast to more stationary generalists'.

Comparisons between land use types

The results of this study indicate that, in the dry period in southern Kalahari, there are significant differences in insect abundance between areas of different land management ($p < 0,001$). Two sample T-tests showed, that there is significant difference in insect abundance between all the land use types investigated ($p < 0,001$), except between the WMAs and CGAs where no significant difference was found ($p = 0,429$). Average insect density varied among land use types accordingly: Commercial Cattle Ranches > Wildlife Management Areas > Community Grazing Areas > National parks. This is *not* consistent with the common inverse relationship between anthropogenic disturbance and wildlife abundance recorded in other insect surveys in grassland environments (Cagnolo et al. 2002, Kreuss et al. 2001). Nor with recent studies of mammals in the same area (Wallgren 2001, Granlund 2001, Viio 2003), indeed at the exact same locations (Bergström A. 2003). Analysis of simultaneously acquired rodent trap data by Bergström A. (2003) show the highest abundances in NP followed by WMA, CGA and CCRs, i.e. roughly the reversed order to that found in this study. What most strikingly differ between national parks and fenced cattle ranches is the amount of large herbivores present (within ranches in the form of cattle). Insect abundance therefore seems to be associated with large herbivores.

In contrast to higher animals, to my knowledge insects are not likely to adapt their lives to human presence in order to escape predation or in other ways be affected by human activity as such. Rather, their occurrence seems mainly to be governed by the availability of suitable habitats and resource abundance (Holland et al. 1999). This suggests that livestock (specifically cattle) provides important resources and/or microhabitats for insects. This would mean that the bulk of the insects caught are saprophagous in general or specifically coprophagous. This is not far fetched considering the severe lack of water and fresh vegetation in the dry period, limiting other food sources.

What speaks against such a straightforward interpretation however is the fact that CGAs have much higher livestock densities than WMAs (Viio 2003). According to the logic applied above, CGAs should show higher insect abundance than WMAs and have higher species richness (since species richness is correlated to abundance, see discussion above). Contrary to this, and as can be seen in figures 5.7 and 5.9, WMAs have both a tendency to higher insect abundances (not significant) and higher species richness ($p = 0,005$) than CGAs. What might explain this relationship, and support the hypothesis presented above, is the trampling effects caused by dense cattle herds, present at several of the CGA pans featured in the study. The hypothesis should thereby be that the WMAs had increased amounts of insects, compared to the natural state of national parks, due to the small but nevertheless present groups of livestock or by livestock occupying bordering CGA areas, while not suffering the negative effect of trampling. Although this is a possibility, it appears a bit contrived and is not supported by environmental data. In addition, trampling in the commercial ranches is likely to be as severe or worse as in the CGAs. Thus, the reasons for the observed abundance and species richness distributions among management types remains not fully explained. It is possible that some undetected factor govern insect occurrence.

Spatial scales

A common feature of insects is variable distribution patterns (Holland et al. 1999). This can be attributed to unevenly distributed resources or habitats, or the relatively high growth rate of insects quickly amplifying random variation. Further, insect variability can be the result of naturally erratic or stochastic population dynamics. Generally, animals of smaller size should also be able to occupy larger areas in relation to their body size and their variation should therefore be measurable at a wider range of spatial scales than with larger animals. Concerning resource distribution of the study area, rainfall distribution can be quite patchy and variable (Pike 1972), at the same time essential for insect communities, possibly contributing to naturally heterogenic distribution patterns.

This leads to a question relevant to this study; At what scales is distribution governed by the environmental factors of focus in this study (e.g. management) and at what scales is distribution a result of natural heterogeneity?

For the scales within transects - distance to pan and microhabitats at roughly the same distance to pan - variation was high and no general pattern was discernable. Figure 5.15 reveal a slight positive correlation between distance to pan and insect abundance in the CCRs. However, these two transects were located relatively close to each other and extended towards the same point, opening for the interpretation that the trend is influenced by local variation. The graph shows that variation in mean abundance is often higher among microhabitats than among different distances to pan fringe. Generally, there were very small correlations between distance to pan and insect catch in regression analysis. This means that for distances at least up to 5 km, possible influence by pans cannot be distinguished from “background” heterogeneity. Even Isoptera showed remarkably low correlation to distance to pan, possibly because of low sample numbers for that taxon.

On the next scale, that of different transects within the same management type, variation is high enough between some transects to generate significant values with ANOVA. Variation among the transects within the same management type indicate that insect occurrence is not likely to be homogenous within these political demarcations of land use. However, most of the transects within the same management type are not significantly different, see figure 5.11 and 5.12. If any transect is to be singled out as particularly “non typical” for its management type, it ought to be Kwakai for its remoteness (approximately 25km west of Hukuntsi). Every other transect in a CGA was much closer a village and had more visible impact from cattle. Although the Kwakai transect indeed had the lowest number of insects of all transects in CGAs, it is not possible to attribute that merely to remoteness since this amount of variation in insect catch was common within other land use areas as well, without them showing as obvious differences in grazing pressure. In fact, as explained, no clear connection between environmental factors and insect density could be established at all.

The transects within the WMA shows higher variation than those within CGAs. This is consistent with the fact that these were sampled over a larger area and thus might represent regional differences. The two transects within the CCRs differ only slightly from another, again consistent with their relative closeness in location. In the NP, variation is relatively high with the most obtrusive transect being the one located farthest apart from any other, the Thupaphedi transect. Considering these facts combined, there is nothing to contradict the supposition that the strongest factor in creating variation among transects within the same management type is their geographical distance to one another.

On the largest scale, that of different land use types, variation of abundance is high enough for the differences to be significant between all land use types but between two, see figure 5.7. Species richness is, as mentioned, significantly different for all management types. The two management types that showed the largest differences in insect occurrence (CCRs and NP) were located farthest apart from each other whereas the management types with least differences (CGA and WMA) were sampled at sites closest to one another. This leaves questions about whether the samples might just reflect a larger distribution pattern governed by for example rainfall, since rainfall is known to vary along a north-south gradient with the driest parts in the south (Pike 1972, BNA 2001). Future studies ought to keep this possibility in mind and cross-sample for variation in rainfall.

Resource and disturbance gradients

The 5 km long transects in this study represents a gradient both in resources and disturbance. At least on a yearly basis, nutrient and water availability and thereby production increases with decreasing distance to pan (Thomas and Shaw 1991, Parris 197?). Since water availability and growth periods are highly seasonal it is not clear that this can be said for the period of this study. Particularly grass cover decreased noticeably close to pans as grazing, both by wild herbivores and livestock is noted to increase around pans (Viio 2003). Large animals' affinity to pans is also the cause for the disturbance gradient and source of the gradient of resources in the form of faeces. However, the results of this study show no sign of effect of these gradients on insect occurrence. Variation in catches between traps at different distances to pan does not differ noticeably from the variation between traps within the same distance. Nothing can thus be said about the relationships between productivity and diversity argued in e.g. Waide et al. (1999) and Abrams (1995).

Abundance and species richness vs. body size

The abundance/body size and morphospecies richness/body size distributions found in this study resemble unimodal patterns. All three most abundant taxa seem to have an intermediate size at which both abundance and species richness peaks. This implies either a diversification around a common ancestor in the three respective taxa, or perhaps more likely (due to the stable environmental conditions of the region on an evolutionary timescale) the divergence around an optimal body size (Siemann et al. 1999). In speculations like this there is a possibility of a sampling bias towards larger individuals. However, the apex of the respective curves is located at slightly different body sizes, suggesting that the result cannot be wholly explained by biased sampling. The reasons for an optimal size may be a combination of any number of physical and ecological factors. In the case of abundance, the energetic equivalence rule states that smaller species generally occur in larger densities. However, this alone would not predict unimodal patterns.

Tilman and Pacala (1993) argue that a decrease in species richness with increased body size can be attributed to the lower population densities associated with larger sized species, since smaller population densities and population numbers is likely to result in higher extinction rates. As mentioned above, smaller species are also likely to show more diversity due to their perception of the world as more heterogenic (Morse et al. 1985, May 1986). Further, smaller species generally have higher growth rate and shorter generation time, in theory opening for faster evolutionary processes, potentially creating more species. Countering these processes is the tendency of smaller species to display more turbulent population dynamics, creating a higher extinction risk (Tilman and Pacala 1993). The de facto relationship between species

richness and body size should be a combination of mechanisms such as these. However, conclusions on this matter ought to be drawn with caution from this study since the values of species richness is only a rough estimation.

Conclusion

It is clear that there are differences in insect abundances and species richness between the different management types. The trends appear to be practically uniform for all major insect taxa present in the area. The trend of these variables goes from Commercial Cattle Ranches (highest), through Wildlife Management Areas, Community Grazing Areas to National Parks (lowest). This trend roughly resembles a disturbance gradient, the question mark being the relative position of WMAs to CGAs. The pattern of more grazing, more insects is not particularly common in other areas and could possibly be explained by a relative high dependence on cattle as a resource provider by the Kalahari insects in the dry period. The high abundances of the WMAs or perhaps more importantly, the low abundances of the CGAs leaves questions about the mechanisms behind insect distribution and suggests that it is not merely a question of cattle dependence. The possibility remains that insect communities have heterogenic distributions due to natural processes even on very large scales. In contrast to recent studies in the area concerning other taxa (Wallgren 2001, Granlund 2001, Viio 2003, Bergström 2003), nothing is found to support the notion that livestock is detrimental to insect communities. Although it is perfectly possible that the recent social development might have been detrimental to insects at some other level overlooked in this study, this leaves us with some light in the gloom.

Future questions

Presumably the ecology of the insects discussed in this paper varies fairly much with season. For example are Scarabaeids well known to be highly connected to precipitation (Doubt 1991, Jankielsohn et al. 2001) and this could probably be said of the insect community as a whole. In this study, while there is a gradient in grazing and disturbance, there is also a gradient in water availability. Water is in this case connected to livestock, by the boreholes of which most areas are dependent for water, and by excrements of livestock. It cannot be excluded that insect occurrence is governed more strongly by local water availability than by grazing pressure. Yet, that explanation would have to deal with the seemingly relative high insect abundances of the WMAs too. As already discussed, the results could also mirror a larger pattern of rainfall, diminishing from north to south. This leaves us with the hope that this study will be followed up by someone in the rainy season. As it is likely that insect abundances would be different, it is also possible that the variances would differ. This fact, subsequently, might have the effect that patterns arise at scales different to those of this study. Thus, it cannot be ruled out that distance to pan have an effect on insect communities at some time of the year. If one is to make recommendations on future studies based on the data of this study, one can say that (if the differences in catch numbers and catch variation stay about the same) fewer sample sites are needed to show differences between Ranches and NPs. The effort should therefore be focused on finding representative sample sites unaffected by factors such as large scale rain patterns and large scale population dynamics.

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References:

Abrams P. A. 1995. Monotonic or unimodal diversity-productivity gradients: what does competition theory predict?. *Ecology* 76, 2019-2019.

Arntzen J., Chanda R., Fidzani H., Magole L., Setshogo M., Skarpe C., Tacheba G. & Totolo O. 1998. Rangeland and livelihood dynamics in the Matsheng area, Botswana. University of Botswana

Brown J. H. and Maurer B. A. 1986. Body size, ecological dominance and Cope's rule. *Nature* 324, 248-250

Bestelmeyer B. T. and Wiens J. A. 2001. Ant biodiversity in semiarid landscape mosaics: The consequences of grazing vs. natural heterogeneity. *Ecological Applications* 11, 1123-1140.

Bergström A. 2003. Small mammal diversity in Kalahari - impact of land use and pans in a semi arid savanna, south-western Botswana. Writing in progress. Uppsala University.

Bergström R. and Skarpe C. 1999. The abundance of large wild herbivores in a semi-arid savanna in relation to seasons, pans and livestock. *African Journal of Ecology* 37, 12-26.

Bergström R. and Skarpe C. 1985. Characteristics of the Kalahari sand in western Botswana. *Meddelande från Växtbiologiska institutionen* 1985:3

BNA. 2001. Botswana National Atlas, PC Atlas 1.0. Department of Surveys and Mapping, Botswana.

- Cagnolo L., Molina S. I and Valladares G. R. 2002.** Diversity and guild structure of insect assemblages under grazing and exclusion regimes in a montane grassland from Central Argentina. *Biodiversity and Conservation* 11, 407-420.
- Cloudsley-Thompson J. L. 2001.** Thermal and water relations of desert beetles. *Naturwissenschaften* 88, 447-460.
- CSO. 2003.** http://www.cso.gov.bw/cso/tab_cens1.4.html at 2003-06-24. Data from 2001. Central Statistics Office, Botswana.
- Doube, B.M. 1991.** Dung Beetles of Southern Africa. In *Dung beetle ecology*. Eds. Hanski I, Cambefort Y. Princeton University Press, Princeton.
- Kreuss A and Tschardt T. 2002.** Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation* 106, 293-302.
- Gause G. F. 1934.** *The Struggle for Existence*. Williams and Wilkins, Baltimore.
- Granlund L. 2001.** The abundance of game in relation to villages, livestock and pans – a study in southwestern Kalahari, Botswana. Minor Field Study No.73, Committee of Tropical Ecology, Uppsala University.
- Haddad N. M., Haarstad J. and Tilman D. 2000.** The effects of long term-term nitrogen loading on grassland insect communities. *Oecologia* 124, 73-84.
- Holland J.M., Perry J.N., Winder L. 1999.** The within-field spatial and temporal distribution of arthropods in winter wheat. *Bulletin-of-Entomological-Research*. 89, 499-513.
- Holm E, Scholtz C. H. 1986.** *Insects of Southern Africa*. Butterworths, Durban.
- Jankielsohn A., Scholtz C. H. and Louw S. V.D.M. 2001.** Effect of habitat transformation on dung beetle assemblages: A comparison between a South African nature reserve and neighboring farms. *Environmental Entomology* 30(3).
- Lawton J.H. 1991.** Species richness, population abundances, and body sizes in insect communities: Tropical versus temperate comparisons. In *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*. Eds. Price P. W. et.al. John Wiley & Sons, Inc. New York.
- Leggett K. edit. 1995.** *The present status of wildlife and its future in Botswana*. Kalahari Conservation Society/ Chobe Wildlife Trust
- May R. M. 1986.** The search for patterns in the balance of nature: Advances and retreats. *Ecology* 67(5).
- Morse D. R., Lawton J. H., Dodson M. M. and Williamson M. H. 1985.** Fractal dimension of vegetation and the distribution of arthropod body lengths. *Nature* 314, 731-733.

- National Parks Board and DWNP. 1997.** Management plan for Kalahgadi Transfrontier Park. National Parks Board, South Africa and Department of Wildlife & National Parks, Botswana.
- Owens M. and Owens D. 1980.** The Fences of Death. *African Wildlife* 34, 25-77.
- Parris R. 197?.** A study of the major components of the Kalahari pan ecosystem. University of Pretoria. (Mimeographed, exact dating has not been possible, somewhere between 1970-1980)
- Perkins S. J. 1991.** The impact of borehole dependent cattle grazing on the environment and society of the eastern Kalahari sandveld, Central District, Botswana. PhD-thesis, unpublished. University of Sheffield.
- Picker M., Griffiths C. and Weaving A. 2002.** Field guide to insects of South Africa. Struik publishers, Cape Town.
- Pike J.G. 1972.** Rainfall over Botswana. *Botswana Notes and Records. Special Edition.* 1, 69-76
- Ricklefs R. 1997.** The economy of nature. 4 ed. Freeman and Co, New York.
- Siemann E., Tilman D. and Haarstad J. 1999.** Abundance, diversity and body size: patterns from a grassland arthropod community. *Journal of Animal Ecology* 68, 824-835.
- Skarpe C. 1992.** Dynamics of savanna ecosystems. *Journal of Vegetation Science* 3, 293-300.
- Skarpe C. 1990.** Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. *Journal of Applied Ecology* 27, 873-885.
- Thomas D.S.G. and Shaw P.A. 1991.** The Kalahari environment. Cambridge University Press. Cambridge
- Tilman D., Pacala S. 1993.** The maintenance of species richness in plant communities. In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, eds. Ricklefs R.E., Schluter D. Univ. Chicago Press. Chicago.
- Waide R. B., Willig M. R., Steiner C. F., Mittelbach G., Gough L., Dodson S. I., Juday G. P., Parmenter R. 1999.** The relationship between productivity and species richness. *Annual Review Ecology and Systematics* 30, 257-257
- Wallgren M. 2001.** Mammal communities in the Southern Kalahari – distributions and species composition. Minor Field Study No. 69, Committee of Tropical Ecology, Uppsala University.
- Viiio T. M. 2003.** Does land use affect mammal diversity in savannah ecosystems? Minor Field Study No. 89, Committee of Tropical Ecology, Uppsala University.
- Williamson D. and Williamson J. 1984.** Botswana's fences and the depletion of the Kalahari wildlife. *Oryx* 18, 218-222.