The Effects of Habitat Change on Bird Diversity and Community Structure in a Mesic Savanna Landscape

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Thesis

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Plates

Plates overleaf:

Plate A: Broadleaf woodland dominated by *Euclea racemosa*, photographed in northern Hluhluwe-Umfolozi Park (site **2b**).

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A

B

Plates overleaf:

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Chapter 1: General Introduction

Many conservation areas are effectively islands in a sea of agricultural or urban development in which natural disturbance regimes have been altered or limited. Managers of such areas often need to artificially maintain disturbance regimes in order to control ecosystem processes such as vegetation succession (Richards *et al.* 1999). The relationship between disturbance, succession, vegetation change and habitat heterogeneity is crucial to managers because together they can influence biodiversity. For example, a break in the disturbance regime could promote woody plant encroachment. Though this might lead to an increase in habitat heterogeneity, the effects on biodiversity could be positive or negative.

Habitat heterogeneity, in this context, can refer to vegetation variability or complexity at a range of spatial scales. At a local scale habitat heterogeneity can describe the relative complexity of the structure of the vegetation and how it relates to faunal diversity via the provision of ecological niches (MacArthur *et al.* 1962). At a regional scale habitat heterogeneity can refer to the pattern of a landscape mosaic (Wiens 1995). In this case, a landscape with four different habitat types, each represented by a number of relatively small patches, would be considered more heterogeneous than a landscape with two different habitat types, both represented by large continuous patches (Addicott *et al.* 1987). In this study I use the term landscape heterogeneity to describe habitat heterogeneity at a landscape scale.

A common assumption is that diversity will be higher in a habitat with more ecological niches (see MacArthur *et al.* 1962), or in a landscape with more habitats (Wiens 1995). Thus, vegetation changes, such as those driven by secondary vegetation succession, can directly affect the biodiversity of a system.

A number of authors have recently dealt with the shift in thinking from a culture of savanna management in which management is directed to a preferred vegetation state (i.e. command-and-control), to on one in which habitat heterogeneity and patchiness are considered key elements (Holling and Meffe 1996, Christensen 1997, Wiens 1997, Andersen 1999).

Because the spatial component of fire management is now considered important (Andersen 1999, Christensen 1997, Wiens 1997), new fire regimes, developed to maximise landscape heterogeneity (or patchiness), are being implemented. The recently proposed patch-mosaic burning strategy (Parr and Brockett 1999) is one such strategy which is aimed at maximising habitat heterogeneity. The assumption is that increasing landscape heterogeneity or patchiness will lead to an increase in biotic diversity.

This study tests the assumption of the argument in the following ways:

1. How does habitat change, caused by secondary succession, influence avian diversity?
2. How important is the spatial distribution of different successional types in the landscape (landscape heterogeneity) to avian diversity?

What, for example, are the biodiversity costs of protecting an open area from fire long enough for woodlands to develop, or allowing a large continuous patch of woodland to become fragmented?

Habitat fragmentation is most often associated with human activity (expansion of agricultural land use and clear felling natural forest and woodlands) but also occurs in natural systems (reviewed by Andren 1994). In the latter case, in addition to habitat loss, reduced patch size and increased distance between patches, fragmentation can increase new habitat (i.e. habitat loss in one habitat is balanced by increase in another habitat) (Andren 1994).

In highly heterogeneous and dynamic savanna ecosystems where many habitat types form a successional series controlled by disturbance such as fire, the risks of vegetation change are particularly evident. Both the faunal and floristic diversity of these habitats and species composition in the different habitat types varies a great deal. Community composition must therefore be taken into account when managers attempt to maximise biodiversity in these systems.

The thorn savanna ecosystem of northern KwaZulu-Natal is a good example of a heterogeneous environment. It contains numerous deciduous and evergreen savanna woodland habitats as well as grassland habitats, growing on common soil types in a fine mosaic. The habitat patches, which range in size from less than 1 ha to 1000 ha, are situated in various different matrix habitats (equivalent to the undivided heterogeneous environment of Addicott *et al.* 1987). The Hluhluwe-Umfolozi Park (HUP), situated 40 km inland in central KwaZulu-Natal, encompasses 96 000 ha of this heterogeneous savanna, and supports the majority of the naturally occurring large mammal species of south-east African savannas. Established in 1895, but only recently completely fenced off from surrounding communally farmed lands, the Park is an ideal site for investigations into savanna dynamics.

Since active management started in the 1940's the Park has been subjected to major herbivore density fluctuations (both due to drought and game removals or additions) and a variety of burning strategies. The current management objectives are to maintain the indigenous diversity of species and habitats. The idea is that the more different habitats the Park contains the more plant and animal species it will support. Secondary aims, such as ensuring adequate game viewing opportunities for visitors, are also given consideration. For example, trees in dense thickets are cleared along roads to improve game viewing.

The objectives of fire management in the Park are not clearly defined but in general, aim to simulate natural fire regimes for the area - i.e. a mix of point source ignitions (lightning and man made) and broad front ignitions (point ignitions that have started outside the Park and have broadened to a front as it spreads across the landscape). One goal of the burning policy is to maintain habitat diversity through creating stands of different post burn age (D.A. Balfour personal communication). Despite management efforts to control bush encroachment (secondary succession) through manual clearing and fire management, a significant increase in woody plant biomass was noted between 1937 and 1983 (Watson and Macdonald 1983, Brooks and Macdonald 1983).

Secondary succession in mesic savannas

In the absence of regular disturbance (fire and herbivore pressure), microphyllous and broadleaf woody shrubs, growing in grasslands or open savannas, escape the fire trap (Bond and van Wilgen, 1996), and grow into trees (Smith and Goodman, 1987; Skowno *et al.*, 1999). The microphyllous species (usually acacia species) are faster growing than the broadleaf species and grow into trees more rapidly than the broadleaf species. The resultant microphyllous woodlands are usually open in structure with the grass sward relatively unaltered. The slow growing long-lived broadleaf species continue to grow beneath the microphyllous canopy until either the short-lived acacia canopy senesces or the broadleaf species overtop and kill the acacia, resulting in the formation of a broadleaf woodland or thicket (Smith and Goodman 1987, Archer *et al.* 1988, Franco-Pizana *et al.* 1996). As long as there is sufficient fuel available the successional process can be reset by an intense fire which would remove the above ground woody plant biomass. In the continued absence of fire the woody plant biomass increases, the amount of light reaching the ground declines and the grass sward becomes sparse, resulting in a reduced fuel load for fires. The result is that once closed canopy broadleaf woodlands have become established they are essentially a permanent feature of the landscape and succession can not reverse to savanna (Archer 1990, Skowno *et al.* 1999).

Why Birds ?

Birds are a highly visible component of the fauna in most ecosystems, they interact with their environment at a similar scale to humans. They respond to elements of their environment which are visible to, and important to humans and are usually a well known component of the biodiversity of a region. Although birds are difficult to census, they are easy to identify and consequently are commonly used as indicator taxa (Noss 1990, Bibby *et al.* 1992). However, the validity of biodiversity indicator taxa has been questioned. Prendergast (1997) states, "that the understanding of the relationship between species richness of different taxa is currently insufficient to support the use of individual higher taxa as biodiversity indicators for conservation planning."

I used birds in this study to help develop a protocol for considering landscape scale effects on faunal diversity. They are known to respond to changes in vegetation structure similar to those taking place as grasslands are converted to woodlands in HUP. They are also known to be sensitive to habitat area. They therefore provided a suitable vertebrate group for exploring the implications of management driven successional change in savanna landscapes.

Literature Review

Vegetation structure

Numerous studies since the early 1960's have linked various aspects of vegetation structure with avian diversity and community organisation (MacArthur and MacArthur 1961, MacArthur *et al.* 1962, Willson 1974, Roth 1976, Wiens and Rotenberry 1981, Ralph 1985, Knick and Rotenberry 1995). MacArthur and MacArthur (1961) were the first to show that bird diversity was related to the structure of the vegetation, initially in various woodland habitats (MacArthur and MacArthur 1961) and subsequently in a series from shrub to forest (MacArthur *et al.* 1962). Subsequent studies have shown that, in general, structurally more complex vegetation supports higher bird diversity. However, Willson (1974) attempted to repeat MacArthur's work and found that foliage height diversity (FHD) and bird species diversity (BSD) were related, but that the addition of trees to a vegetation series had a disproportionate effect on the addition of bird species. When she excluded treeless habitats from her analysis she found that FHD and BSD were not related. Ralph (1985) showed, in his study of a range of habitats from grassland to mature *Nothofagus* forest, that when open treeless sites are removed from the correlation of foliage height diversity and bird species diversity, the slope goes from significantly positive to significantly negative. This means that in wooded habitats BSD decreased as FHD increased, and that BSD reached its maximum at some intermediate FHD level. Wiens and Rotenberry (1981) suggest that most bird - habitat relations are apparent only if a wide range of habitat types are considered, and that within habitat variations in bird diversity may be related to factors other than vegetation structure (e.g. floristics, productivity and disturbance). Three separate studies conducted in South African forest habitats support this view (Cody 1983a, Koen and Crowe 1987, Kruger and Lawes 1997).

Species - Area relationships

The relationship between habitat patch area and bird species is also well documented (Ambuel and Temple 1983, Willson *et al.* 1994, McCoy and Mushinsky 1994, Knick and Rotenberry 1995, Schieck *et al.* 1995, Macnally and Watson 1997, Helzer and Jelinski 1999). In many systems, when patch area increases so does bird diversity (Ambuel and Temple 1983, Willson *et al.* 1994, Helzer and Jelinski 1999). However, a number of studies have shown that there is no simple relationship between species and area (Schiek *et al.* 1995, Macnally and Watson 1997). For example Schiek *et al.* (1995) found that there were fewer generalist birds in the centre of large patches of forest than at the centre of small patches, but that the species richness of small and large patches was not different. Macnally and Watson (1997) found no relationship at all between bird species richness and patch area. Watson and Peterson (1999) in a study of humid forest birds of Mesoamerica found that the area effects are scale dependant. They state that, "Area and similar patch level effects may be influential for smaller patches, but not once they exceed a particular threshold.......[and that] patch scale characteristics such as area and isolation may be critical in the short term, but over longer time periods may be superseded by other factors, such as disturbance regime and geographic context."

Patch Shape

Many authors have suggested that it is not the area of a patch but rather the shape of the patch that is important in determining faunal diversity (Sousa 1985, Wiens 1985, Forman and Godron 1986, Bender 1998, Helzer and Jelinski 1999). Ecological processes are often different at the edge and interior of a habitat, leading to differences in plant species composition and abundance. The structure of the vegetation is often different as well. In wooded environments for example, the edge is often more open than the interior. As a result bird communities are often different in edge and interior environments (Bender 1998). Shape is important because it relates to edge effect, but because it is difficult to measure it is under studied (Forman 1995). Edge effect is important even if habitat patch shape is kept constant because small patches have a greater ratio of edge to area than do larger patches (Sousa 1985). If small and large patches are sampled equally it is likely that edge species will contribute more to faunal diversity in a small patch than in a large patch. Helzer and Jelinski (1999) show that overall grassland bird species richness is best predicted by the perimeter-area ratio of a habitat patch, and state that, "....species richness is maximised when patches are large (>50 ha) and shaped so that they provide abundant interior areas, free from the impact of edges."

Andren (1994) in a review of habitat fragmentation effects, suggests that the shape of the habitat patches (and hence edge effects) only become important when the habitat is rare in the landscape. He goes further to state that for mobile organisms (such as birds), the effects of isolation may appear only in landscapes with highly fragmented habitats.

Related work on mammals

There are also a number of studies, based on small mammals, which provide further insight into the importance of vegetation structure, habitat heterogeneity and habitat patch size in controlling species diversity (Bond *et al.* 1980, Andren 1994, McCoy and Mushinsky 1994, Lindenmayer *et al.* 1999). Bond *et al.* (1980) found that small mammal diversity was closely related to vegetation structure, and that individual species chose structurally similar rather than floristically similar habitats. Both McCoy and Mushinsky (1994), and Lindenmayer *et al.* (1999), found that small mammal diversity was higher in large habitat patches than in small habitat patches. Hirst (1975) and Scogings *et al.* (1990) both suggest that south-east African ungulates select habitats on the basis of vegetation structure. Ungulate species can readily be divided into those that prefer open savannas and grasslands (i.e. with low tree density) and those that prefer woodlands or well wooded savannas (Hirst 1975, Scogings *et al.* 1990).

General Aims

The initial motivation for this work was the need to better understand the effects of vegetation change on avifaunal communities and species diversity in HUP. The two most obvious elements of vegetation change are 1) the physiognomic changes associated with secondary succession in savanna habitats, and 2) habitat fragmentation (the subdivision of continuous habitat into smaller pieces) and the associated loss of habitat and isolation of remaining habitat patches in grasslands and *A. nilotica* woodlands.

It follows that my aims were to 1) investigate the importance of vegetation structure and floristics in determining bird community composition in a range of habitats, and 2) to investigate the relationship between habitat patch size / isolation and bird species diversity. In other words, to what degree is bird community organisation linked to vegetation structure and floristics, and is bird species diversity related to habitat patch size and isolation? The answers to these questions are then used to explore the effects of landscape heterogeneity on conserving biodiversity in the context of recent proposals for maximising landscape heterogeneity as a means of conserving diversity.

Thesis structure

Chapter 1 - General Introduction

Chapter 2 - Site Description and General Methods

The study area is described in detail and placed in context geographically. The design of the study is discussed and the general methodology, bird censusing techniques and habitat measurement are described in full.

Chapter 3 - The importance of vegetation structure and composition in shaping savanna bird communities

In this chapter I focus on bird community composition and its controlling factors in three woodland and one grassland habitat. The importance of various measures of vegetation structure, as well as floristic elements, in shaping bird communities are investigated using ordination techniques. The changes in bird community composition associated with secondary succession in vegetation are discussed.

Chapter 4 - The effects of habitat patch size, patch isolation and vegetation structure on savanna bird diversity

Chapter 4 looks at bird species diversity between and within habitat types. The bird diversity of four habitats is related to foliage height diversity. Bird diversity in *A. nilotica* woodland and grassland patches of various sizes is investigated. What controls diversity between habitats and within habitats is discussed. Correlations such as species vs. area for grassland and *A. nilotica* woodland, and vegetation structure measures (FHD) vs. species diversity are presented.

Chapter 5 - Landscape model

In this chapter a landscape model is constructed in order to investigate the responses of woodland and grassland bird diversity to total area in a landscape and to average patch size in a landscape.

Chapter 6 - Conclusion

Chapter 6 includes a discussion of the implications of vegetation change and habitat fragmentation on bird community composition and diversity in HUP. Other potential threats to the avifauna of the Park, in particular, the invasion of *Chromolaena odorata* inside the Park and the regional effect of habitat loss out side the park are discussed.

Chapter 2: Site Description and General Methods

Introduction

In this chapter I describe the study site and place it in context geographically. I outline the general methods, such as census procedures and habitat measurement, that apply to all the following chapters. I also present some preliminary census findings which I use to design the final censusing technique, as well as a series of foliage profiles and photographic plates of the vegetation types included in the study.

Site description

The study was conducted in the Hluhluwe-Umfolozi Park (HUP), situated 40 kilometres from the coast in KwaZulu-Natal, South Africa (28°00 - 28°10 S, 32°00 - 32°10 E) (Figure 1). The Park, bounded by game proof fencing, is surrounded by rural KwaZulu where population densities are high and subsistence agriculture is extensive. The altitude of the Park varies from 90 m a.s.l. in the river valleys, to 580 m a.s.l. on the hill tops in the north east and extreme south. The Park is generally hilly with some relatively flat areas on the flood plains of the major rivers. There is a strong rainfall gradient in the Park, ranging from 910 mm (mean annual rainfall) in the high lying areas to < 600 mm in the low river valleys in the south west (Park records 1932-1990). The wet season runs from October to March. The mean annual temperature is 18.5 °C. The warmest month is January with a monthly mean temperature of 25.9 °C. September is the coolest month with a monthly mean temperature of 11.5 °C (King 1987).

The vegetation of the Park consists mostly of savanna woodlands, with some evergreen forest and grassland communities, and falls into the Tongaland - Pondoland regional mosaic of White (1983).

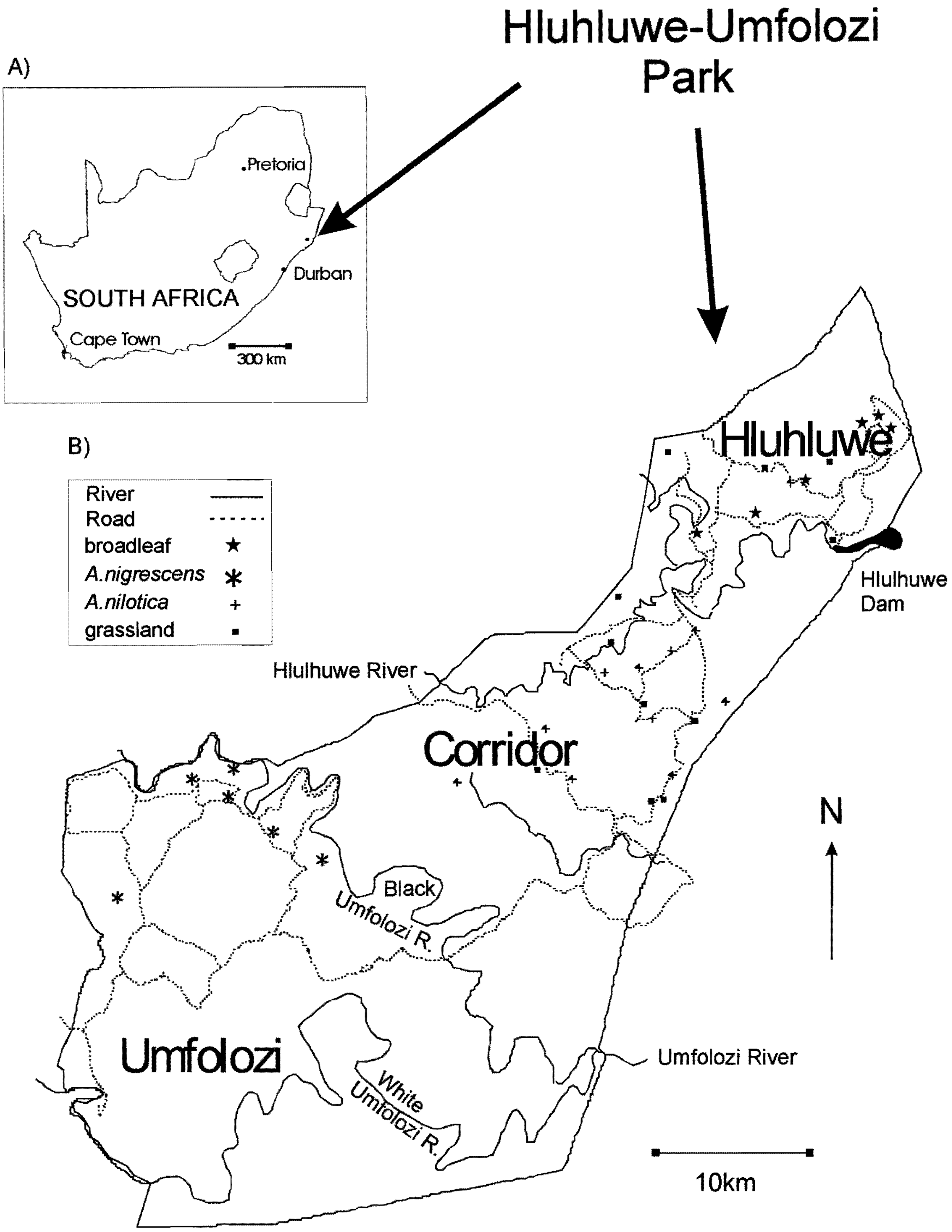

Figure 2: a) Map showing location of Hlulhuwe - Umfolozi Park in South Africa, **b)** map of HUP showing study sites, major rivers, sections and roads.

Through a series of re-introductions, the Park houses most of the large mammalian fauna, indigenous to the region. Zoogeographically, on the basis of avifauna, the region is classified as the southern sub - district of the East African Coastal District (Winterbottom 1974). The Park actually lies very close to the point of convergence of four of Winterbottom's (1974) districts and sub districts. The Mozambique sub district of the East African District begins just to the north, the South Central Highlands District lies just to the NW and the Southern Temperate District just to the west. The Park is known to support over 400 bird species, and is considered important for the conservation of a number of large, wide ranging species. These include Cape Vulture (*Gyps coprothees)*, Hooded Vulture (*Necrosyrtes monachus)*, Whitebacked Vulture (*Gyps africanus)*, Whiteheaded Vulture (*Trigonoceps occipitalis)*, Lappetfaced Vulture (*Torgos tracheliotus)*, Tawny Eagle (*Aquila rapax)*, Martial Eagle (*Polemaetus bellicosus)*, Bateleur (*Terathopius ecaudatus)*, African Marsh Harrier (*Circus ranivorus)*, Grass Owl (*Tyto capensis)*, Ground Hornbill (*Bucorvus leadbeateri)* and Secretary Bird *(Sagittarius serpentarius)* (Johnson *et al.* 1998).

Study design

A total of 36 habitat patches, ranging in area from 2 to 538 ha (mean size 19.7 ha), was chosen from four different vegetation types in the HUP (the physical details of each site are presented in Appendix 1). Initially six sites were selected in each of the following vegetation types: 1) broadleaf woodland (Plate A), 2) *Acacia nigrescens* (Oliv.) **Mimosaceae** woodland (Plate B), 3) *Acacia nilotica* (L.) **Mimosaceae** woodland (Plate C) and 4) open grassland (Plate D). These 24 patches were used in the bird community investigation which constitutes Chapter 3. An additional 12 patches, 6 of *A. nilotica* woodland and 6 of open grassland, were subsequently chosen. These 12 patches, together with the original 6 *A. nilotica* and 6 grassland patches, were used in the investigation of habitat area and isolation effects in winter (Chapter 4).

The vegetation types were defined by the dominant tree layer (Whateley and Porter 1983). The broadleaf woodlands are dominated by *Euclea divinorum* (Hiern) and *Euclea racemosa* (Murray), and cover extensive areas around the Hluhluwe River, particularly below the 200m contour (Whateley and Porter 1983). *E. divinorum* and *E. racemosa* are evergreen members of the Family **Ebenaceae**. *E. divinorum* commonly forms multi-stemmed shrubs up to 2 m in height, and can grow into multi or single stemmed trees of up to 8 metres in height (Pooley 1993). *E. racemosa* typically forms single stemmed trees up to 12 metres in height and is common in the more mesic woodlands in the Park (Pooley 1993). In this study the grasslands with no tree layer, or scattered trees separated by over 40m, were chosen. These grasslands are common in the Corridor region of the Park (Figure 1).

The *Acacia nilotica* woodlands have an almost monospecific overstory of *A. nilotica,* and are common in the Park north of the Black Umfolozi River (Figure 1). The grass layer of these woodlands is typically dense but areas with short grass do occur. Areas where a mixture of acacia and broadleaf canopy species are found together are common through out the Park. However in order to simplify the study, sites were selected in near monospecific stands only. The *A. nigrescens* woodlands, which are confined to the dolorite derived soils in the catchment areas of the Black and White Umfolozi Rivers, consist of near monospecific stands of *A. nigrescens* or of mixed stands of *A. nigrescens* and *A. tortilis* (Figure 1). Again in order to simplify the study, sites were chosen in the near monospecific stands only. The *A. nigrescens* woodlands are taller than the *A. nilotica* woodlands and usually have a less dense grass layer.

Suitable patches of vegetation were identified using aerial photographs, orthophotographs, and a digital vegetation map of the Park based on LANDSAT-TM images (Meyer 1999), viewed using the GIS programme ARC VIEW (version 3.1.1, Environmental Systems Research Institute 1999, Redlands, Calif.). Ground based investigation of potential patches was necessary in order to determine the level of dominance of the woodland tree species (i.e. *E. racemosa* and *E. divinorum*, *A. nilotica* and *A. nigrescens*) and whether the area had been recently burnt. All patches in which the herbaceous layer had burnt within last 3-4 months were excluded. Patches close to the existing road network were selected in order to reduce travelling times. 400 meter long transects were randomly placed in each patch. When possible the transects were placed more than 200m from the edge of the patch.

Bird censuses and habitat measurements were completed during the wet and dry seasons in 1998 and 1999. Summer or wet season censuses were completed between 11th December 1998 and 25th January 1999, and winter, or dry season, censuses between 17th May and 25 th June 1999 (Table 1). The 6 broadleaf and 6 *A. nigrescens* patches were censused only during the summer study. The original 6 *A. nilotica* and 6 grassland patches were censused both in summer and winter studies. An additional 6 *A. nilotica* and 6 grassland patches were censused only in winter. Because of the large number of species potentially encountered during censusing, over 3 months in total was spent in the Park before censusing commenced in preparation for the study and getting to know the bird calls.

Table 1: The number of sites censused in each habitat during the study

Summer Censuses		**Winter Censuses**	
Broadleaf woodland	6	*A. nilotica* woodland	12
A. nigrescens woodland	6	Grassland	12
A. nilotica woodland	6		
Grassland	6		

Methods

Bird census procedures

Bird were censused using fixed width transects approximately 400 metres long and 50 metres wide (25 metres on either side of the path chosen). 20 minutes was spent walking each transect census. The slow walking speed and frequent pauses allowed me to detect shy woodland species, while the length of the transect ensured useful censusing of the grassland patches. This method is a compromise between the long transects usually used in grassland bird censuses and the stationary point counts used in woodlands and forests (Bibby 1992, Pomeroy 1992). Although there are numerous arguments for and against every census technique, (Bibby 1992, Pomeroy 1992), I believe this method is best suited to this study in that it allows direct comparison of the avifaunas of different habitat types. For the small patches (i.e. those less than 10 ha) it was often necessary to walk 'U' or 'L' shaped transects. However extreme care was taken to avoid censusing the same birds twice. Transects were walked and birds censused on four consecutive rainless mornings in the period of maximum activity and vocalisation between sunrise and two and a half hours after sunrise. Aerial feeding birds (swifts, swallows and martins) and raptors were excluded from the census because of the difficulties in assigning sightings to a particular patch. All bird censuses were done by the Author.

Species Accumulation Rates

The number of times that each transect is censused is particularly important when different habitats are being compared directly. The number of new bird species encountered on each successive day (species accumulation rates) gives an indication of how complete the census is. Species accumulation rates were calculated for broadleaf woodland, *A nilotica* woodland and grassland prior to beginning the study. The species accumulation curves constructed during these preliminary studies in July 1998 suggested that four days was the minimum number of days over which a habitat patch could be censused (Figure 2). After four days of censusing the curve levels off, especially in the grassland (Figure 2). It was decided to restrict censusing to four days at each site to allow a greater range of habitat types and patch sizes to be included in the study.

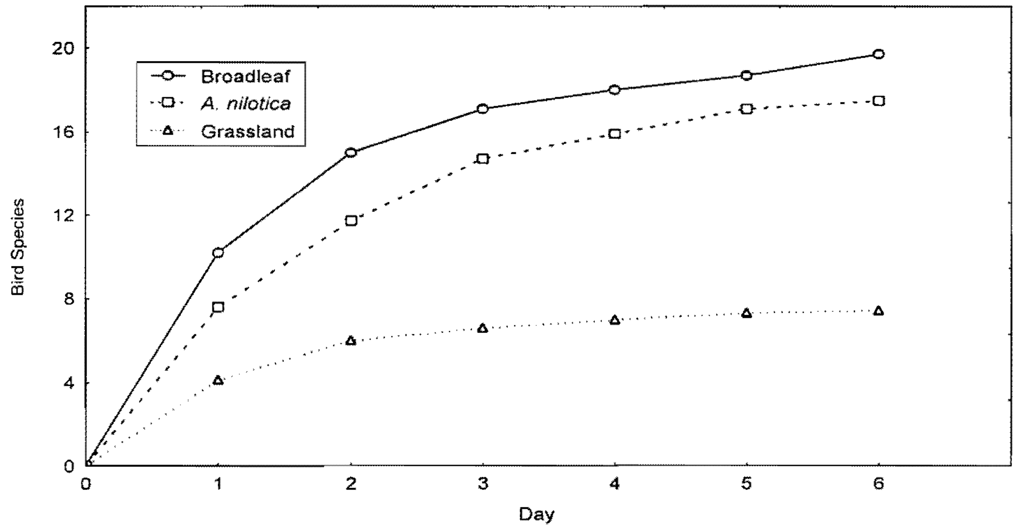

Figure 2: Species accumulation rates based on preliminary censuses in winter 1998. The y -axis is the average cumulative number of bird species observed at 4 grassland, 4 *A. nilotica* woodland and 4 broadleaf woodland sites in winter.

Once the censusing proper began it became clear that while four days was sufficient for grassland bird communities it was less than optimum for woodland communities (Table 2).The comparisons of bird diversity between habitat types must therefore be cautiously made. In general the avian diversity of the woodlands is underestimated relative to that of the grasslands.

Table 2: Average number of new species encountered on each successive day of censusing, in both summer and winter censuses

Day	Broadleaf	*A. nig*	*A. nil*	Grassland	*A. ni* (win)	Grass(win)
1	1.77	12	10.2	6.3	8.3	4.4
2	4.7	4.7	5	2.7	3.9	1
3	2.3	2.2	2.5	1	3.2	1
4	2.3	2	2	0.7	1.8	0.5

Habitat measurement

Habitat measurements were taken once along each transect. The structure of the vegetation was quantified using the method devised by MacArthur and MacArthur (1961), and modified by Ralph (1985). This method has been used extensively and is widely accepted as the standard method for quantifying vertical vegetation structure. At eight points, (every 50 meters), along each transect I assessed the vegetation to the right and left of the transect line. At each point I estimated the distance at which a 30 x 30 cm board was 50% obscured by foliage at various heights. These heights were 0, 0.5, 1, 1.5, 2, 3, 5, 8 and 12 meters. If the distances were greater than 40 metresthey were given a value of 100. The average distance for each height was calculated for each transect. This was translated to foliage density using the following formula :

$$\mathbf{k = 0.69315 / D} \qquad \mathbf{(1)}$$

where **k** is foliage density (m^2/m^3), **D** is the distance to the imaginary board and **0.69315** is the natural logarithm of 2 ($\log_e 2$).

A vertical vegetation profile was then constructed by plotting height above the ground (on the y axis) against the logarithm of vegetation density (on the x axis) (Figure 3), and joining the points on the scatter. These foliage profiles illustrate the major differences in structure of the four habitats studied.

In addition to foliage density; canopy cover (CC), canopy height (Cn ht) grass height (Gr ht), grass cover (GC), grass density (Gr den), tree density (Tr den), shrub density (Sh den) and plant species composition were measured along each transect. Percentage canopy cover was estimated by noting the presence or absence of canopy cover every 10 m along the transect. Canopy height and grass height were estimated in a similar manner. Percentage grass cover was estimated in a $1m^2$ quadrat every 50 meters. The distance to the nearest tree and shrub in each of the cardinal directions was also measured every 50 meters. For the purposes of this study woody plants over 3m in height were considered trees. Plants between 2 and 3 metresin height were classed as trees if they had one stem and as shrubs if they were multistemmed. Woody plants less than 2m in height were classed as shrubs. The reciprocal of the average distance between trees was taken as a measure of density. The same was done for shrubs.

All trees, woody shrubs and grasses were identified in eight $50m^2$ quadrats along the transect. While the trees and shrubs were simply identified and counted, the grasses were ranked in terms of dominance in each quadrat. The most abundant species was scored as 10; the 2nd as 8; the 3rd as 5; the 4th as 3; the 5th as 2; and the remaining species a score of 1. The abundance of each grass species was the sum of its scores along a transect.

Habitat measurements taken at the same site in summer and again in winter proved to be identical. Consequently grassland and *A. nilotica* woodland sites measured in summer were not remeasured in winter. There were significant late summer rains in the Park in 1999 and as a result the vegetation had not dried out significantly by May and most of the deciduous tree species had not lost their leaves. If the winter study had been conducted in late winter this may not have been the case.

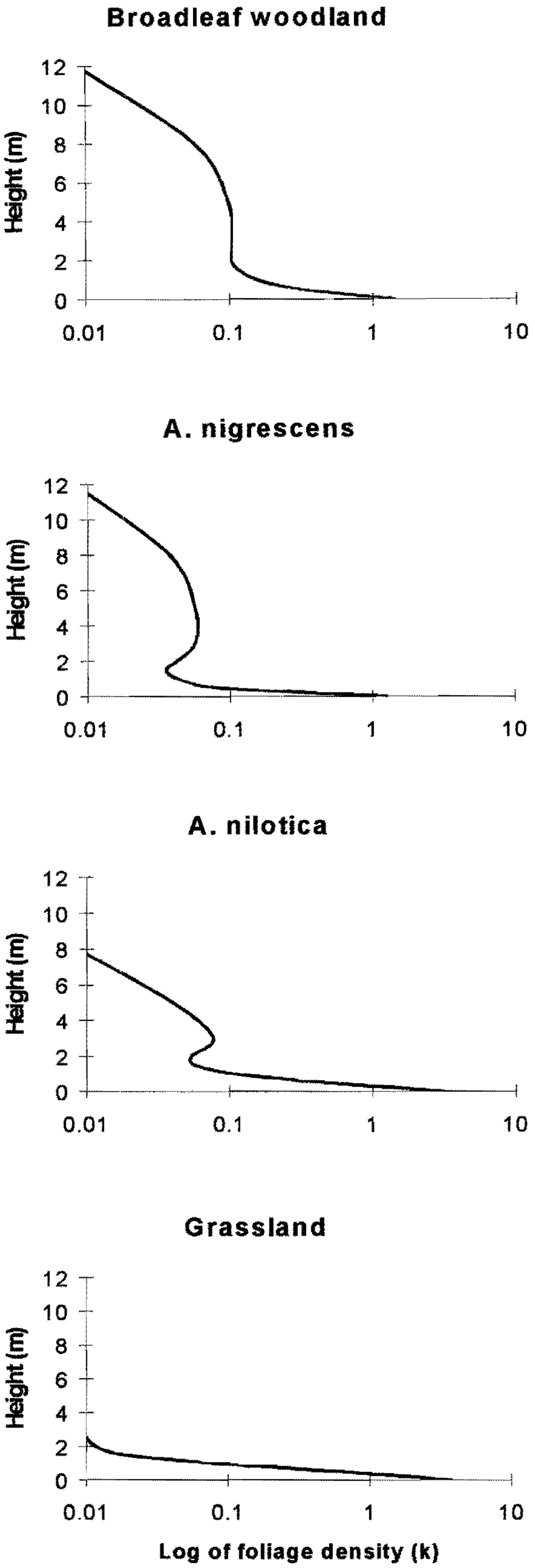

Figure 3: Foliage profiles of broadleaf, *Acacia nigrescens* and *Acacia nilotica* woodland, and grassland. Constructed from the average density (k) of foliage at 0, 0.5, 1, 2, 3, 5, 8 and 12 meters above the ground. The log of k is used due to the large difference between herbaceous and non-herbaceous foliage density.

Data Analyses

Overall bird species richness of a patch was calculated as the sum of all species encountered on a particular transect over the four days of sampling. Abundance was similarly calculated. This simply means that species richness of a patch is the total number of bird species encountered in 80 min of dawn sampling. Because all the patches were censused equally the number of species encountered and the number of individuals counted can be compared. However, the underestimation of diversity in thorn woodlands, relative to the grassland and broadleaf woodlands should be noted.

Species diversity and foliage height diversity were calculated using the Shannon - Wiener information theory formula (Equation 2).

$$H' = -\sum_{i=1}^{s} p_i \log_{10} p_i, \quad (2)$$

where **s** is the number of categories and p_i is the proportion of the observations in the i^{th} category. The p_i used in the bird species diversity equation was the proportion that each species contributed to the total abundance at each site. Magurran (1988), in a review of species diversity measurement, suggests that, although there are numerous suitable alternatives, the Shannon -Wiener index is useful expression of diversity when relative abundance of the species needs to be taken into account. It is also widely used and understood, and has become the standard method in many fields of ecology (Magurran 1988).

In order to calculate foliage height diversity (FHD) a foliage profile was drawn by plotting the foliage density against height (Figure 3). The area of the profile is then divided into three horizontal layers, 0 -1m, 1-2m , > 2 m, and the proportions of the whole that each constitutes is the p_i used in the Shannon Wiener diversity formula. The resulting value is known as the FHD (MacArthur and MacArthur 1961). Numerous variations of the standard FHD were calculated, in order to asses its sensitivity to the herbaceous layer. One of these variations, termed non-herbaceous FHD was calculated using the proportion of the total density that each layer above 1m contributes as $\mathbf{p}_{i.}$ (i.e. foliage density at 1m 1.5, 2, 3, 5, 8, and 12m). This is essentially a foliage height profile which, by excluding the herbaceous layer, represents the structural diversity of the woody element of the vegetation.

Chapter 3 : The importance of vegetation structure and composition in shaping savanna bird communities

Abstract

Multivariate analyses were used to determine the relative importance of vegetation structure and floristic composition in defining bird communities in a savanna ecosystem. Birds were censused, plant species were identified and vegetation structure was measured in four different habitat types in Hluhluwe - Umfolozi Park (HUP) in northern Kwazulu Natal, South Africa. Detrended correspondence analysis (DCA), was used to determine the dominant community groupings of the plant and bird species. Detrended canonical correspondence analysis (DCCA), a direct type of gradient analysis, was used to relate vegetation structure to bird community organisation. The bird communities of the four vegetation types are relatively sharply defined, and are linearly arranged on the first axis of the DCCA. Canopy cover and Foliage height diversity (FHD) are strongly correlated with this axis suggesting a successional series from grassland to *Acacia nilotica* woodland to broadleaf woodland. The sites are not arranged in the same linear series on the basis of their plant communities. The broadleaf and *Acacia nigrescens* sites each have relatively distinct plant communities, and occupy opposite ends of the ordination diagram. The *A. nilotica* and grassland sites group together forming a single central plant community in the ordination diagram.

There is a high degree of dissimilarity in the bird community composition between the vegetation types. Vegetation change associated with secondary succession could thus lead to major changes in bird community composition. The results suggest that it is the physiognomic changes which drive the turn over in bird species not the floristic changes.

Introduction

Woody plant encroachment is a well documented phenomenon in the mesic savannas of southern Africa (see Chapter 1, page 5, for references). In HUP, the shift from open grassland with scattered trees to closed canopy woodlands can occur in as little as 40 years (Skowno *et al.* 1999). In this dynamic savanna ecosystem the structure and composition of the vegetation are largely controlled by disturbances such as fire and by herbivore densities, with soil playing a minor defining role (Whateley and Porter 1983). For the purposes of this study it is important to note that once a broadleaf woodland has formed it is effectively a permanent change. The encroachment of woody species into grassland areas is not as difficult to reverse and managers routinely use fire and manual clearing to combat this process which is perceived as a problem.

It is widely believed that the structure of the vegetation, its complexity and vertical arrangement are the primary defining factors in bird communities (MacArthur and MacArthur 1961, MacArthur *et al.* 1962, Willson 1974, Wiens and Rotenberry 1981, and Roth 1976). Yet, there are also studies showing that floristic composition plays an important role (Herremans 1993, Ralph 1985), especially when fruit bearing plant species are involved (Willson *et al.* 1994).

The main aim of this study is to determine the role that vegetation structure versus floristic composition play in defining the bird communities of the Park, and in this way investigate the current and potential effects of secondary succession of vegetation on one faunal component.

The first step in determining the impacts of vegetation change on bird communities is defining the bird communities of the various vegetation types present. These vegetation types are usually defined by their structure and a dominant floristic element. For example, the presence or absence of a tree layer would lead to a grassland / woodland distinction, and the density of the tree layer would lead to a savanna woodland / open / closed canopy woodland distinction. By using multivariate community analyses such as gradient analyses, it is possible to determine: 1) how the bird and plant communities vary in terms of species composition within and between vegetation types, and 2) which components of vegetation relate best to the observed pattern of bird community organisation.

Methods

See Chapter 2 for a full site description and general methods. The habitat measurements and summer bird censuses in broadleaf woodland, *Acacia nigrescens* woodland, *Acacia nilotica* woodland and grasslands, were used in this chapter.

Data Analysis Methods

Ordination

ter Braak and Prentice (1988) review data analysis techniques for the interpreting of community composition in terms of species' responses to environmental gradients. The authors introduce a new type of gradient analysis, constrained ordination, which not only constructs axes of variation in overall community composition (like indirect Gradient analysis), but optimises the fit to supplied environmental data (ter Braak and Prentice 1988). In this study both the bird and plant communities were analysed. The environmental data to be incorporated in the analysis of the bird communities were various measures of vegetation structure.

The computer programme CANOCO for Windows (version 4.0, Microcomputer Power, Ithaca, NY, USA) was used for all ordinations.

Detrended correspondence analysis (DCA) was used to extract the dominant patterns of variation in community composition from the bird and plant species data. DCA is favoured for the analysis of unimodal species data sets with a large number of zero values, as it avoids the problems of interpretation due to the arch effect produced by correspondence analysis (ter Braak and Verdonschot 1995). DCA is an indirect gradient analysis which ordinates only the species data (bird or plant) (ter Braak and Verdonschot 1995).

In order to relate the bird community composition and vegetation structure directly I used detrended canonical correspondence analysis (DCCA). DCCA is a direct gradient analysis technique in which a set of species data is related directly to a set of environmental variables. This method detects the patterns of variation in species data which can be explained by environmental variables.

In this study the bird species data are the total number of individuals of each bird species encountered over four consecutive days of censusing in 6 grassland, broadleaf woodland, *A. nilotica* woodland and *A. nigrescens* woodland sites during summer (see Appendix 3). In order to run an analysis of the whole plant community the species abundance values were converted to presence absence. This was necessary because different methods were used to measure the abundance of woody and herbaceous plants. The environmental variables (here after referred to as the structural variables) used together with the bird species data in the DCCA are FHD-1, FHD-3, GC, Gr den, Sh den, Tr den, CC, Gr ht, Sh ht, Cn ht, which are measures of vegetation structure at each site (see Table 1 for a description of the structural variables used, and Appendix 2 for structural variable values).

Table 1. Vegetation structure variables used in analyses.

Variable	Description
FHD-1	Foliage height diversity - MacArthur's (1961) original technique
FHD-3	Non-herbaceous foliage height diversity
GC	% Ground cover
Gr den	Grass density
Sh den	Shrub density
CC	% Canopy cover
Gr ht	Grass height
Sh ht	Shrub height
Cn ht	Canopy height
Tr den	Tree density

The ordination diagrams produced by the DCAs show a scatter plot of the sites, the sample scores (from which the sites are plotted) are derived from the bird or plant species data. In the ordination diagram produced by a DCCA the sites and/or species are represented by points and the environmental variables by arrows. The eigen vector scores used to produce a sample - environmental variable biplot are linear combinations of the structural variables with the regression coefficients (ter Braak and Smilauer 1998). In other words the site scores in the DCCA are derived from both the environmental variables and the species data. In this study the samples represent the 24 sites and the vegetation structural variables are the environmental variables. The distribution of the sites along each environmental gradient are shown in the ordination diagrams.

Two separate DCAs were performed. The first used the bird species data, and the second used the plant presence-absence data. The data in all the analyses were not transformed and were detrended by segments. In order to asses the importance of each structural variable, an initial DCCA including all the variables was run. The intraset correlations between the first two DCCA axes and the structural variables are effectively a measure of importance for each variable. Intraset correlations are the interset correlations divided by the species environment correlation of the axis and tend to be a more stable measure than interset correlations (ter Braak 1987).

Distance analysis

Another direct method of gradient analysis for community data is distance analysis. It is considered direct analysis because the communities are predefined. The relative distance between the communities and amount of variation within a community are the products of the analysis. The computer programme Releve Manager (ter Braak 1988, Agricultural Mathematics Group DLO, Wagenigen) was used for the distance analysis which, in this case, produces the percentage dissimilarity between the bird and plant communities in the four different vegetation types. These dissimilarity measures were used in conjunction with the ordinations, the difference being that in the dissimilarity analysis one assumes that the birds and plants found in each vegetation type are members of the same community, while the DCA and DCCA make no such assumption and treat all the sites equally. To allow comparison of plant and bird communities the bird species data were converted to presence-absence data.

Results

General

A total of 92 bird species was encountered in the four vegetation types censused in summer. The most abundant species were the Rattling Cisticola (*Cisticola chiniana*) and Blackeyed Bulbul (*Pycnonotus barbatus*). The most abundant broadleaf species was the Greenbacked Bleating Warbler (*Camaroptera brachyura*), while the Croaking Cisticola (*Cisticola natalensis*) was the most abundant species in the grasslands. The Rattling Cisticola was the most abundant bird in the *A. nigrescens* woodland, and *A. nilotica* woodland. The number of species and individual birds encountered is presented in Table 2. The broadleaf woodlands supported the highest number of individual birds while the *A. nilotica* woodlands had the highest total number of species encountered. A full list of birds, their abundance and the sites at which they were encountered is given in Appendix 1.

Table 2. The total number of bird species, and individuals encountered in each of the four vegetation types over four consecutive mornings in mid summer.

Habitat type	**species**	**Individuals**
n=6		
Broadleaf woodland	45	624
A. nigrescens woodland	46	453
A. nilotica woodland	59	564
Grassland	24	385

Table 3 shows the total number of plant species (divided into grass and non grass species) identified in the four vegetation types in summer. The Acacia woodlands have similar numbers of both grass and woody plant species. Not surprisingly the grasslands have the highest number of grass species, while the broadleaf woodlands have the highest number of woody species.

Table 3. The total number of grass species and woody plant species encountered in each vegetation type during summer.

Habitat type	**grass species**	**woody species**	**total plant species**
n=6			
Broadleaf woodland	14	35	49
A. nigrescens woodland	25	24	49
A. nilotica woodland	22	24	46
Grassland	31	12	43

Ordination Results

1) DCA - Bird communities (Figure 1).

The eigenvalues of the first and second ordination axes of the DCA using bird species abundances, were 0.778 and 0.249 respectively. These are relatively high eigenvalues, indicating that the observed patterns are well supported. The first two ordination axes explained 30.8 % of the variance in the species data, which is relatively high for this type of analysis. Figure 1 shows the distribution of the 24 sites in ordination space. The site names have been abbreviated, broadleaf woodland (**b**), *Acacia nigrescens* woodland (**g**), *Acacia nilotica* woodland (**n**) and grassland (**o**). A gradient of increasing vegetation structural complexity is evident from right to left in the diagram. The grassland sites form a distinct cluster on the right of the diagram, and the broadleaf woodlands form a cluster on the left hand side. The two Acacia woodlands occupy the ordination space between the open and the broadleaf clusters. The *A. nilotica* sites and *A nigrescens* sites separate out on the 2nd ordination axis, except for one A. nigrescens site (**6g**) which is placed amongst the nilotica cluster. What this means is that 1) the bird communities in the four vegetation types sampled are relatively sharply defined and distinct from one another, and 2) that there is a high degree of turnover in bird species along the successional gradient of increasing foliage complexity.

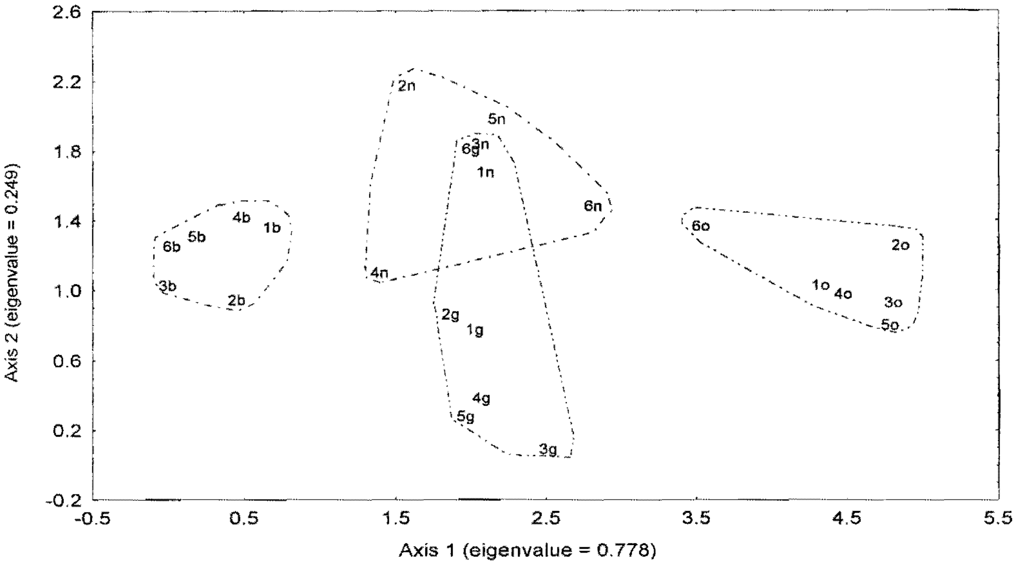

Figure 1: Detrended correspondence analysis (DCA) ordination of the first two axes of the summer bird censuses. The sites are labelled as follows: 1b-6b, broadleaf woodland sites; 1g-6g, *A. nigrescens* woodland sites; 1n-6n, *A. nilotica* woodland sites; 1o-6o, grassland sites.

2) DCA - Plant communities based on presence absence data (Figure 2).

In the ordination by DCA of plant community presence absence data, the first and second ordination axes explained 20 % of the variation in the plant species data. The first and second eigenvalues for the ordination were 0.513 and 0.238 respectively. The main clusters formed were again those of the four vegetation types (Figure 2). However, on first axis the grassland and *A. nilotica* sites formed a single cluster between the *A. nigrescens* sites on the left and the broadleaf sites on the right. There was little separation of sites along the 2nd axis. These axes are more difficult to explain than those of the bird community DCA, as no true environmental variables were measured. However one possibility for the first axis could be a rainfall gradient, from the dry *A. nigrescens* woodlands on the right to the mesic broadleaf woodlands on the left of the diagram.

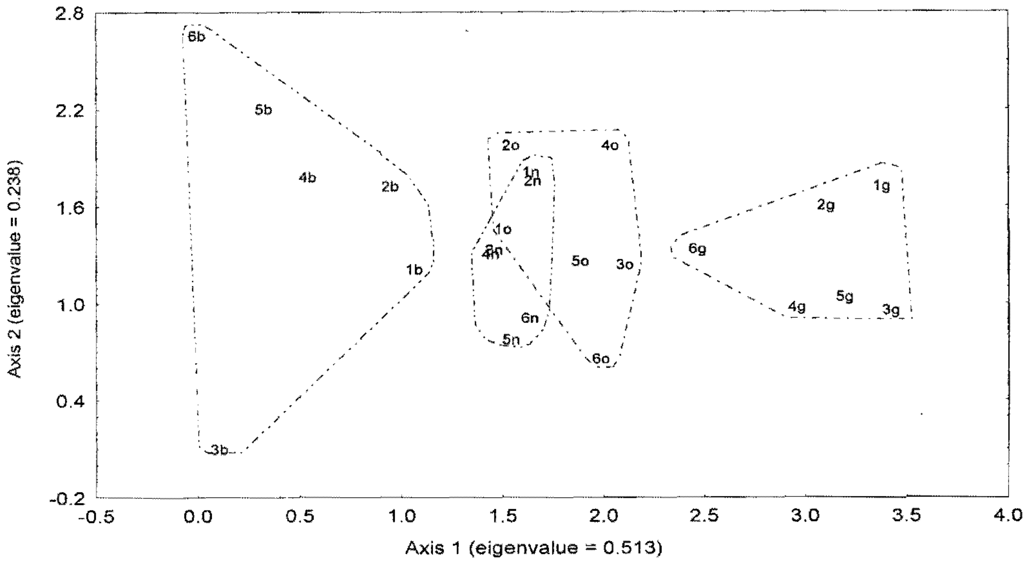

Figure 2: Detrended correspondence analysis (DCA) ordination of the first two axes of the plant presence / absence data from 24 sites sampled. 1b-6b, broadleaf woodland sites; 1g-6g, *A. nigrescens* woodland sites; 1n-6n, *A. nilotica* woodland sites; 1o-6o, grassland sites.

3) DCCA - Bird and vegetation structure (Figure 3).

For the bird data the complete set of vegetation structural variables produced eigenvalues of 0.767 and 0.249 for the first and second axes of the DCCA. The structural variables explained over 62 % of the variance in the bird data (sum of all canonical eigenvalues divided by the inertia). A Monte Carlo permutation test of the F-ratios of the first axis eigenvalue and trace statistic (the sum of all eigenvalues) were both significant ($P<0.01$), indicating that the complete set of structural variables adequately explain the variation in the species data. The determinants of the DCCA axes are most likely those variables with the highest (intraset) correlations, namely CC and FHD-1 (axis 1 $R = -0.957$, $R = -0.911$) and Gr ht (axis 2 $R = 0.829$). The Intraset correlations of all the structural variables and the first two axes are presented in Table 4.

Table 4. Intraset correlations between the vegetation structural variables and the first two axes of the DCCA. All structural variables included.

	Axis 1	Axis 2	
Eigenvalue:	0.776	0.287	
Vegetation structure variable:			
FHD-1	-0.911	-0.265	*
FHD-3	-0.860	-0.312	
Gr den	0.479	0.537	
Gr ht	0.397	0.829	*
GC	0.527	0.625	*
Tr den	-0.907	0.188	
Sh den	-0.769	0.347	*
CC	-0.957	0.134	*
Cn ht	-0.679	-0.532	
Sh ht	-0.446	0.388	

* included in biplot of sites and structural variables (Fig. 3)

The variables Cn ht, Sh ht and Gr den showed weak intraset correlations with both the first and second ordination axes and were thus excluded from the ordination diagram (Table 4). FHD 3 and Tr den were excluded due to colinearity with other variables (FHD 1 and CC respectively). This left a set of five vegetation structural variables (Gr ht, CC, FHD 1, Sh den and GC) which were included in the species - vegetation structure biplot of the 24 sites (Figure 3). The similarities of the sites in terms of the birds found there and the structure of the vegetation is indicated by the spatial relationship of the letters, each of which represents a different community.

The arrows represent the vegetation structure gradients. The relative lengths of the arrows are important as they indicate the relative strengths of the gradients.

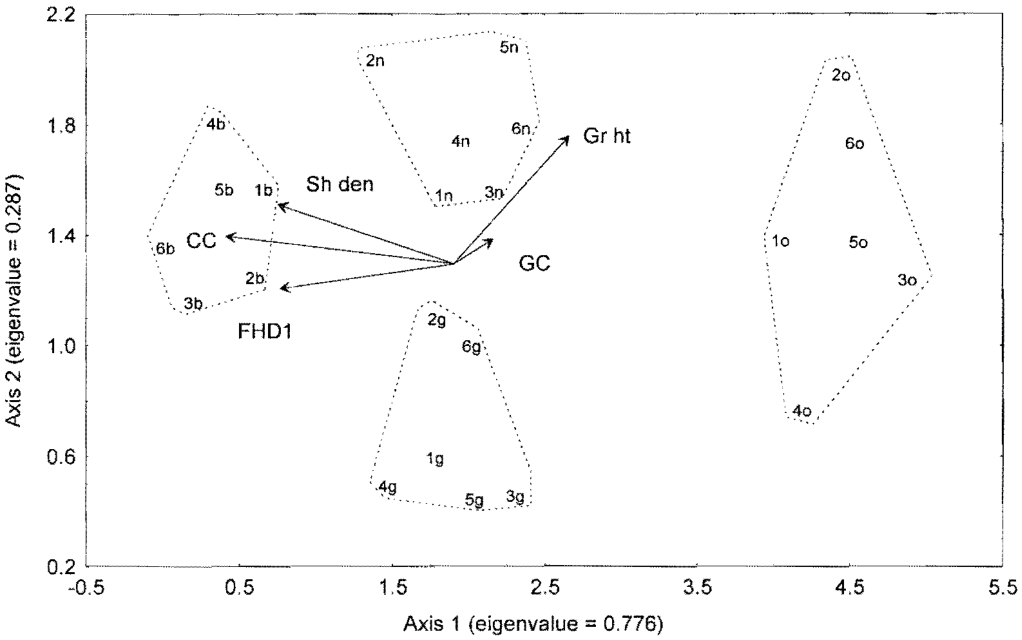

Figure 3: Detrended canonical correspondence (DCCA) ordination of the first two axes of the summer bird census data. Arrows indicate direction and relative magnitude of selected vegetation structural gradients. Site vs. structural variable biplot which shows avifaunal similarities among sites and their relationship to the selected structural variables. FHD-1, total foliage height diversity; Sh den, shrub density; CC, canopy cover; Gr ht, grass height; GC, ground cover.

In the DCCA biplot (Figure 3), the four vegetation types form sharply defined groups. Broadleaf woodlands group together on the left hand side of the diagram, the *A. nilotica* and *A. nigrescens* woodlands occupy the central region (the *A. nilotica* woodlands above the *A. nigrescens* woodlands), and the grasslands group together on the right hand side of the biplot. Canopy cover, Foliage height diversity and Shrub density all support a successional series, of increasing woody plant biomass from the grassland sites on the right, through the *A. nilotica* woodlands in the centre to the broadleaf woodlands on the left. The *A. nigrescens* communities, clustered below the *A. nilotica* woodland sites, do not form part of this series, and occupy a position of intermediate canopy cover and of low grass height. The similarity of the DCA of bird data and the DCCA indicates that the vegetation structural variables are correlated with the organisation of the bird communities.

Key bird species associated with these communities included:

Broadleaf woodland - Redfronted Tinker Barbet (*Pogoniulus pusillus*), Terrestrial Bulbul (*Phyllastrephus terrestris*), Natal Robin (*Cossypha natalensis*), Greenbacked Bleating Warbler (*Camaroptera brachyura*), Cape White eye (*Zosterops pallidus,* Southern Boubou (*Laniarius ferrugineus*), Gorgeous Bushshrike (*Telophorus quadricolor*),).

***A. nigrescens* woodland** - Striped Kingfisher (*Halcyon chelicuti*), African Hoopoe (*Upupa africana*), Pied Barbet (*Tricholaema leucomelas*), Sabota Lark (*Mirafra sabota*), Plumcoloured Starling(*Cinnyricinclus leucogaster*), Greyheaded Sparow (*Passer diffusus*).

***A. nilotica* woodland** - Burntnecked Eremomela (*Eremomela usticollus*), Yellowbellied Eremomela (*Eremomela icteropygialis*), Willow Warbler (*Phylloscopus trochilus*), Chinspot Batis (*Batis molitor*), Orange Breasted Bushshrike (*Telophorus sulfureopectus*), Golden Breasted Bunting (*Emberiza flaviventrus*).

Grassland - Rufousnaped Lark (*Mirafra africana*), Croaking Cisticola (*Cisticola natalensis*), Fantailed Cisticola (*Cisticola juncidis*), Grassveld Pipit (*Anthus cinnamomeus*), Yellow Throated Longclaw (*Macronyx croceus*), Redcollared Widow (*Euplectes ardens*), Redshouldered Widow (*Euplectes axillaris*).

Dissimilarity analysis

The percentage dissimilarity of the four habitat types based on plant and bird presence absence are presented in Tables 5 and 6. In addition to the percentage dissimilarity between vegetation types, the dissimilarity of the sites within each vegetation type are presented. The percentage dissimilarity of the sites within a vegetation type is a measure of the variability in species composition of a vegetation type.

Bird Communities - Table 5

The dissimilarity analysis of the bird communities agrees with the clusters formed in the DCA (Figure 1). The % dissimilarity within the *A. nilotica* woodland sites (62%) is higher than the dissimilarity between the *A. nilotica* and *A. nigrescens* sites (61%), indicating that the bird communities of the two Acacia woodlands are relatively similar. The grassland sites are very different to all the woodlands. There is an 87 %, 83 % and 78 % dissimilarity between grasslands and the broadleaf, *A. nigrescens* and *A. nilotica* woodlands respectively. In contrast to this the *A. nilotica* and *A. nigrescens* woodlands are only 60 % dissimilar.

Table 5. Percentage dissimilarity of habitat types based on **bird** species presence absence data, and the % dissimilarity of the sites within each vegetation type *

	dissimilarity %			
	Broadleaf	*A. nigrescens*	*A. nilotica*	Grassland
Broadleaf	41.1*	77.5	71.9	88.6
A. nigrescens		43.3*	60.6	83.0
A. nilotica			62.1*	73.7
Grassland				44.3*

Table 6. Percentage dissimilarity of habitat types based on **plant** species presence absence data, and the % dissimilarity of the sites within each vegetation type *

	dissimilarity %			
	Broadleaf	*A. nigrescens*	*A. nilotica*	Grassland
Broadleaf	51.9*	78.2	62.8	80.9
A. nigrescens		46.7*	67.5	80.0
A. nilotica			37.5*	52.2
Grassland				53.1*

Plant Communities - Table 6

Table 6 indicates that the plant communities of *A. nilotica* woodlands and grasslands are relatively similar (52% dissimilarity), and that the grassland sites and broadleaf woodland sites vary a great deal in their composition (53% and 52% dissimilarity respectively within sites). As expected the grassland and broadleaf woodland sites are most dissimilar in terms of plant community composition (81%). Interesting differences between the tables are that in *A. nilotica* woodland the sites have similar plant communities (37% dissimilarity) but relatively different bird communities (61% dissimilarity).

Discussion

The principle findings of this study are that, 1) the four vegetation types censused have relatively sharply defined bird communities, 2) the bird communities are linearly arranged along a successional gradient of increasing foliage complexity, and are not related to plant community composition and 3) plant communities of the *A. nilotica* and grassland sites are relatively similar whereas the broadleaf and *A. nigrescens* communities are sharply defined and distinct.

Bird data

The ordination diagrams resulting from the DCA of bird data and DCCA of bird data and structural variables are very similar. The addition of the structural variables did not change the general pattern of community organisation evident in the bird species data. The one *A. nigrescens* site (g6) which was placed among the *A. nilotica* sites in the DCA was placed among the *A. nigrescens* sites in the DCCA. The site (g6) is in a stand of *A. nigrescens* on the upper slopes of a hill, it has low canopy and well developed grass layer. None of the bird species that require open ground (e.g. Sabota Larks) or tall canopies (e.g. Striped Kingfishers) were present resulting in a community similar in composition to the majority of *A. nilotica* woodland sites. It follows therefore that the site would shift from the *A. nilotica* cluster on the DCA to the *A. nigrescens* cluster in DCCA.

The importance of the vegetation structural complexity in defining bird communities is well illustrated by the DCCA biplot. The variables CC and FHD are closely correlated with the ordination axis 1 along which the sites are linearly distributed. This arrangement of the sites agrees with the well established secondary successional sequence in the Park (Chapter 1, page 4). Along this vegetation series, there is rapid turn over in bird species associated with the addition of a tree layer (i.e. between the open grassland avifauna and the acacia woodland avifauna). Willson (1974), who first observed this phenomenon, noted that the turnover was driven by the addition of new feeding guilds of birds, rather than the expansion of guilds already present in shorter vegetation.

Plant data

Despite being structurally very different, the grassland and *A. nilotica* woodland sites are floristically similar. Because the plant community analysis was based on presence absence data, obvious differences in species dominance between grasslands and woodlands were not taken into account. Many of the trees and shrubs characteristic of the *A. nilotica* woodlands in the Park are already present, as shrubs, in the grasslands but in low numbers. Broadleaf woodlands on the other hand are floristically distinct from the other vegetation types, although they are variable in their composition. Secondary succession from an *A. nilotica* woodland to a broadleaf woodland would therefore involve a large turn over in plant species. There is, however, no clear linear arrangement of the sites that would support a sequential change in plant community composition. The endpoints in the plant and bird ordinations (Figures 1 & 2) are different. It is therefore unlikely that the change in bird community composition between vegetation types is driven by a change in the flora.

A. nigrescens woodlands have a relatively distinct flora, which has some elements in common with grasslands and *A. nilotica* woodlands but very little in common with the broadleaf woodlands. The *A. nigrescens* woodlands are generally considered to occupy dry areas in the Park, while broadleaf woodlands are most common in mesic areas, suggesting that the first axis of the plant DCA (Figure 2) represents a moisture gradient, increasing from right to left.

Conclusion

The four vegetation types included in the study have relatively distinct avifaunas. A number of generalist species utilise all four vegetation types, but the majority of birds are restricted to one or two vegetation types. Birds seem to be choosing the habitats they use on the basis of vegetation structure rather than floristics. Sites with similar avifaunas do not necessarily have a similar flora. In contrast sites with similar FHD have very similar avifaunas. As canopy cover, shrub density and FHD increase there is a clear turn over in bird community composition. In the case of secondary succession, open areas would be converted to structurally more complex Acacia woodlands, which, despite being floristically similar to the grasslands, have very different avifaunas. Therefore, in order to maximise avifaunal diversity in the Park, the full range of vegetation types should be maintained, and secondary succession or bush encroachment should be controlled when possible.

Loiselle and Blake (1994) suggest that a range of successional stages is necessary to support the full compliment of bird species that can occur in a given area. Maintenance of a mosaic of habitat types in a particular region or Park may require substantial and active management intervention (Loiselle and Blake 1994). In HUP intervention usually comes in the form of burning which is thought to limit the invasion of woody plants into grasslands and savannas. The frequency and intensity of the burns vary, but traditionally the

burns are cool (in order to allow effective control) and take place in early spring. Other common management intervention includes bush clearing, in which woody plants (usually *Dichrostachys cinerea* and *Acacia karroo*) are cut and removed, leaving the grass layer and canopy layer intact.
This constant disturbance, which produces a spatial mosaic of patches of varying structure in the Park is expensive to conduct. It has been suggested that the managers take more of a hands off approach and allow the successional process to proceed. Broadleaf woodlands would probably increase in area and grasslands would definitely suffer a loss of area. My results show that this would result in the loss of plant and bird species from the Park.

Wiens and Rotenberry (1981) state that , "If habitat structure is either directly or indirectly associated with the niche parametresimportant to the coexistence of species and the structuring of communities.........we should find rather close associations between the co-distribution of species sets or variations in community attributes and patterns of change in habitat configuration". Wiens and Rotenberry's own analyses produced very little support for these expectations. My findings on the other hand provide supporting evidence for the expectations. When the full range of habitat types (from grassland to broadleaf woodland) are considered, co-distributed species sets are closely associated with "habitat configuration" or foliage height diversity.

Chapter 4 : The effects of vegetation structure, habitat patch size and patch isolation on savanna bird diversity

Abstract

Bird communities were censused in four different savanna habitats in order to determine the influence of vegetation structure and patch area on bird species diversity. Between-habitat variation in bird diversity, is mainly a function of vegetation structure. Various foliage height diversity (FHD) measures were positively correlated with both bird species richness and bird species diversity, when all four habitat types were included in the analysis. However, it is primarily the addition of a tree layer (shift from grassland habitats to wooded habitats) which explains the increase in bird species diversity. Within-habitat diversity seems to be controlled by patch area and isolation. Habitat area was positively correlated with the number of specialist bird species in grassland patches, while isolation and specialist bird diversity were negatively correlated in *Acacia nilotica* woodland patches. Due to edge effects in smaller patches, total bird species diversity was not significantly correlated with patch area or isolation. For managers of conservation areas the results suggest that in order to maximise specialist avian diversity 1) large continuous areas of grassland (ca >65 ha) must be encouraged, 2) *Acacia nilotica* woodland patches of < 65 ha are adequate if they are relatively close to "source" areas of over 65 ha, and 3) that physiognomic changes in the vegetation, such as those that occur as a result of secondary succession, could lead to major changes in the avian diversity and community composition and should be closely monitored and controlled.

Introduction

The previous chapter focused on the bird communities of HUP, and the factors relating to their structure and composition. In this chapter the emphasis is on bird species diversity. Investigating species diversity is in many ways simpler than whole community analyses, and for this reason the majority of studies into the relationship between bird communities and their environments focus on diversity. The most commonly asked questions are how vegetation structure and plant diversity, and habitat patch size and isolation, relate to bird species diversity. The objective of such studies is usually to gain insight into the factors controlling niche separation in birds or to gain insight into the effects that landscape modification has on birds.

Most bird diversity work has been conducted in forest environments and habitat fragments separated by urban or agriculturally transformed lands (see Harrison and Bruna 1999 for review) It remains to be seen whether the bird diversity in naturally fragmented heterogeneous landscapes, such as savanna woodlands, responds to patch area and vegetation structure in the same way.

Savanna woodlands are made up of physiognomically very different habitats, from treeless grasslands to thicket vegetation. They are therefore ideal for investigating the relationship between vegetation structure and bird species diversity. Species - area relationships are equally interesting in heterogeneous savanna systems where a complex mosaic of woodland and grassland patches ranging from 1 -1000 ha, mix together. The landscape heterogeneity of the Park is dynamic and can be manipulated by limiting the extent of disturbance events and varying the disturbance regime.

When considering patches of a particular habitat type, situated in a matrix of different, but natural, vegetation, the normal species area concept is misleading (McCoy and Mushinsky 1994). Instead of a linear relationship between species and log patch area, there is a curvilinear relationship, with species reaching a saturating level, rather than increasing indefinitely (McCoy and Mushinsky 1994). This point of saturation is a consequence of a limited pool of species that are present in a particular region that can occupy any patch.

It is likely that the factors controlling bird diversity within a particular habitat will be different to those controlling diversity between habitat types (Wiens and Rotenberry 1981). In this chapter I will first consider between habitat variation in bird diversity, using three woodland communities and a grassland community, and secondly, investigate the variations in bird diversity within one woodland habitat type and one grassland habitat type.

Aims

In Chapter 3 the effects of vegetation change (largely due to successional change) on the bird communities of the Park were investigated. In this chapter I deal briefly with the diversity costs of this vegetation change. More specifically I ask the question "Do habitats with high structural diversity support more species than those of low structural diversity ?" As mentioned in the introductory chapter, numerous authors have asked this question and a positive correlation between the two is expected. What makes the question worth asking in this situation is that the vegetation types included form part of a successional series with rapid changes from one type to another depending, partly, on management decisions. The basic biodiversity implications of such change are at present a matter of speculation.

The central aim of this chapter is to investigate the avifaunal diversity implications of increasing habitat heterogeneity at a landscape level. In terms of Park management this means:

Are heterogeneous landscapes, in which habitat patches are relatively small, and many habitats are represented in a 100 ha area, for example, preferential to landscapes in which habitat patches are large and continuous and each cover over 100 ha? I do this by investigating the relationship between habitat patch size and specialist bird diversity in *A. nilotica* woodlands and grasslands in Hluhluwe-Umfolozi Park (HUP).

Methods

Bird census procedures and habitat measurement techniques are presented and discussed in Chapter 2. Methods specific to this chapter are presented below.

Turnover in bird species

In the previous chapter (Chapter 3) I discussed the turnover in bird species associated with the increase in foliage height diversity. In order to measure this turnover in the bird communities of grassland, *A. nilotica* woodland and broadleaf woodland were arranged along an axis of increasing FHD-1 (Cody 1983b)(*A. nigrescens* woodlands were excluded as they do not form part of the successional series from open grassland to broadleaf woodland). Only the summer data (sites: 1o-6o, 1n-6n and 1b-6b) were used in this analysis to allow the comparison of grassland, *A. nilotica* and broadleaf woodland sites. The turnover in bird species between adjacent sites (in terms of FHD-1) was measured using Wilson and Shmida's (1984) formula which is a modification of Cody's (1983b) beta diversity index (Equation 1).

$$\beta = [\, g(H) + l(H) \,] \,/\, 2.\alpha \qquad (1)$$

where β is the beta diversity between sites, **g(H)** is the number of species gained along gradient **H, l(H)** is the number of species lost along gradient **H**, and α is the mean sample richness of all the samples along the gradient. β Diversity is independent of alpha diversity (as measured by the Shannon Wiener index at a particular site), and sampling intensity (Wilson and Shmida 1984). β Diversity (turnover) was plotted against the higher FHD-1 of each pair of sites. For example, sites 3o and 2o have FHD-1 values of 0.08 and

0.14 respectively; the turnover between these sites was plotted against the FHD-1 value of site 2o.

Patch area and isolation

The area and perimeter of each patch was measured using digital vegetation maps (Meyer 1999) in conjunction with black and white 1:10000 orthophotogaphs. The program ARC VIEW (version 3.1.1, Environmental Systems Research Institute 1999, Redlands, Calif.) made this possible. Using ARC VIEW a circle with a diameter of 1 km , centred at the mid point of the transect was drawn. The area within this circle, covered by the same vegetation type as the patch was calculated in Km^2. This area (a) was divided by the total area inside the circle ($\Pi \times 0.5^2 = 0.785$), and multiplied by 100 to get a percentage value. In this study the reciprocal of this percentage is used as a measure of relative isolation of the habitat patches (Equation 2).

$$\mathbf{I = 100 - ((a / T) . 100)} \qquad \mathbf{(2)}$$

Where **I** is relative isolation, **a** is area (in km^2) covered by vegetation type x, and **T** is the area of a circle with diameter 1 km. Using this method one is able to distinguish between two patches of equal area where one patch has numerous similar patches within 500m, while the other has no similar vegetation within 500m. Large patches will therefore usually have low isolation.

Bird habitat selectivity

In order to determine habitat specialists in each habitat type Jacob's (1974) modification of Ivlev's selectivity index was used (Equation 3)(see Velasquez *et al.* 1991). This selectivity index takes the area of a particular vegetation type into account as well as the frequency at which the vegetation type is selected by each species. Habitat selectivity for each of the bird species encountered was calculated in the following way.

$$\mathbf{E_i = (p_i - q_i) / (p_i + q_i - 2p_i . q_i),} \qquad \textbf{(3)}$$

where $\mathbf{p_i = N_i / N_t}$ and $\mathbf{q_i = A_i / A_t}$
$\mathbf{N_i}$ is a measure of abundance of a species in a particular habitat and $\mathbf{N_t}$ is a measure of total abundance for a species. In this study I used encounter per unit time as a measure of abundance. $\mathbf{A_i}$ is the area of habitat **i**, and $\mathbf{A_t}$ is the total area. $\mathbf{E_i}$ ranges from -1 to +1, with positive values indicating preference and negative values indicating avoidance of a particular habitat. This method was used successfully by Velasquez *et al.* (1991) for determining waterbird habitat selectivity.

In the grassland sites bird species with an $\mathbf{E_i} > 0.3$ were considered 'specialists'. In the *A. nilotica* sites a species with an $\mathbf{E_i} > 0.1$ was sufficient to be classed as 'specialist'. Because woodland birds tend to use more than one type of habitat, the $\mathbf{E_i}$ cut off could not be as high as for the highly selective grassland birds. Species in which fewer than five individuals were observed during the whole census period were excluded from the selectivity calculations.

It is important to note that the term 'specialists' refers only to distribution patterns of birds in relation to habitat types in HUP. Savanna woodland birds in this region are rather cosmopolitan in distribution and occupy a wide range of habitat types across the sub continent. Although general preferences for thorn or moist broadleaf or mature riverine woodland have been noted for most bird species (Harrison *et al.* 1997), few, if any are restricted to particular woodland habitats (e.g. *A. nilotica*, *A. nigrescens*, or *Euclea* woodlands) across their entire range.

Data Analyses

Using the habitat selectivity of each bird species encountered, a list of species which preferentially utilise each habitat can be drawn up (Appendix 4). In this way the overall and specialist bird species richness and diversity of the four vegetation types can be determined.

For the majority of the scatterplots generated a standard linear regression model was applied. However, for scatterplots of log (patch area) and isolation versus bird species diversity in grasslands, relationships were non linear declining or increasing to an asymptote. A range of non-linear equations was fitted to determine the most appropriate curve. The best fitting curve was determined by eye.

Results

General

A total of 56 and 26 species respectively were encountered during the winter census of *A. nilotica* and grassland patches (Table 1). The most abundant species in winter were the Rattling Cisticola (*Cisticola chiniana*) and Blackeyed Bulbul (*Pycnonotus barbatus*). In winter the most abundant bird species in the grassland patches was the Fantailed Cisticola (*Cisticola Juncidis*), while in the *A. nilotica* woodland the Rattling Cisticola was the most abundant.

Table 1: Species richness and abundance of birds in each habitat in winter, based on encounters during 80 min of dawn censusing per site, with 12 sites per vegetation type.

	All birds	
Habitat type	**species**	**individuals**
Winter (n=12)		
A. nilotica woodland	56	847
Grassland	26	397

Foliage height diversity relationships

There are strong positive correlations between bird diversity, richness and abundance, and foliage height diversity (FHD). The relationship FHD-1 and bird species diversity (BSD) is shown in figure 1a ($R^2 = 0.70$, df 22, $P < 0.00001$), and that between FHD-3 and BSD in figure 1b ($R^2 = 0.67$, df 22, $P < 0.00001$). Richness and abundance of birds was also significantly correlated with both FHD-1 and FHD-3 (Table 2).

Table 2: Correlations between Foliage height diversity (both FHD-1 and FHD-3) and bird abundance and bird species richness (BSR)(FHD-3 is non herbaceous FHD, FHD-1 is total FHD).

Variables	**R**	**df**	**P**
FHD-1 vs. BSR	0.76	22	***
FHD-1 vs. abundance	0.50	22	*
FHD-3 vs. BSR	0.73	22	***
FHD-3 vs. abundance	0.52	22	**

- $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS $P > 0.05$

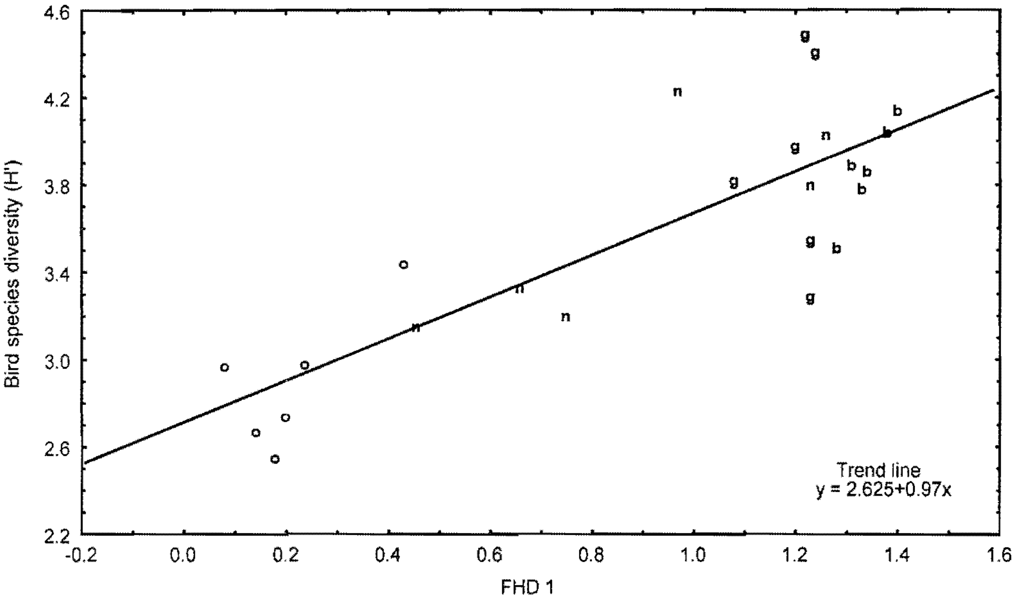

Figure 1a: Relationship between FHD-1 (total FHD) and bird species diversity (BSD) in broadleaf woodland (b), *A. nigrescens* woodland (g), *A. nilotica* woodland (n) and grassland (o) sites ($R^2 = 0.70$, df 22, $P<0.05$).

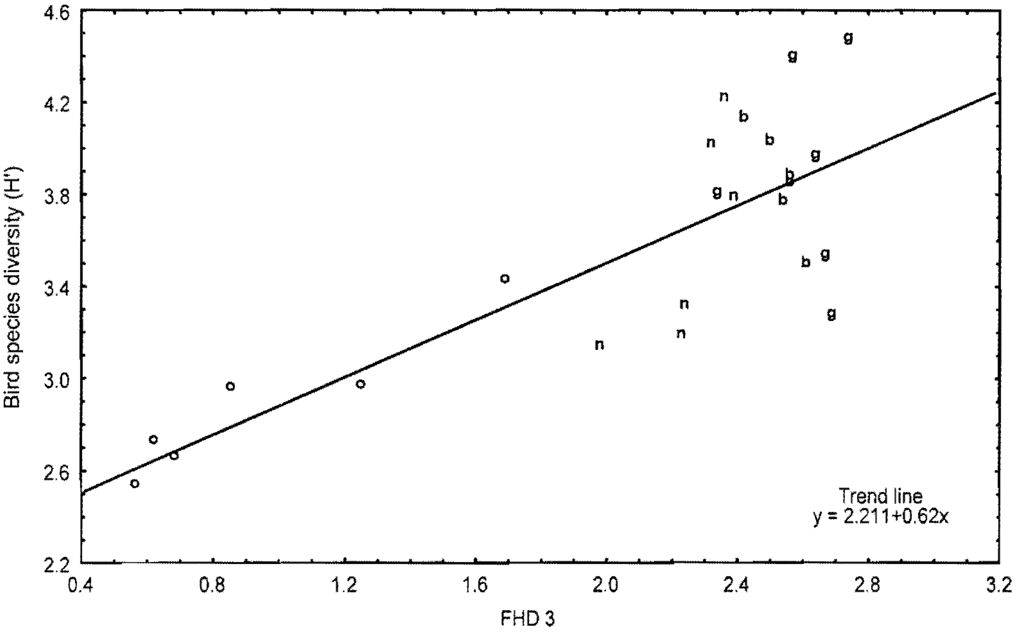

Figure 1b: Relationship between FHD-3 (non-herbaceous FHD) and bird species diversity (BSD) in broadleaf woodland (b), *A. nigrescens* woodland (g), *A. nilotica* woodland (n) and grassland (o) sites ($R^2 = 0.67$, df 22, $P<0.05$).

When grassland sites are excluded from the above correlations (Figures 1a & 1b) (i.e. only wooded sites are considered), both relationships weaken, with

FHD-1 vs. BSD remaining significant (R^2 = 0.34, df 16, P=0.01), and FHD-3 vs. BSD becoming non-significant. (R^2 = 0.18, df 16, P=0.08). This indicates that the relationship between FHD and BSD is poorly supported in habitats with high tree density.

Turnover of species

Figure 2 shows the turnover of bird species along a gradient of increasing foliage height diversity. Areas of interest on figure 2, are 1) the high species turnover rates at the transition from grassland to woodland (at FHD-1 ≅ 0.45), 2) the decrease in turnover at the transition from *A. nilotica* to broadleaf woodland and 3) the dramatic increase in species turnover at the maximum FHD. This figure suggests that the most rapid turnover in bird species is at the grassland / woodland transition, but that there is also high turnover in bird species among sites with very high FHD.

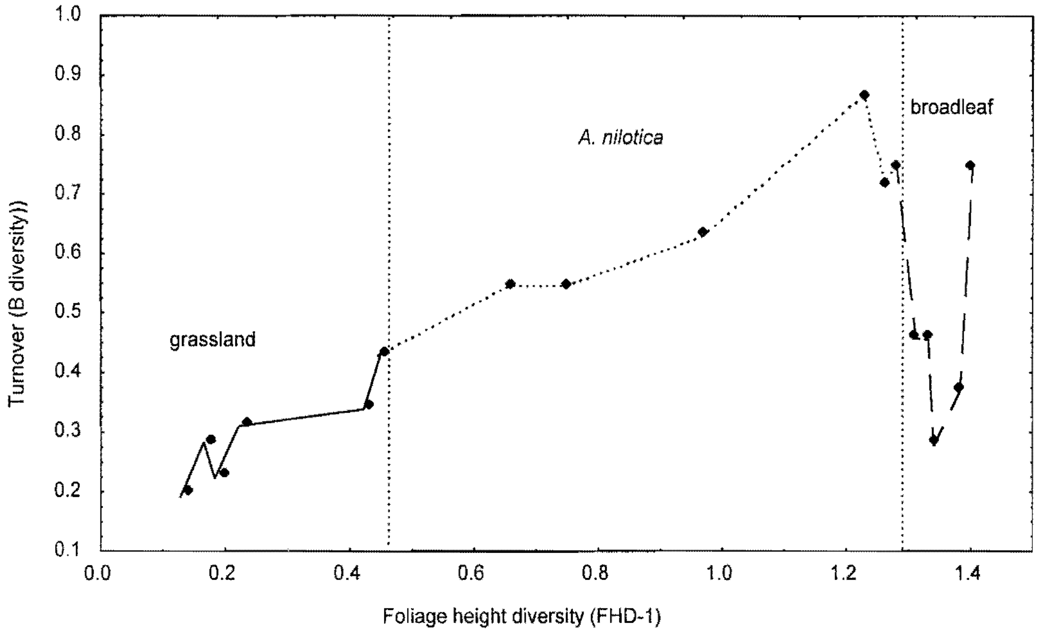

Figure 2: Turnover in bird species along a gradient of increasing foliage height diversity (FHD-1). Turnover in this case is β diversity (Wilson and Shimda 1984) between adjacent sites. β diversity is plotted against the higher FHD of each pair of sites. Figure based on summer censuses in grassland, *A. nilotica* woodland and broadleaf woodland (n = 17).

Herbaceous layer structure

Grass density, grass height and % ground cover are all negatively correlated with bird diversity (Table 3). However, there is a strong link between the structure of the herbaceous layer and the canopy structure (Table 4). Wooded sites with high FHD, tree density, canopy cover and canopy height have lower grass height, grass density and % ground cover than grassland sites which have intrinsically low FHD.

Table 3: Herbaceous layer structure vs. bird species diversity (BSD). Gr den is grass density, Gr ht is average grass height and % GC is percentage ground cover.

Variables	**R**	**df**	**P**
Gr den vs. BSD	-0.55	22	**
Gr ht vs. BSD	-0.57	22	**
% GC vs. BSD	-0.65	22	***

* $P < 0.05$, ** $P< 0.01$, *** $P < 0.001$, NS $P > 0.05$

Table 4: Relationship between herbaceous layer structural variables (GC, ground cover; Gr den, grass density) and canopy structural variables (CC, canopy cover; FHD-1, total foliage height diversity).

Variables	**R**	**df**	**P**
FHD-1 vs. % GC	-0.67	22	***
% CC vs. Gr den	-0.42	22	*

* $P < 0.05$, ** $P< 0.01$, *** $P < 0.001$, NS $P > 0.05$

Plant Species Richness residual analysis

Plant Species Richness (PSR) and bird species diversity (BSD) are significantly positively correlated ($R^2 = 0.27$, df 22, $P=0.0087$). However, it is clear from Figure 3 that PSR accounts for none of the residual variation in the FHD-1 vs. BSD correlation (Figure 1a). The wooded sites contain more plant species than the open sites, and usually have a more complex foliage profile. Thus although plant species diversity alone is a fair predictor of bird diversity it is because PSR is high when FHD is high, and when this is taken into account, PSR contributes nothing further. In other words habitats with different numbers of plant species will have the same bird diversity if they have the same FHD.

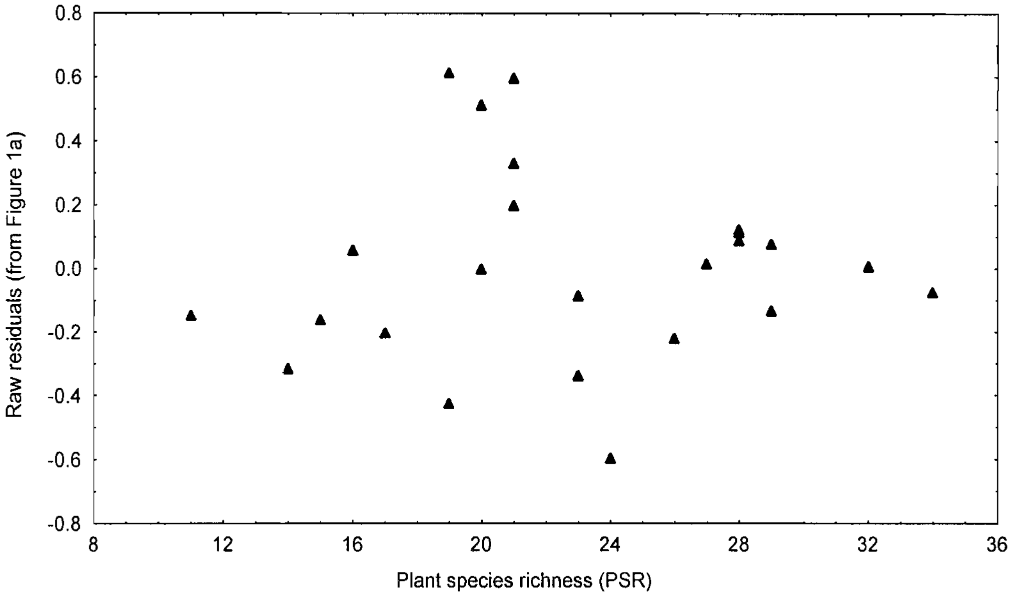

Figure 3: Scatter plot showing plant species richness vs. the raw residuals of FHD-1 vs. bird species diversity (BSD). Based on the summer censuses in grassland, *A. nilotica, A. nigrescens* and broadleaf woodland. (R^2 = 0.001, df, 22, NS).

Area and isolation

Grassland Sites

Area

Overall species diversity and log area were not significantly correlated in the grassland patches during winter (R^2 = 0.16, df 10, P=0.2) (Figure 4a). On the other hand species diversity of "specialist" birds, according to the selectivity index, was positively correlated with log patch area (R^2 = 0.48, df 10, P=0.01)(Figure 4b). Bird abundance relates similarly to log area with no correlation between overall abundance and log patch area, and a significant positive relationship between abundance of specialists and log patch area (R^2 = 0,12 and R^2 = 0.37 respectively).

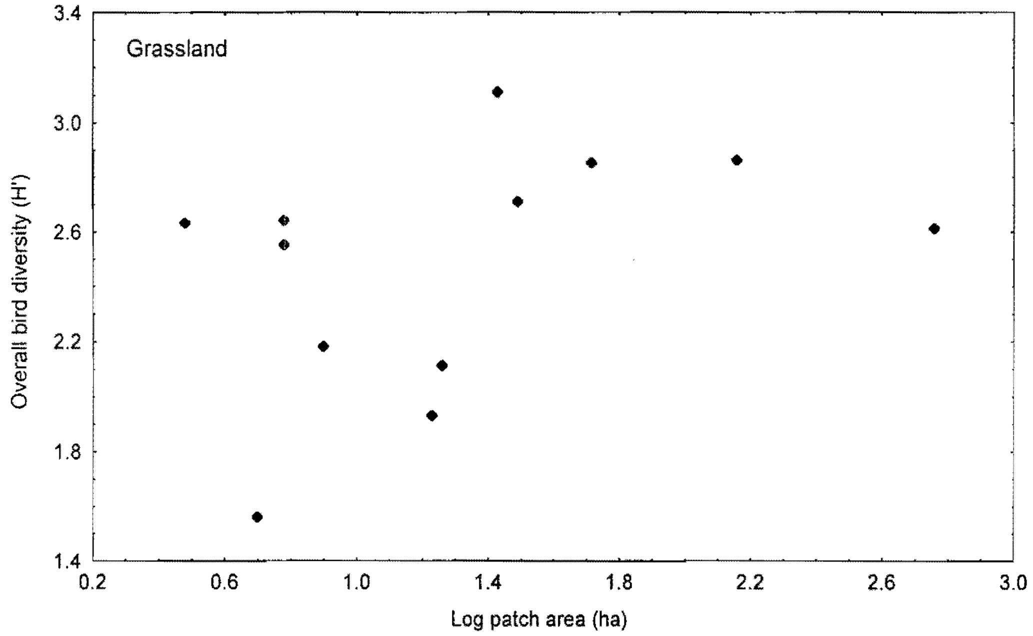

Figure 4a: Relationship between log patch area and **overall** grassland bird diversity (R^2 = 0.16, df 10, NS).

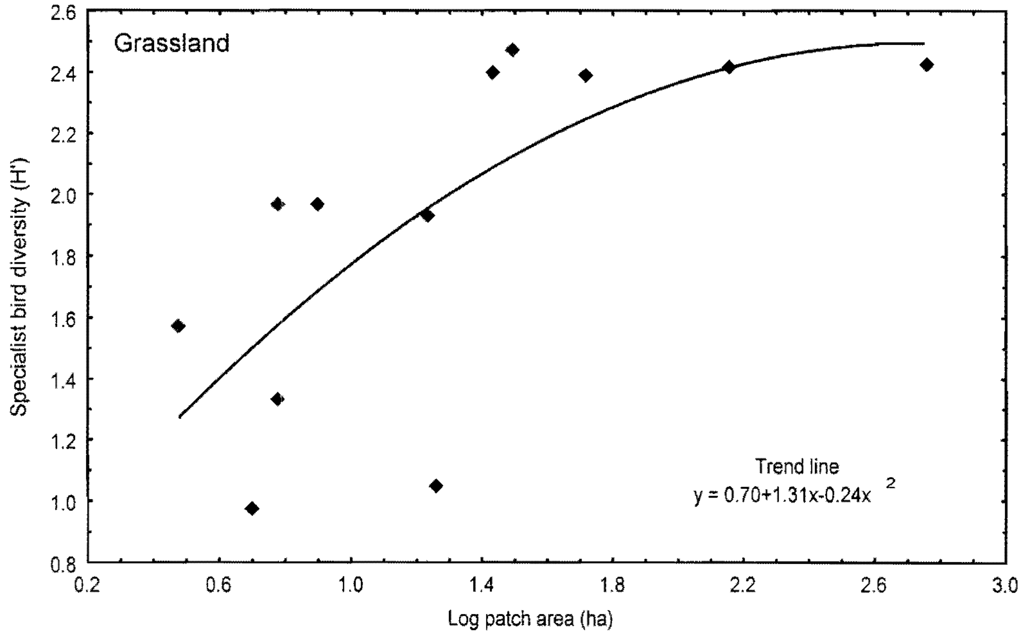

Figure 4b: Relationship between log patch area and **specialist** grassland bird diversity (R^2 = 0.48, df 10, P<0.05). The model used is: $y = ax^2 + bx + c$.

Patch isolation (% isolation) is not significantly related to specialist bird diversity in the grassland sites ($R^2 = 0.07$, df 10) (Figure 5). Small grassland patches such as sites 11 and 12 have low bird diversity despite being with in 500m of a number of open areas.

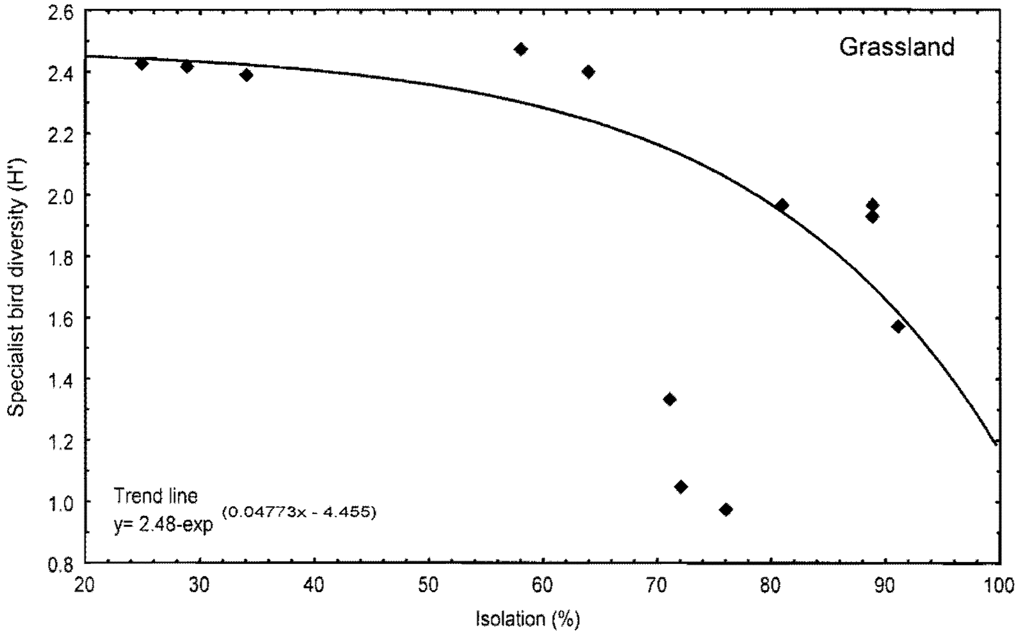

Figure 5: Relationship between percentage patch isolation and **specialist** grassland bird diversity. The fitted trend line uses the model: $y = A - \exp^{(bx-c)}$, where A is (y^{max} + 0.01).

A. nilotica Sites

Area

In the *A. nilotica* woodlands there was no significant Relationshipbetween overall bird diversity and log area of patch (Figure 6a)($R^2 = 0{,}03$, df 10, P=0.62). The diversity of specialists, calculated by the selectivity index, also showed no significant correlations with log patch area (Figure 6b)($R^2 = 0.08$, df 10, P=0.37).

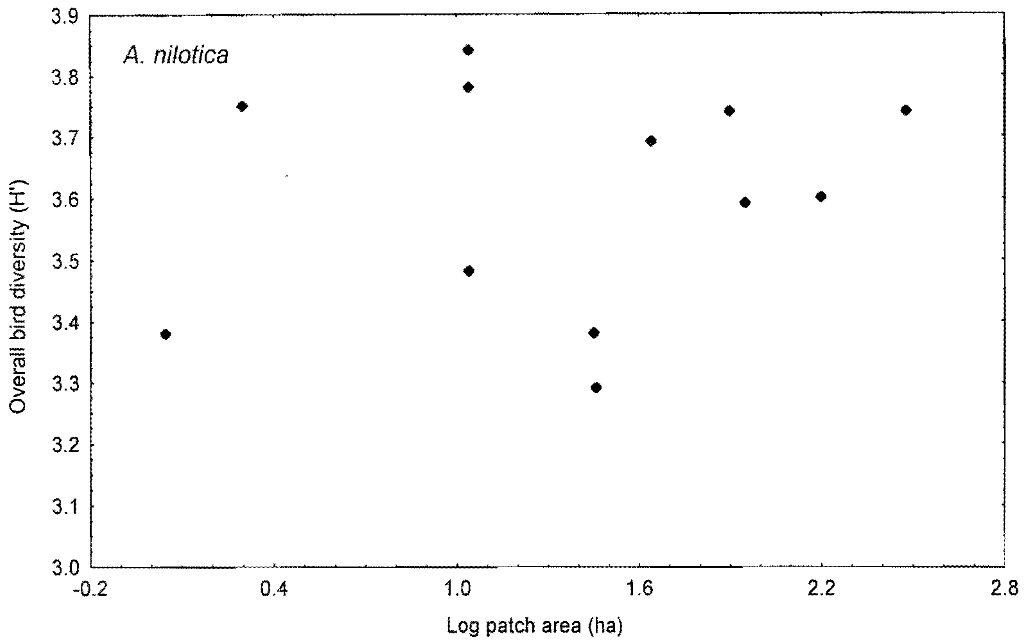

Figure 6a: Relationship between log patch area and **overall** *A. nilotica* woodland bird diversity (R^2 = 0.02, df 10)

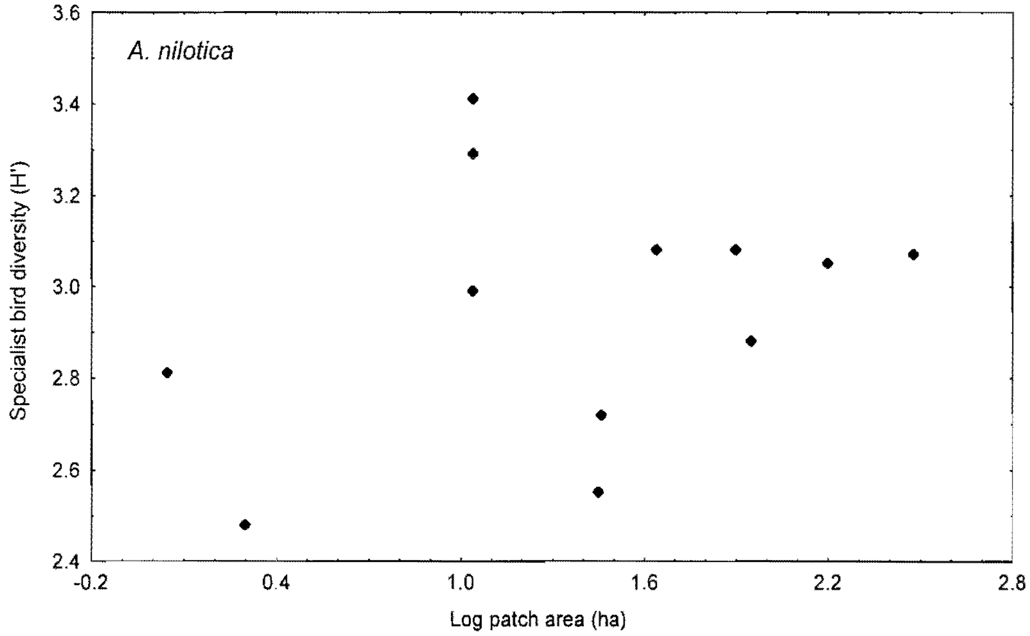

Figure 6b: Relationship between log patch area and **specialist** *A. nilotica* woodland bird diversity (R^2 = 0.08, df 10)

The total number (i.e. abundance) of individual birds encountered at each site was not correlated with log patch area (R^2 = 0.05, df 10, P=0.477). Similarly, there was no between abundance of specialist *A. nilotica* birds and log patch area (R^2 = 0.15, df 10, P=0.2). Thus, the large patches of woodland did not support significantly more or less individual birds than the small woodland patches.

Isolation

Patch isolation explains a significant amount of the variation in *A. nilotica* woodland specialist bird diversity (Figure 7)(R^2 = 0.52, df 10, P=0.0085). Medium and small *A. nilotica* patches which have low isolation values, because they're close to large *A. nilotica* stands (e.g. site 8, site 10 and site 12), have relatively high specialist bird diversity. This suggests that specialist *A. nilotica* woodland birds are capable of moving between the patches in an archipelago of *A. nilotica* patches situated in a matrix of broadleaf woodland or grassland.

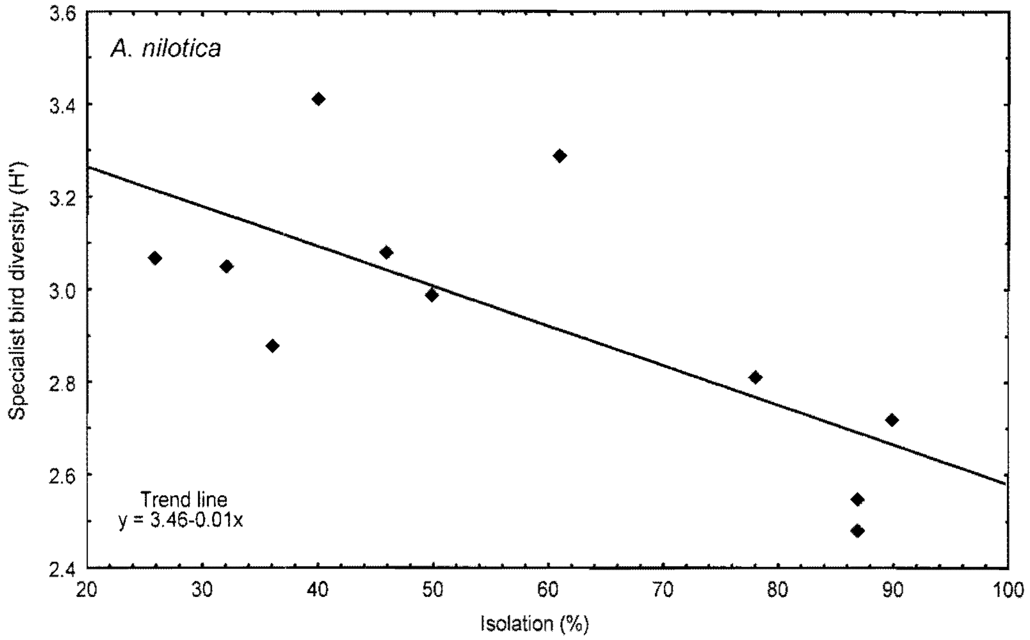

Figure 7: Relationship between percentage patch isolation and **specialist** *A. nilotica* woodland bird diversity (R^2 = 0.52, df 10, P<0.05).

Patch Shape

The effects of patch shape on diversity were not studied. The area effect in the grasslands and isolation effect in the *A. nilotica* woodland probably mask any effects that may be present. In order to understand the influence of patch shape, a number of patches of comparable area would have to be included in the study. Some possible effects would be higher numbers of generalist or edge species in patches with high perimeter to area ratios.

Discussion

Vegetation Structure

FHD and vegetation structure

The results show that when a range of habitat types are considered, sites with high foliage height diversity have higher bird species diversity than sites with low FHD (Figure 1a and 1b, Table 2). This relationship is well documented. However, as noted by Willson (1974) and Ralph (1985), it is the addition of a tree layer which is largely responsible for the relationship. Figures 1a & 1b show that as FHD increases along the vegetation successional series, in general, grassland sites have the lowest FHD, the broadleaf woodlands the highest and the *A. nilotica* woodlands an intermediate FHD.

The ordinations in the previous chapter (Figure 1, Chapter 3) show that the bird communities in each of these successional stages are relatively distinct from one another. Therefore, although bird diversity increases from grassland to *A. nilotica* to broadleaf habitats (Figure 1a), the bird community composition alters as well.

Bird species turnover

The first peak in figure 2 is the transition between grassland and woodland habitats. At this transition the turnover in species is at its highest level as grassland species are lost and woodland species are gained. After the transition the turnover in species increases more gradually to a peak and then decreases. This suggests that, to birds, the addition of the tree layer is the most important aspect of vegetation change (see Willson 1974). The implication of this is that if shrubs in grasslands are allowed to grow into trees there will be a significant change in the avifauna.

The second transition in figure 2 is more difficult to explain, but indicates that the sites with very high FHD values have a relatively distinct avifaunas (i.e. there is a high turnover between the broadleaf sites with FHD-1 less than 1.3 and those with FHD-1 above 1.35). One possible explanation for this is that the sites with FHD over 1.35 are more similar to forest habitats than woodland habitats (in this region evergreen forests are part of the landscape and there is a distinctive avifauna associated with the forests).

Herbaceous layer structure

The correlations in table 3 indicate that there is a significant negative relationship between the density of the herbaceous layer and BSD. However, it is unlikely that increased bird diversity in woodlands in relation to grasslands is related to the thinning of the herbaceous layer. It is more likely that the structure of the herbaceous layer is linked to the canopy structure. In general, when considering a wide range of habitat types, dense or complex canopies are associated with a sparse herbaceous layer (Table 4). For this reason it is likely that the relationships between grass density, ground cover and grass height, and bird species diversity (Table 3) may simply be a result of the low FHD of sites with sparse or non-existent canopy (Table 4).

To complicate the issue further, the herbaceous layer in *A. nilotica* woodlands is determined to a large degree by the altitude of the site (altitude is a good predictor of rainfall in this area). Low lying sites, which receive less rainfall than higher altitude sites, often have a reduced grass sward and low percentage ground cover, despite having relatively open canopy structure.

Differences in vegetation structure (canopy and herbaceous structure) between the 12 *A. nilotica* woodland sites, censused in winter, were not significantly related to bird diversity or abundance. This suggests that within a particular vegetation type, variation in FHD and other structural elements is not important to birds.

Like the *A. nilotica* woodlands, the various measures of vegetation structure did not relate directly to BSD in the grassland sites, censused in winter.

Effect of plant species richness (PSR) on bird diversity

Bird species diversity does not seem to be related to plant species richness, although there was a significant correlation between them. The residual analysis (Figure 3) indicates that when vegetation structure is taken into account, plant species richness explains no additional variance in bird diversity. Habitats of the same foliage profile therefore have the same BSD whether composed of a few or many plant species. This is an example of the now widely accepted phenomenon that diversity patterns vary independently in different taxa (see Lawton 1998, and Cummings *et al.* 1997). Ideally a habitat with high FHD and low PSR should be included in an analysis of the relative importance of structural diversity and plant species diversity in determining bird species diversity. (One such habitat, which could be investigated in future, in this savanna system are the tall (12m), largely monospecific *Spirostachys africana* (Sond.) **Euphorbiaceae** woodlands)

Area and isolation

Grassland sites

The interesting findings in the winter study of the grassland habitats, were; 1) that large patches do not have significantly higher overall bird diversity than small patches, but 2) that the diversity of **specialist** grassland birds was significantly higher in large grassland patches than in small grassland patches, 3) that small patches which are not isolated still have depressed **specialist** bird diversities.

The relatively high total species diversity in small patches is interesting. Biological edge effects have been widely shown to influence bird diversity in small habitat patches (Ambuel and Temple 1983, Saunders *et al.* 1991, McCoy and Mushinsky 1994). In this case birds (usually generalist species) from surrounding habitats tend to utilise small patches of "inappropriate" habitat. For example the small grassland patches tended to have higher numbers of woodland generalists such as Rattling Cisticolas (*Cisticola chiniana*) and Blackeyed Bulbuls (*Pycnonotus barbatus*) than the large grassland areas. Woodland understory species such as Rattling Cisticolas and Tawnyflanked Prinias (*Prinia subflava*) were commonly observed in the shrub layer of small grassland patches, and were absent in the large grassland areas.

The bird species which preferentially occupy grasslands (Appendix 4) according to the habitat selectivity index, are for the most part considered grassland birds by texts on South African birds (see Harrison *et al.* 1997). It is the diversity of these species which one would expect to be affected by patch area.

My results indicate that small grassland patches have lower specialist bird species diversity than large grassland patches. It is clear from the scatter plot that the specialist bird diversity vs. log area curve levels off at approximately

65 ha (Figure 4b). Because the y axis in this example is specialist bird diversity of a particular habitat type, one would expect an upper limit of bird diversity to be reached when the area was so large that it included all the grassland and open savanna birds that have been recorded in the region. The relationship is therefore not a true species - area relationship, rather a type of incidence function. The probability of encountering new species decreases as patch size increases.

The weak relationship between specialist bird diversity and patch isolation (Figure 5) is difficult to explain. Small grassland sites such as sites 10 and 11, which are separated from other large grassland patches by relatively short stretches of woodland, have specialist bird diversities comparable to highly isolated small or medium patches (sites 8 and 9). This suggests that the specialist grassland birds found in a patch (regardless of its size) do not utilise other adjacent patches. This is in contrast to the situation in *A. nilotica* woodlands where birds seem to utilise adjacent patches on a daily basis. This finding may indicate a type of source-sink model (Pulliam 1988, Danielson 1992), in which large species-rich patches provide colonists for small patches (which are more prone to whole-patch disturbance events). If this were the case, groups of small patches may be of limited value in conserving grassland birds and large continuous areas of grassland (> 65a) may be required in the Park to maintain grassland bird diversity.

***A. nilotica* woodland sites**

None of the correlations between bird diversity and patch area were significant in the *A. nilotica* woodlands (Figure 6a and Figure 6b). Specialist bird species diversity, on the other hand, is clearly related to patch isolation (Figure 7). Isolated patches of *A. nilotica* woodland (such as sites 6 and 7) have fewer specialists than patches which are close (less than 500m) to patches of the same woodland type (e.g. sites 12 and 8). This indicates that woodland birds move between adjacent woodland islands on a regular basis but seldom reach the more isolated patches. For this habitat type the fragmentation of a large continuous area of woodland into an archipelago of small patches, close together, would not severely affect bird diversity. This is the reverse of the situation for the grassland habitats. Large continuous patches of *A. nilotica* woodland are still desirable, in that they contain the majority of specialist birds. However, a range of patch sizes in the landscape would be sufficient to maintain bird diversity, provided the small patches do not become highly isolated.

The matrix vegetation in which a small patch of *A. nilotica* woodland is situated is also important in determining the overall bird diversity of the patch. Patches surrounded by broadleaf woodland have the highest diversity because many broadleaf specialists can utilise thorn woodlands. These are considered edge species (some examples include Cape White Eyes *Zosterops pallidus*, Collared Sunbirds *Anthreptes collaris*). On the other hand *A. nilotica* patches surrounded by grassland do not gain many "edge" species as grassland birds seldom utilise woodlands of any kinds. Occasional exceptions include Croaking Cisticolas (*Cisticola natalensis*) and Redcollared Widows (*Euplectes ardens*).

Implications

Current secondary successional trends in HUP, could conceivably result in the alteration of existing bird communities and the loss of numerous grassland specialist birds. However managers currently manipulate disturbance regimes (fire frequencies and intensities) and herbivore densities in order to maximise habitat heterogeneity, ensuring that a wide range of successional stages are maintained within the Park. Yet, it remains to be seen whether this will be enough to ensure that avian diversity in the Park will be conserved. Within-habitat variation in bird diversity seems to be related to patch area in grassland environments and patch isolation in *A. nilotica* woodlands. My findings, based on bird diversity suggest that in order to maximise bird species diversity in the Park managers should aim to 1) prevent large grassland environments from being fragmented into sections smaller than ca. 65 ha, and 2) encourage the creation of archipelagos of small patches of woodland, if the fragmentation of a large continuous patch of *A. nilotica* woodland is unavoidable.

Maximising diversity of one component of the biota does not necessarily maximise that of others. Lawton *et al.* (1998) showed that species turnover along a disturbance gradient differs among taxonomic groups. Cummings *et al.* (1997) on the other hand found that both bird and ant species richness was significantly lower in elephant altered woodlands than in unaltered woodlands, and that bat and mantid richness was lower although not significantly so. Herremans (1993) showed that while increased elephant disturbance resulted in a decline in plant diversity, bird diversity did not decline. However, Herremans (1993) also noted avifaunal compositional changes in disturbed vs. undisturbed areas, with migrants being especially sensitive to habitat change. It is reasonable to assume that birds and large mammals in HUP would be the main groups affected by habitat change.

My findings suggest that managing a conservation area with the aim of maximising biodiversity requires the protection of not only the full spectrum of habitat types but of large continuous areas of each habitat as well. Management aimed at maximising habitat heterogeneity may not achieve the desired effect of conserving diversity if the patch area and /or isolation of different habitat types falls below acceptable thresholds.

These findings are based on a limited series of censuses which provide insight into only the relatively abundant component of the avifauna. The censusing procedures are easily repeatable, and provide a sampling frame work for the investigation of other taxa.

Chapter 5: Landscape Model

Introduction

The influence that landscape heterogeneity has on biotic diversity is largely a matter of speculation. In general a heterogeneous landscape is thought to house more species than a homogeneous landscape (Rosenzweig 1995). In the previous chapters I have shown that woodlands tend to have higher avian diversity than grasslands, that grassland specialist bird diversity is largely a function of habitat patch area and that *A. nilotica* woodland specialist bird diversity is a function of habitat patch isolation. In order to relate these findings to savanna management it may be useful to create a simplified model of the landscape which covers a range of landscape heterogeneity.

The recently proposed patch mosaic burning strategy (Parr and Brockett 1999) aims to increase biotic diversity by maximising landscape heterogeneity. The assumption is that the more habitats present in a landscape the more species the landscape will support. Yet the scale of the landscape heterogeneity that managers of savanna conservation areas should aim for remains unclear. For example, do managers aim for a coarse grained landscape with individual patches over 50 ha or a fine grained landscape with individual patches of 10 ha? This difference could be crucial to biodiversity conservation if, for example, some species had a minimum patch size requirement of 30 ha, and thus were lost in the fine grained landscapes.

The aim of this chapter is to link the avian species / area relationship, for two habitats, to landscape heterogeneity, and in this way predict what landscape configurations may be best suited to conservation. To do so, one needs to ask this question: "what do we want to conserve?" Wiens (1997) highlights three foci for conservation: species (as in single species conservation), biodiversity and ecosystem function. In the context of this study bird species diversity is of principle interest. A further aim of this chapter is to determine a measure of diversity which takes differences in community composition between habitats into account.

Model design

I created simulated "landscapes" varying in amount and configuration of two habitat types. The habitat types represent grassland and woodland. The landscapes were represented in a grid 10 cells wide and 14 long where each cell is either "grassland" or "woodland". 10 grids were created, each representing a landscape in which the amount of woodland increases and the amount of grassland decreases from the first (96% grassland and 4 % woodland) to the last grid (6 % grassland and 94 % woodland) (Figure 1a). For each habitat type in each landscape the total amount of the habitat (**TA**), the largest continuous habitat patch (**LP**) and the average size of the patches (**AV**) can be measured (Table 1). **TA** is calculated as the sum of all the cells of a particular habitat, for **LA** only the largest "patch" of cells is counted, and for **AV** the average number of cells per "patch" is calculated. In this model only directly adjacent cells form part of the same "patch", cells diagonally adjacent are not considered to be part of the same "patch".

The grain of habitat patchiness is potentially important for controlling diversity. For example, a landscape with an equal amount of woodland and grassland (Grid 6) is interesting as it can have a large range of grain sizes (e.g. 70 grassland and 70 woodland patches or 1 grassland and 1 woodland patch). In order to explore the effects of landscape grain a series of landscapes with equal amounts of woodland and grassland, but with differing patch sizes were created (Figure 1b). The differences between these landscapes is only evident when the largest patch (**LP**) or average patch size (**AV**) is considered as the total amount of each habitat (**TA**) is equal (Table 1).

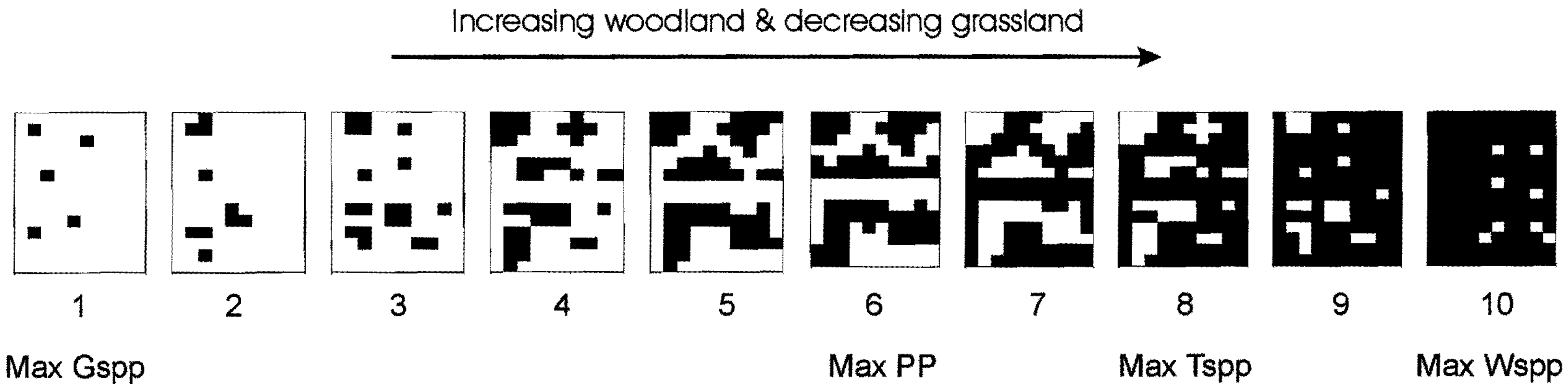

Figure 1a: Range of landscapes included in the model, dark cells represent woodland and clear cells grassland. Grid 6 has an equal number of woodland and grassland cells. Gspp = grassland species, Wspp = woodland species, PP = product of proportion of grassland and woodland species, Tspp = total species. Refer to figure 2 for details.

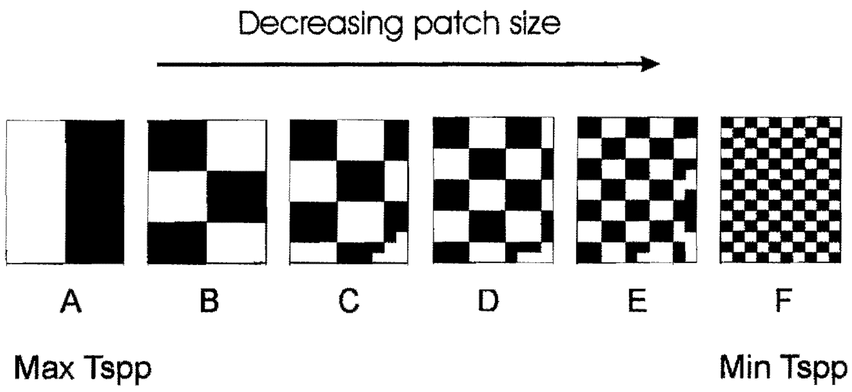

Figure 1b: Range of landscapes with equal amounts of grassland and woodland. Tspp = total number of species in landscape.

Table 1: The total amount (**TA**), the largest patch (**LP**), the number of patches (**NP**) and the average patch size (**AV**) of woodland and grassland in each landscape in Figure 1a and Figure 1b (units are number of cells).

Grid	Woodland				Grassland			
number	TA	LP	NP	AV	TA	LP	NP	AV
1	5	1	5	1	135	135	1	135
2	10	3	5	2	130	130	1	130
3	20	4	9	2.2	120	120	1	120
4	40	8	8	5	100	100	2	100
5	60	28	5	12	80	59	2	40
6	70	34	4	17.5	70	27	3	23.3
7	80	59	2	40	60	28	5	12
8	100	100	1	100	40	8	8	5
9	120	120	1	120	20	4	9	2.2
10	132	132	1	132	8	1	8	1
A	70	70	1	70	70	70	1	70
B	70	25	3	23.3	70	25	3	23.3
C	70	16	6	11.7	70	16	6	11.7
D	70	9	10	7	70	9	10	7
E	70	6	18	3.9	70	6	18	4.1
F	70	1	70	1	70	1	70	1

Landscape Scale

How animals perceive landscapes is an important consideration when defining optimal landscape configurations for conserving diversity. If, for example, an animal utilises all the patches of suitable habitat in a landscape, regardless of patch size, then the total area (**TA**) is the appropriate predictor of the potential number of species in a landscape. In terms of the model this means that total area (**TA**) is the appropriate measure of area to include in the species / area curve. If, however, an animal is sensitive to patch size (group of cells), and there is a threshold habitat size below which it does not occur, then the largest patch size in the landscape (**LP**) is the best predictor of potential number of species in a landscape and **LP** would be the appropriate measure of area. In other words if a set of species were restricted to continuous habitat patches the size of the largest patch in a landscape would be a better measure of area than the total amount of habitat in the landscape.

The scale at which animals perceive patchiness is also important. For example, an animal that ranges over a relatively large area may recognise the patches in a mosaic, whereas a less mobile animal may be restricted one patch (Wiens 1997). "Thus, what is a highly fragmented landscape to one kind of organism may be relatively homogeneous (or at least continuous) to another" (Wiens 1997, page 103). For this reason the model concentrates on habitat specialists which are likely to respond to landscape patchiness in a similar way because they are, in general, restricted to continuous habitat patches.

Objectives

The model was used to explore different patch area responses of birds in two different habitat types. In my study, woodland habitats had consistently higher species richness than grasslands, although grassland specialists showed stronger responses to patch area than *A. nilotica* woodland specialists (Chapter 4). The main response variable in the model is the rate at which grasslands accumulate species with area relative to woodlands. For example, what proportion of grassland is required in the landscape if grasslands accumulate species at half the rate of woodlands, and is this proportion more or less than if grasslands accumulate species at twice the rate of woodlands? The model was also used to explore the effects of landscape grain on specialist bird "diversity": "do fine grained landscapes support higher or lower "diversity" than coarse grained landscapes?

Basis of the model

To explore the effects of different habitat configurations on simulated diversity, I varied the number of specialist species present in the smallest patch of a particular habitat type ($\mathbf{S}_{min}$) and the total number of specialists in a particular habitat in the "region" in which the landscape is situated ($\mathbf{S}_{max}$). I assumed that species were habitat specialists, restricted to either grassland or woodland. Habitat generalists (or species that utilise more than one habitat) would not respond to landscape patchiness as clearly as the specialists although one would expect them to increase as landscape heterogeneity increased. I assumed that the species area curves in both habitats were power functions, and that species increased with area, between $\mathbf{S}_{min}$ and $\mathbf{S}_{max}$, according to the species area curve $\mathbf{S = cA}^{b}$. The shape of the species area curve, and the slope (**b**) of the species area curve was calculated from $\mathbf{S}_{min}$ and $\mathbf{S}_{max}$. (Equation 1, 2 & 3).

The general equation is,

$$\mathbf{S = c.A}^{b} \qquad \textbf{(1)}$$

where **S** = number of species in a particular grid, **c** = $\mathbf{S}_{min}$, **A** = landscape area ($\mathbf{A}_{max}$ = 140 cells), and **b** = (log $\mathbf{S}_{max}$ - log $\mathbf{S}_{min}$) / log $\mathbf{A}_{max}$

For grassland, the slope is given by,

$$\mathbf{b}_g = (\log \mathbf{G}_{max} - \log \mathbf{G}_{min}) / \log 140 \qquad \textbf{(2)}$$

where $\mathbf{G}_{min}$ is the number of grassland species found in the smallest grassland habitat patch, $\mathbf{G}_{max}$ is the number of species found in the largest grassland patch and $\mathbf{b}_g$ is the slope of the species-area curve.

For woodland, the slope is given by

$$\mathbf{b}_w = (\log \mathbf{W}_{max} - \log \mathbf{W}_{min}) / \log 140 \qquad \textbf{(3)}$$

where $\mathbf{W}_{min}$ is the number of woodland species found in the smallest woodland habitat patch, $\mathbf{W}_{max}$ is the number of woodland species found in the largest woodland patch and $\mathbf{b}_w$ is the slope of the species-area curve.

Once the slope of the species area curve has been calculated for each habitat, it can be used, together with amount of each habitat (**TA**), the largest patch of each habitat (**LP**) or the average patch size of each habitat (**AV**), to calculate the number of grassland and woodland species present in a landscape ($\mathbf{G_{spp}}$ and $\mathbf{W_{spp}}$ respectively) (Equation 4 & 5).

For grassland,

$$\mathbf{G_{spp} = G_{min} \cdot H_g} \qquad \mathbf{(4)}$$

where $\mathbf{G_{spp}}$ is the number of grassland species found in habitat **H** and $\mathbf{H_g}$ is the total amount **(TA)** of grassland in the landscape, or the largest patch **(LP)** of grassland in the landscape, or the average grassland patch size **(AV)** in the landscape.

For woodland,

$$\mathbf{W_{spp} = W_{min} \cdot H_w} \qquad \mathbf{(5)}$$

where $\mathbf{W_{spp}}$ is the number of woodland species found in habitat **H** and $\mathbf{H_w}$ is the total amount **(TA)** of woodland in the landscape, or the largest patch **(LP)** of woodland in the landscape, or the average woodland patch size **(AV)** in the landscape.

Measuring Richness

In the model I have two measures of biodiversity. The first, total species present in a particular landscape (**Tspp**), does not take differences in species composition in different habitat types into account. If, for example, woodlands contained many more species than grasslands, a landscape made up of woodland alone would have the maximum **Tspp**, despite the loss of grassland specialists. Despite this short-coming it is a commonly used approach to measuring the "biodiversity "of a landscape (Noss 1991, Pressey *et al.* 1993).

The second approach is to take account of species composition and changes in composition in different habitat types. Assuming that habitats contain relatively distinct sets of species, the goal is to find a landscape in which the maximum number of species specific to each habitat are present. There are several possible ways of devising a single index for measuring how well a particular landscape conserves the specialist species. For example, adding the proportion of the total grassland species present to the proportion of the total woodland species present in a landscape $[(\mathbf{G_{spp}}/\mathbf{G_{max}}) + (\mathbf{W_{spp}}/\mathbf{W_{max}})]$. However, this measure is flawed because a landscape with a low proportion of grassland specialists (e.g. $\mathbf{G_{spp}}/\mathbf{G_{max}}=0.2$) and a high proportion of woodland specialists (e.g. $\mathbf{W_{spp}}/\mathbf{W_{max}}=0.8$) would have the same "sum of proportions" as a landscape with moderate proportions of both grassland and woodland specialists (e. g. $\mathbf{G_{spp}}/\mathbf{G_{max}}=0.5$; $\mathbf{W_{spp}}/\mathbf{W_{max}}=0.5$). I suggest that a better way of measuring how well a landscape conserves diversity is to multiply the proportion of the total grassland species present in a landscape by the proportion of the total woodland species present in a landscape (Equation 6). For example, if $\mathbf{G_{max}}$ were 20 and $\mathbf{W_{max}}$ were 40 in a particular region, and a landscape in that region housed 4 grassland and 32 woodland species, then the "product of the proportions" (**PP**) for the landscape would be: (4/20) multiplied by (32/40) (**PP** =0.16, **Tspp** =36). If, on the other hand, a landscape contained 10 grassland and 20 woodland species, the "product of the proportions" (**PP**) in would be 0.25 (**Tspp** =30). Therefore, if **PP** were used as a measure, the second landscape would have a higher "diversity" than the first despite having fewer total species. In other words, grasslands and woodlands contribute equally to **PP** despite the fact that grasslands have fewer species than woodlands. Thus, **PP** emphasises the relative diversity of each of the habitats in a landscape, and can be described as:

$$\mathbf{PP} = (\mathbf{G_{spp}} / \mathbf{G_{max}}) \cdot (\mathbf{W_{spp}} / \mathbf{W_{max}}) \qquad \mathbf{(6)}$$

The model was run for a range of $\mathbf{G_{min}}$, $\mathbf{G_{max}}$, $\mathbf{W_{min}}$ and $\mathbf{W_{max}}$

values which I considered to be realistic for the savanna ecosystem in which the study is based. Because of the assumption that woodlands have more specialist species than grasslands, $\mathbf{W}_{max}$ was always higher than $\mathbf{G}_{max}$. The $\mathbf{G}_{min}$ varied from 1-6, $\mathbf{G}_{max}$ from 7-15, $\mathbf{W}_{min}$ from 1-20, and $\mathbf{W}_{max}$ from 10-40. The size of $\mathbf{G}_{min}$ and $\mathbf{W}_{min}$ is related to minimum patch size. If, for example, one cell is considered to be a 1 ha patch, $\mathbf{G}_{min}$ will be low (e.g. 1), if, on the other hand, one cell is considered to be an 8 ha patch, $\mathbf{G}_{min}$ would be high (e.g. 6). The same applies for $\mathbf{G}_{max}$ and $\mathbf{W}_{max}$, the larger each cell is considered to be the higher the $\mathbf{G}_{max}$ and $\mathbf{W}_{max}$ will be. The model was set up in a speadsheet programme (Microsoft Excel, version 5.0a) allowing the input of various different $\mathbf{G}_{min}$, $\mathbf{G}_{max}$, $\mathbf{W}_{min}$ and $\mathbf{W}_{max}$ values, as well as **TA**, **LP** and **AV** values representative of different landscape configurations (see Figure 1 a&b and Table 1).

Assumptions of the model

- Landscape consists of two habitats only, woodland and grassland.
- One grid cell is the minimum habitat unit (i.e. patch).
- Only directly adjacent cells can link to form patches (i.e. diagonally adjacent cells are not considered to be in contact).
- Patch shape is not included in the model. The assumption is that the habitat patches are free from edge / interior effects.
- The landscape ends at the edge of the grid (i.e. the landscape is considered to be two dimensional).
- $\mathbf{W}_{max}$ is always higher than $\mathbf{G}_{max}$, although $\mathbf{W}_{min}$ may be greater than or equal to $\mathbf{G}_{min}$. This follows from the general finding that bird species richness increases with foliage height diversity (FHD) from grassland (G) to woodland (W).
- Woodland birds utilise only woodland and grassland birds utilise only grassland. Species that utilise ecotones or that utilise a number of habitats are not included in the model. The assumption is that these species will be

less sensitive to the scale of landscape heterogeneity than habitat specialists

- In the **TA** model patch size is not taken into account
- The landscapes are free of isolation effects (i.e. distance between patches does not factor into the model).

Results

Total area model

Figure 2 illustrates the output generated by the model. The output in figure 2, based on the model using total area (**TA**), shows grassland species decreasing with decreasing habitat area (From Grid 1 to 10) and woodland species richness increasing. Total species (**Tspp**), the sum of grassland and woodland species, is maximised in Grid 8, a landscape composed of 72 % woodland. However, **PP**, which takes account of different species in each habitat type, is maximal at Grid 6 (50% woodland), which has significantly more grassland than Grid 8. The landscape with maximal **Tspp**, in this example, would be full of "woodland" birds and diversity of grassland birds would be minimal. Therefore, to conserve the largest fraction of species from both habitat types, requires a more "grassy" landscape. The models using the largest patch and average patch size (**LP** and **AV**) produced practically identical results when the range of landscapes in Figure 1a are considered. This is because, as woodland increases in a landscape the **LP** and **AV** increase together with **TA**. The difference is that **TA** increases more steadily than **LP** and **AV** (Table 1).

Table 2 shows how the different input values affect **PP** and **Tspp** in the total area (**TA**) model. Figure 2 is an example of the graphic output of the (**TA**) model. Table 3 shows how **LP** and **AV** affect **Tspp** and **PP** in the patch size model.

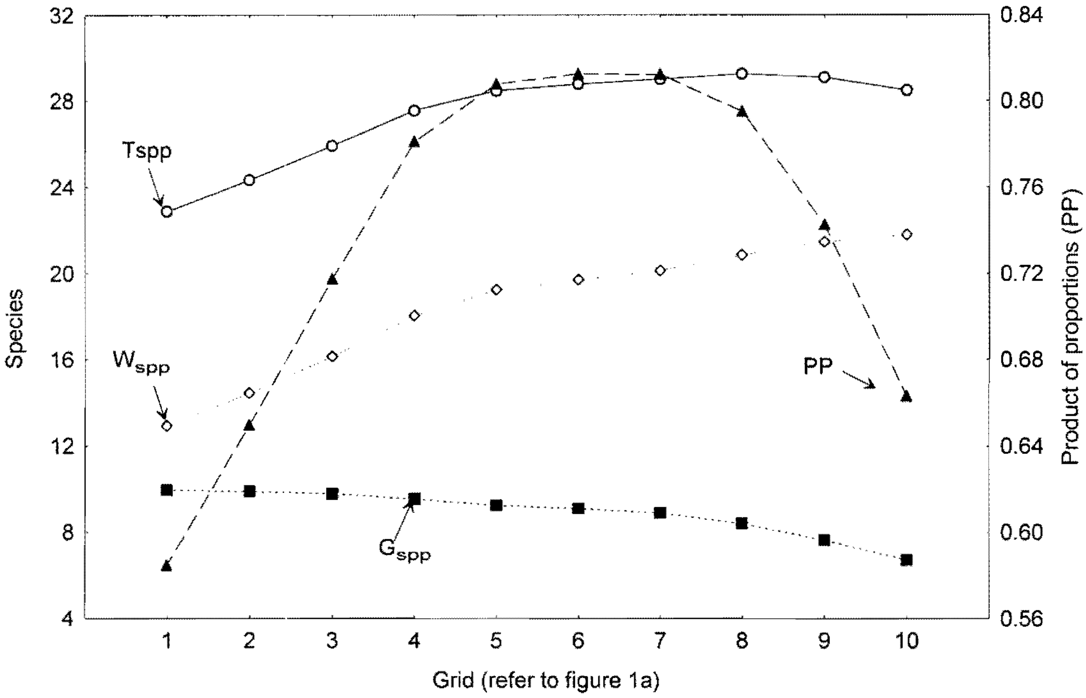

Figure 2: Example of the output of the model. $\mathbf{G}_{min}$ was set at 5, $\mathbf{G}_{max}$ at 10, $\mathbf{W}_{min}$ at 10 and $\mathbf{W}_{max}$ 22. The slopes of the species area curves are 0.14 ($\mathbf{b}_g$) and 0.16 ($\mathbf{b}_w$) for grassland and woodlands respectively. $\mathbf{G}_{spp}$ is the number of grassland species present, $\mathbf{W}_{spp}$ the number of woodland species present, **Tspp** the total number of species present and **PP** the product of the proportions of grassland and woodland species present. **PP** is plotted on the secondary y-axis, the x-axis is the Grid number of the landscapes in Figure 1a.

The TA model (Table 2) shows that as the slope of the grassland species area curve steepens in relation to the woodland species area curve (i.e. $\mathbf{b}_g > \mathbf{b}_w$), the product of the proportions (**PP**) moves in the direction of increasing grassland. More specifically if $\mathbf{b}_g = \mathbf{b}_w$ then the maximum **PP** is in a landscape with equal amounts of grassland and woodland. If $\mathbf{b}_g > \mathbf{b}_w$ then maximum **PP** is in a landscape with 40 % woodland (60 % grassland) (Grid 5). If $\mathbf{b}_g < \mathbf{b}_w$ then maximum **PP** is in a landscape with 60 % woodland (40 % grassland) (Grid 7)(Table 2). Because of the assumptions of the model (woodlands richer than grasslands), the total number of species (**Tspp**) is always on the right of the figure (i.e. in the landscapes dominated by woodland)(see figure 2). Thus, the landscape configurations which maximise biodiversity are determined to a large degree by the relative slopes of the species area curves for the different habitats. The measure of diversity is also important; in this model maximum **PP** is always in a more grassy landscape than maximum **Tspp**. The same trends are evident in the **LP** and **AV** models.

Table 2: Optimum landscape configuration (Grid number) using total area of grassland and woodland in each landscape grid. The grid in which **PP** and **Tspp** were at a maximum was estimated using variations of figure 2, and the "landscapes" in figure 1a.

		$b_g = b_w$	$b_g < b_w$	$b_g < b_w$	$b_g < b_w$	$b_g > b_w$	$b_g > b_w$	$b_g > b_w$
			diff. large	diff. medium	diff. small	diff. large	diff. medium	diff. small
	INPUT							
Species Parameter	G_{min}	5	5	5	5	5	5	5
	G_{max}	15	10	10	10	15	15	15
	W_{min}	10	10	10	10	10	10	10
	W_{max}	30	40	30	22	17	20	28
	b_g	0.22	0.14	0.14	0.14	0.22	0.22	0.22
	b_w	0.22	0.28	0.22	0.16	0.11	0.14	0.20
	OUTPUT							
Optimum Landscape	Grid # PP max	6	8	7	6	6	5	4
	Grid # Tsppmax	8	10	9	8	8	6	4
	PP max	0.74	0.76	0.78	0.81	0.74	0.78	0.81
	Tsppmax	39	46	37	29	38	31	29

Patch size models

The comparison of six landscapes with equal amounts of grassland and woodland and varying patch number / size (see figure 1b) shows that landscapes with larger patches house more species than those consisting of many small patches. Coarse grained landscapes (e.g. Grid 1-3) have higher **Tspp** (total species) and **PP** (product of proportions), regardless of the richness of the habitats, than fine grained landscapes (e.g. Grids 4-6)(Table 3).

Table 3: The total species (**Tspp**) and **PP** in Grids A - F using the largest patch size (**LP**) and average patch size (**AV**). Gmin and Gmax were set at 5 & 10, Wmin and Wmax were set at 10 & 30 respectively.

Grid	LP	AV	**Tspp** LA	**PP** LP	**Tspp** AV	**PP** AV
A	70	70	34.	0.78	34	0.78
B	25	23.3	28	0.54	27	0.52
C	16	11.7	25	0.46	24	0.41
D	9	7	23	0.37	21	0.34
E	6	3.9	21	0.32	19	0.27
F	1	1	15	0.17	15	0.17

Discussion

Despite the simplifications, the model indicates that the slope of the species area curves for habitats are crucial to understanding how different landscape configurations effect diversity.

The model based on the total amount of woodland / grassland in the landscape indicates that landscapes in which woodland and grassland are approximately equally represented (Grid 5, 6, 7) have the highest **PP** despite having below maximal **Tspp** (total species). The model also indicates that because woodlands have more species than grasslands, landscapes dominated by woodland have the highest total number of species. If the management goal is to conserve the maximum number of species then the amount of woodland in the landscape should be maximised. The conservation cost of allowing savanna to convert to woodland (via secondary succession) would be that more specialist grassland birds would be lost from the landscape. However, if the goal is to conserve as many grassland and woodland bird species as possible in a single landscape, then a landscape with approximately equal proportions of woodland and grassland is required. This implies (if **PP** is considered) that a relatively greater area is needed to conserve the species in a species poor habitat. It is important to note that **PP** and **Tspp** converge when the species area curves for the two habitat are equal, and that discussions are based on the assumption that woodlands contain more species than grasslands.

The model also shows that in landscapes with equal amounts of woodland and grassland those with large habitat patches (coarse grained) are richer in species and have higher **PP** than those with small habitat patches (fine grained). This finding is not surprising when the species area curve is considered as the number of species increases with area. Yet, the implications of this are worth considering. Disturbance regimes such as patch-mosaic burning are supposed to increase landscape heterogeneity (Parr and Brockett 1999, Christensen 1997). However, if increasing landscape heterogeneity means reducing the grain of the landscape, the largest patch size and average patch size of the landscape would decrease, resulting in reduced diversity for those species restricted to continuous habitat patches (usually habitat specialists)(Hansson 1997, Wiens 1997).

Therefore, in order to predict the diversity effects of increasing landscape heterogeneity, one needs to have some idea of how species (habitat specialists in particular) respond to patch area.

The model described above is a general model addressing a general problem. The relationships between bird diversity and patch area, described in preceding chapters, were used to parameterise the model. As it is presented above, the model is an attempt to further understand the relationship between landscape heterogeneity and biodiversity. Enormous potential remains to extend the model and make it more realistic. For example, it would be interesting to try and incorporate patch isolation, variance in patch size, and more than two habitat types.

This simple simulation also suggests that scale must be taken into account when measuring landscape heterogeneity (Wiens 1997). Geographic Information Systems (GIS) systems are now widely available and can be used to measure landscape patchiness (Pulliam 1997). Features such as largest patch in landscape and average patch size are relatively easy to measure, and would be particularly informative to managers if the area response of the species or taxon of interest were known (Pulliam 1997).

Chapter 6 : Conclusion

"The pragmatism of the conservation manager is based on the need for action dictated by the problem at hand, not the completeness of the understanding to which ecologists aspire" (Rogers 1997, page 66).

Previous studies in HUP have described how grasslands, *A. nilotica* woodlands, and broadleaf woodlands are part of a successional series (Whateley and Porter 1983, Skowno *et al.* 1999). I have shown that in general the canopy cover, tree density and foliage height diversity increase along this successional series. Associated with these changes in vegetation structure is an increase in bird species diversity and species richness. Birds seem to be responding to structural vegetation changes rather than floristic changes between habitats. Yet, I have also shown that the bird communities of grasslands, *A. nilotica* woodlands and broadleaf woodlands are relatively sharply defined, and that while diversity may increase along the successional gradient, bird species characteristic of the early successional stages may be lost. If the successional changes in savannas are allowed to proceed throughout the Park the overall avian diversity of the Park will decrease because of the loss of habitat specialists.

At a landscape scale secondary succession and prescribed burning are causing the fragmentation of grasslands and *A. nilotica* woodlands. Current disturbance regimes encouraged by management may also be causing a reduction in the average habitat patch size by limiting the extent of fires. This study indicates that fragmentation could have major effects on bird diversity in certain habitats. If large continuous areas of a particular habitat are fragmented the number of specialist bird species using the patch may decline. Due to biological edge effects small patches tend be utilised by generalist species, and tend be depauperate in habitat specialists (Ambuel and Temple 1983, Schieck *et al.* 1995, Hansson 1997). It is clear from my results that simply ensuring that all habitat types are preserved is not sufficient for maintaining bird diversity in the Park. The model in chapter 5 indicates that an approximately equal proportion of grassland and woodland should be maintained in the landscape if both grassland and woodland specialist birds are to be conserved. It also indicates that the total number of bird species may be maximal when woodland dominates the landscape. Managers therefore have to take a definite stance on whether the maximum number of species are to be conserved or whether specialist species are to conserved.

Managers also need to consider the implications of landscape grain. Coarse grained landscapes, consisting of relatively large habitat patches (>65 ha), are likely to support more specialist species than fine grained landscapes in which individual habitat patches are relatively small (<65 ha). My results (in Chapter 4) suggest that this is particularly important in grassland habitats where specialists tend to utilise continuous habitat patches. However, in *A. nilotica* woodlands a fine grained landscape is not as detrimental to specialist birds because they tend to utilise habitat patches separated by "unsuitable" matrix vegetation.

Regional isolation effects:

Habitat patch isolation as a result of fragmentation within the Park is a local phenomenon. At a regional scale the Park as a whole is becoming progressively more isolated as the surrounding land is transformed. A large proportion of the communally farmed lands bordering the Park were sparsely inhabited range lands until about 20 years ago. At this time, the bird diversity out side the Park was high, especially for grassland birds (Macdonald and Birkenstock 1980). This situation allowed far ranging species, such as raptors, Ground Hornbills and Secretary Birds to utilise the Park while nesting elsewhere. The increase in sugar farms and the general degradation of the land outside the Park will eventually leave very little habitat for birds and other animals. In addition to the general habitat destruction there is also considerable "hunting" pressure on the birds out side the Park. It is widely appreciated that reserves such as HUP are essential for the conservation of large mammals, but are of limited value for the conservation of birds. Yet, if the current trends of population growth and land degradation continue, the Park will become significant for the conservation of all but the most adaptable bird species.

Chromolaena odorata:

Another potentially major threat to the avian diversity of the Park is the alien invasive shrub *Chromolaena odorata*. Introduced from the Caribbean earlier this century it has only become a major problem in the Park in the last 10 years. Mesic areas of the Park (the riverine vegetation of rivers in the northern section of the Park) are being invaded by this difficult to control resprouting shrub. Thiollay (1998) singles *Chromoleana* out as a major threat to bird diversity in the Lamto Park, Cameroon. It dramatically alters the structure of the understory of mesic woodlands and riverine forests, and acts as a fuel load for very intense fires (Thiollay 1998).

To promote specialist bird diversity in the Park heterogeneous landscapes and large continuous areas of each habitat should be promoted. Vegetation change resulting from secondary succession is managed and this management should continue. In particular the shift from *A. nilotica* woodland to broadleaf woodland should be combated because it is a difficult change to reverse. An intensified burning regime, concentrating on fire intensity rather than frequency has been proposed to maintain open Acacia savanna in the Park (Skowno *et al.* 1999). Large mammal management can also play a role in controlling secondary succession. Smith and Goodman (1987) suggested that the loss of elephants (*Loxodonta africana*), through hunting early last century, from a savanna reserve similar to HUP, may have contributed to secondary successional vegetation changes. As elephants are thought to maintain open areas in savannas by their destructive feeding mode. In the context of HUP, it has been suggested that the density of herbivores in the Park can influence vegetation succession (Watson and Macdonald 1983).

Watson and Macdonald (1983) and Brooks and Macdonald (1983) suggest that high herbivore densities in the Park in the 1960's helped to maintain open savannas, and that the rapid increase in woody vegetation between the 1960's and 1980's was caused, to a degree, by a dramatic reduction in herbivore densities throughout the Park in the late the 1960's. Thus, by controlling both large herbivore densities and the fire regime managers can control vegetation change in the Park.

The biodiversity costs of successional change are substantial, at least for avifauna. I propose that changes in the biota should be measured not as number of species but as kinds of species present. The landscape context is important for overall biodiversity, and landscape scale implications of habitat management must be considered. For example, large numbers of tourist roads fragment open grassland habitats and impede the progress of fire, increasing the probability of woody plant encroachment.

Patterns of avian species diversity and community composition and structure in HUP indicate that landscape level changes, driven by vegetation succession could negatively impact the biodiversity of the Park.
But how applicable are my findings, based on birds, to other taxa? Do large mammals, for example, respond similarly to vegetation change and landscape heterogeneity and patchiness? With regard to single species conservation, there is evidence that secondary succession and woody plant invasion in grasslands have influenced mammals in the Park (Brooks and Macdonald 1983). For example, Common Reedbuck (*Redunca arundinum*), an antelope which requires large homogeneous grasslands has declined in the Park since the 1930's as a result of habitat loss (Deane 1966, Brooks and Macdonald 1983). Emsley (1996) showed that the decline in Black Rhinoceros (*Diceros bicornis*), which, are one of the principal species which Park managers aim to conserve, was due to loss of suitable browse of acacia shrubs in grasslands that was caused by vegetation change (Emsley 1996). This highlights the importance of vegetation management and how it relates

to vertebrate management, in a Park where vertebrates and vegetation are usually managed separately.

Birds and mammals, in general, respond to similar landscape scales (Andren 1994, McCoy and Mushinsky 1994). However, smaller, less mobile taxa, such as invertebrates and amphibians, are more likely to respond to local habitat conditions rather than to landscape patchiness (Wiens 1997). Samways (1989) suggests that insects respond to landscape patchiness, but that it is the alteration of environmental conditions in these patches which affect insects rather than the change in landscape pattern.

Increasing landscape heterogeneity promotes biodiversity by creating successional beta diversity and increasing total species. But the scale of the patchiness in a heterogeneous landscape is more important than habitat diversity per se., especially when habitat specialists are the main focus of conservation in an area.

I suggest that in order to conserve the vertebrate diversity of savanna areas such as HUP, managers need to have some idea how species select habitats and how they respond to changes in habitat patch area. For species rich taxa it may only be practical to measure patterns in “specialist” diversity, as in this study, because measuring the individual responses of numerous species would require considerable effort and time. For less diverse taxa, such as large mammals, the individual responses of each species could conceivably be measured.

As suggested by Parr and Brockett (1999), if the goal is to maximise biodiversity, a heterogeneous landscape with the full compliment of habitat types and successional stages should be aimed for by managers. However, as Weins (1995 & 1997) points out, the grain of the landscape is important to biodiversity. If the size of the patches in the landscape falls below a “certain level” habitat specialists will be lost, resulting in an overall loss of diversity.

Determining this “level” requires an understanding of how species and or taxa respond to landscape scale heterogeneity and patchiness. Further research into such fields will be of great importance to conservation and should be incorporated into studies of landscape ecology.

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Appendix 1: Study site details , all sites included. Season censused s=summer, w=winter and s/w=summer and winter. Latitude and Longitude in decimal degrees.

Site	Code	Area (ha)	Altitude (m)	Latitude S	Longitude E	Season censused	Dominant grass sp.	Dominant shrub sp.	Dominant tree sp.
Broadleaf woodland 1	1b	302.0	220	28:06:12.07	32:05:06.32	s	*Eragrostis curvula*	*Euclea divinorum*	*Euclea racemosa*
Broadleaf woodland 2	2b	63.1	16	28:05:06.40	32:04:11.24	s	*Panicum maximum*	*Diospyros lycioides*	*E. racemosa*
Broadleaf woodland 3	3b	173.8	260	28:08:17.26	32:01:47.59	s	*P. maximum*	*E. racemosa*	*E. racemosa*
Broadleaf woodland 4	4b	6.2	190	28:03:38.95	32:07:07.78	s	*Panicum deustum*	*Hippobromus pauciflorus*	*Berchemia zeyheri*
Broadleaf woodland 5	5b	17.0	200	28:03:52.51	32:07:18.57	s	*P. maximum*	*H. pauciflorus*	*E. racemosa*
Broadleaf woodland 6	6b	3.6	220	28:04:17.82	32:07:24.77	s	*P. deustum*	*E. racemosa*	*E. racemosa*
A. nigrescens woodland 1	1g	51.3	110	28:16:01.54	31:50:36.55	s	*Panicum coloratum*	*Grewia bicolor*	*Acacia nigrescens*
A. nigrescens woodland 2	2g	100.0	150	28:15:04.51	31:48:42.38	s	*Themeda triandra*	*Dichrostachys cinerea* sb. *africana*	*A. nigrescens*
A. nigrescens woodland 3	3g	50.1	180	28:13:21.49	31:46:13.19	s	*Sporobolus nitens*	*Commiphora harveyi*	*A. nigrescens*
A. nigrescens woodland 4	4g	12.9	130	28:13:05.30	31:47:35.14	s	*P. maximum*	*D. cinerea* subsp. *africana*	*A. nigrescens*
A. nigrescens woodland 5	5g	36.3	160	28:13:37.76	31:47:43.67	s	*Urochloa mosambicensis*	*Grewia villosa*	*A. nigrescens*
A. nigrescens woodland 6	6g	7.1	280	28:16:42.59	31:44:09.33	s	*P. deustum*	*Mayteus senegalensis*	*A. nigrescens*
A. nilotica woodland 1	1n	89.1	210	28:01:49.93	32:00:26.72	s/w	*E. curvula*	*Acacia karroo*	*Acacia nilotica*
A. nilotica woodland 2	2n	79.4	200	28:09:50.09	32:00:56.32	s/w	*T. triandra*	*D. cinerea* subsp. *africana*	*A. nilotica*
A. nilotica woodland 3	3n	158.5	240	28:13:52.57	31:58:00.08	s/w	*P. maximum*	*A. nilotica*	*A. nilotica*
A. nilotica woodland 4	4n	2.0	250	28:05:09.25	32:04:50.38	s/w	*Bothriochloa bladhii*	*A. karroo*	*A. nilotica*
A. nilotica woodland 5	5n	28.8	380	28:13:30.10	31:54:15.69	s/w	*P. maximum*	*Euclea crispa* subsp. *crispa*	*A. nilotica*
A. nilotica woodland 6	6n	28.2	340	28:12:41.76	31:56:59.92	s/w	*P. maximum*	*D. cinerea* subsp. *africana*	*A. nilotica*
A. nilotica woodland 7	7n	300.2	200	28:10:56.21	32:03:15.51	w	*Dactyloctenium aegyptium*	*D. cinerea* subsp. *africana*	*A. nilotica*
A. nilotica woodland 8	8n	10.7	260	28:13:22.93	32:01:14.98	w	*P. maximum*	*D. cinerea* subsp. *africana*	*A. nilotica*
A. nilotica woodland 9	9n	44	200	28:10:23.54	31:58:51.20	w	*D. aegyptium*	*D. cinerea* subsp. *africana*	*A. nilotica*
A. nilotica woodland 10	10n	10.8	220	28:10:18.68	32:00:24.66	w	*P. maximum*	*D. cinerea* subsp. *africana*	*A. nilotica*
A. nilotica woodland 11	11n	3	130	28:09:06.57	32:02:04.62	w	*S. pyramidalis*	*Euclea divinorum*	*A. nilotica*
A. nilotica woodland 12	12n	11.1	205	28:09:26.94	31:58:44.74	w	*D. aegyptium*	*D. cinerea* subsp. *africana*	*A. nilotica*
Grassland 1	1o	52.5	315	28:11:18.58	32:00:09.83	s/w	*T. triandra*	*A. karroo*	
Grassland 2	2o	31.1	335	28:04:49.75	32:03:56.35	s/w	*Hyparrhenia hirta*	*D. cinerea* subsp. *africana*	
Grassland 3	3o	569.8	325	28:12:46.12	31:56:35.10	s/w	*T. triandra*	*A. karroo*	
Grassland 4	4o	27.1	180	28:11:37.22	32:01:47.11	s/w	*Hyparrhenia filipendula*	*D. cinerea* subsp. *africana*	
Grassland 5	5o	6.1	138	28:04:39.28	32:06:02.19	s/w	*S. pyramidalis*	*D. cinerea* subsp. *africana*	
Grassland 6	6o	3.4	95	28:06:54.53	32:06:14.10	s/w	*Panicum subalbidum*	*M. senegalensis*	
Grassland 7	7o	146	370	28:04:05.79	32:00:58.57	w	*T. triandra*	*Heteropyxis natalensis*	
Grassland 8	8o	17	430	28:03:53.27	32:01:57.80	w	*T. triandra*	*D. lycioides*	
Grassland 9	9o	17.7	260	28:08:39.60	31:51:59.70	w	*H. filipendula*	*D. cinerea* subsp. *africana*	
Grassland 10	10o	8.1	260	28:13:53.53	32:00:52.97	w	*Paspalum scrobiculatum*	*D. cinerea* subsp. *africana*	
Grassland 11	11o	5	280	28:13:53.40	32:01:09.32	w	*T. triandra*	*D. cinerea* subsp. *africana*	
Grassland 12	12o	6.4	190	28:09:38.46	31:58:46.03	w	*E. curvula*	*A. karroo*	

Appendix 2: Structural variables measured at each site, full variable names are given below.

Site	FHD1	FHD3	Gr den	Gr ht (m)	GC %	Tr den	Sh den	CC %	Cn ht (m)	Sh ht (m)
1b	1.40	2.47	0.31	0.39	70	0.11	0.27	69	5.9	1.3
2b	1.31	2.56	0.99	0.39	78	0.16	0.28	71	5.4	1.4
3b	1.28	2.61	0.64	0.25	51	0.08	0.28	71	8.3	1.2
4b	1.38	2.50	0.54	0.80	80	0.17	0.27	75	4.2	1.4
5b	1.34	2.56	0.72	0.46	82	0.14	0.29	81	6.0	1.2
6b	1.33	2.54	0.56	0.31	59	0.14	0.30	79	5.7	1.2
1g	1.23	2.69	0.28	0.12	47	0.06	0.08	38	6.8	1.2
2g	1.23	2.67	0.64	0.33	84	0.09	0.15	57	6.7	1.5
3g	1.20	2.64	0.25	0.05	61	0.05	0.07	33	7.2	1.2
4g	1.22	2.40	0.37	0.14	69	0.06	0.07	59	6.8	1.0
5g	1.24	2.57	0.30	0.08	50	0.05	0.10	27	6.6	1.0
6g	1.08	2.34	0.97	0.48	81	0.08	0.10	47	5.6	1.2
1n	0.84	2.32	1.07	0.52	73	0.11	0.16	47	4.2	1.4
2n	1.26	2.32	0.80	0.54	70	0.10	0.31	50	4.4	1.4
3n	0.47	2.24	2.09	0.59	94	0.08	0.11	57	4.3	1.4
4n	0.97	2.36	0.96	0.97	83	0.09	0.14	47	5.2	1.3
5n	0.75	2.23	1.19	0.70	88	0.07	0.18	60	4.4	1.1
6n	0.45	1.98	2.57	1.16	91	0.06	0.14	47	4.9	1.3
7n	0.83	2.26	1.11	0.34	82	0.09	0.16	64	4.2	1.2
8n	0.82	2.33	1.45	0.96	79	0.08	0.22	67	4.9	1.5
9n	0.95	2.24	0.75	0.28	80	0.06	0.28	64	4.3	1.6
10n	0.67	2.20	1.33	0.49	87	0.13	0.09	60	4.3	1.0
11n	1.01	2.40	0.65	0.31	78	0.07	0.22	53	4.5	1.6
12n	1.10	2.25	0.51	0.17	71	0.08	0.18	60	4.6	0.9
1o	0.24	1.25	2.22	0.86	96	0.01	0.17		3.8	1.1
2o	0.14	0.68	1.19	0.11	92		0.07			1.1
3o	0.08	0.86	1.27	0.45	84		0.03			0.6
4o	0.43	1.69	0.57	0.42	82	0.01	0.07		4.5	1.0
5o	0.18	0.56	1.13	0.79	87		0.01			1.3
6o	0.20	0.62	2.56	0.12	99		0.01			1.4
7o	0.17	0.00	1.07	0.56	79		0.05			0.9
8o	0.09	0.73	2.03	0.48	87		0.04			0.9
9o	0.13	0.80	1.30	0.68	74		0.07			0.8
10o	0.12	1.41	1.60	0.48	85		0.05			1.1
11o	0.09	1.20	1.71	0.81	84		0.09			1.0
12o	0.13	1.30	1.56	0.63	81		0.10			1.0

FHD1 = total foliage height diversity, FHD3 = non-herbaceous foliage height diversity, Gr den = grass density, Gr ht = grass height, GC = ground cover, Tr den = tree density, Sh den = shrub density, CC = canopy cover, Cn ht = canopy height, Sh ht = shrub height

Appendix 3: Results of the summer bird censuses in broadleaf, *A. nigrescens*, *A. nilotica* woodland and grassland sites.

	Broadleaf Sites							*A. nigrescens* Sites							*A. nilotica* Sites							Grassland Sites					
Bird Species	1b	2b	3b	4b	5b	6b	**Total b**	1g	2g	3g	4g	5g	6g	**Total g**	1n	2n	3n	4n	5n	6n	**Total n**	1o	2o	3o	4o	5o	6o
Andropadus importunus	**10**	12	12	20	13	13	80											2	3		5						
Anthus cinnamomeus																2					2				2		
Apalis flavida	**4**			1	1	7	13									1		2			3						
Apalis thoracica				2	1		3																				
Batis capensis				2			2																				
Batis molitor	**3**						3	**3**	6	1	2	4	5	21	**7**	9	17	2	10		45						
Bostrychia hagedash															**2**						2						
Buphagus erythrorhynchus								**1**			2	8		11	**2**						2						
Camaroptera brachyura	**14**	12	21	10	25	22	104								**2**	4			4		10						
Campephaga flava	**4**	3					7		2		1		2	5				2			2						
Campethera abingoni	**2**		1		2	3	8					2		2	**1**						1						
Centropus burchellii																	1				1						
Chrysococcyx caprius												1		1						1	1						
Chrysococcyx klaas				1	2		3									1					1						
Cinnyricinclus leucogaster									2	18		8		28				2			2						
Cisticola chiniana	**8**	4		7	1	4	24	**18**	9	4	6	12	32	81	**31**	20	34	9	18	27	139	5		2	4	2	2
Cisticola juncidis																						7	4	11	9	12	
Cisticola natalensis																			1	2	3	38	19	12	23	8	
Colius striatus				4			4						1	1				2			2						
Coracias naevia													1	1													
Cossypha humeralis	**1**	2		4	1	1	9		1				1	2						2	2						
Cossypha natalensis	**2**	4	5	3	4	8	26																				
Cuculus clamosus	**1**	3	1				5					2		2													
Dendropicos fuscescens								**1**						1		2					2						
Dicrurus adsimilis		7			2		9	**2**		3	3	4	5	17	**1**	2	3	6			12						
Dryoscopus cubla	**2**			1			3		3		3		4	10	**1**						1						
Emberiza flaviventris											1			1			2	3			5						
Eremomela icteropygialis						1	1									2					2						
Erythropygia leucophrys		2		1	1		4																				
Esrilda astrild																				5	5	2	6				5
Euplectes ardens																			5	1	6	5	19	4	4	1	
Euplectes axillaris																						20	27	8	3	7	
Eupodotis melanogaster																								1	8		
Francolinus natalensis		1			1	7	9																				
Francolinus sephaena																							2				
Halcyon chelicuti										5	1			6													
Hippolais icterina													1	1			2		3		5						
Lagonosticta rubricata															**1**			4			5						1
Lamprotornis corruscus																		4			4						
Lamprotornis nitens								**5**	2	5	2	3	1	18													

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Bird Species cont....	1b	2b	3b	4b	5b	6b		1g	2g	3g	4g	5g	6g		1n	2n	3n	4n	5n	6n		1o	2o	3o	4o	5o	6o
Laniarius ferrugineus		1	7	4	5	9	26																				
Lanius collaris															**1**						1	1					
Lanius collurio										4	4	4	2	14	**11**	1	3			9	24				5	2	1
Lybius torquatus																				6	6						
Macronyx croceus				2			2													2	2	4	5	1	5		2
Malaconotus blanchoti													3	3	**1**						1						
Melaenoris pallidus	**1**				1		2	**2**	3		4	1		10	**2**						2				1		
Melaenoris pammelaina								**1**		4		2		7													
Mirafra africana																								3	1		
Mirafra rufocinnamomae																							2	1			
Mirafra sabota										3		2		5													
Muscicapa caerulescens	**1**						1																				
Myioparus plumbeus										1				1	**1**						1						
Nectarinia bifasciata				6			6																				
Nectarinia senegalensis			4				4	**7**	3	2	2	3		17		1		1			2						
Nectarinia talatala	**4**	5					9									2		2			4						
Nectarinia veroxii	**1**		5	5	3	1	15											1			1						
Nicator gularis		5	3	2	4		14																				
Nilaus afer	**1**						1	**2**		2	1	3	2	10	**2**		4	1			7						
Oriolus larvatus	**2**				1		3									2					2						
Parus niger	**1**	1		2			4	**1**		2	3	3		9	**1**		4	2			7						
Passer diffusus											7	5		12													
Petronia superciliaris								**1**		6	9	5	2	23	**3**			2			5	3					
Phyllastrephus terrestris		1	2		4	3	10																				
Phylloscopus trochilus																	3	2	1		6						
Ploceus ocularis																						2					
Pogoniulus pusillus			2	1	1		4																				
Prinia subflava			2	4	10	5	21				1		3	4	**3**	10		8	2	4	27		1				
Prionops plumatus													4	4	**4**	4					8						
Pycnonotus barbatus	**18**	18	12	17	20	12	97		1	4	7	4	9	25	**19**	21	12	11	19	11	93	12	2	1	2		3
Quelea quelea																									10		
Rhinopomastus cyanomelas	**3**						3			2	2			4	**5**	2			2		9						
Serinus mozambicus										15	4		4	23			3	7	7	12	29	12		3	5	2	3
Streptopelia capicola	**1**	2					3	**5**	4	11	3	6	1	30			3			5	8	1					
Streptopelia semitorquata								**2**						2			2				2						
Streptopelia senegalensis		1					1				1			1													
Sylvietta rufescens								**2**	3	1	2	3	1	12	**4**	2		2	1	2	11						
Tauraco porphyreolophus	**2**			3	1	1	7										1				1						
Tchagra australis	**2**						2						3	3		2	2				4						
Tchagra senegala															**1**						1						

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Bird Species cont....	1b	2b	3b	4b	5b	6b		1g	2g	3g	4g	5g	6g		1n	2n	3n	4n	5n	6n		1o	2o	3o	4o	5o	6o
Telophorus quadricolor	1	3	2	3	9	6	24								1						1						
Telophorus sulfureopectus	2						2						2	2		4	1	2			7						
Terpsiphone viridis											2			2													
Trachyphonus vaillantii												3		3													
Tricholaema leucomelas										4	2		1	7													
Turtur chalcospilos	1	3		1	2		7		1		3	2	1	7			1				1						
Turtur tympanistria	1						1																				
Upupa africana										1				1													
Uraeginthus angolensis										3				3	2		2				4						
Urocolius indicus																		6			6						
Vidua macroura																									1	1	4
Zosterops pallidus	9	9	9		3	8	38											11			11						
Total species	**28**	**21**	**15**	**24**	**25**	**17**	**45**	**15**	**13**	**22**	**26**	**23**	**24**	**46**	**25**	**20**	**19**	**25**	**13**	**14**	**59**	**13**	**10**	**11**	**15**	**8**	**8**

Appendix 4: Results of the winter bird censuses in grassland and *A. nilotica* woodland, each site was censused on four concecutive mornings. Grassland specialist birds are followed by an O and A. nilotica woodland specialists by an N in the Specialist column.

		A. nilotica Sites													*Grassland* Sites												
Species	Specialist	1n	2n	3n	4n	5n	6n	7n	8n	9n	10n	11n	12n	**Total n**	1o	2o	3o	4o	5o	6o	7o	8o	9o	10o	11o	12o	**Total o**
Andropadus importunus			3						1		1			**5**													
Anthoscopus caroli			4											**4**													
Anthus caffer	N							3					7	**10**									1			4	**5**
Anthus cinnamomeus																		9									**9**
Anthus lineiventris									1					**1**													
Apalis flavida		2			4	2		2						**10**													
Batis molitor	N	9	3	7		8	2	16	10	5	4	3	9	**76**													
Camaroptera brachyura					1						1			**2**													
Campethera abingoni		1	1						1					**3**													
Centropus burchellii			1		1		1							**3**													
Cisticola aberrans	O				4		1							**5**	1	3	3				2	10					**19**
Cisticola chiniana	N	14	9	26	6	14	10	20	15	8	17	3	20	**162**	4	5		1	5	2			4	9	3	11	**44**
Cisticola juncidis	O															1	8	17	7		11	7	13	5		12	**81**
Cisticola natalensis	O			6	2		4							**12**	3	3	6	1	5	5	4	4	4	3	3		**41**
Cisticola sp. (? lais)																					3						**3**
Colius striatus	N					7	8							**15**													
Cossypha humeralis	N		1	1				2	2	4	2	3	2	**17**													
Dendropicos fuscescens	N	4		2	2			3		1		1	1	**14**													
Dicrurus adsimilis		1		4	3				2	5		2		**17**													
Dryoscopus cubla		2	2			1								**5**													
Emberiza flaviventris	N												2	**2**													
Eremomela icteropygialis	N			4										**4**													
Eremomela usticollis	N			5					2				8	**15**													
Esrilda astrild																				4							**4**
Euplectes axillaris	O														4												**4**
Euplectes sp.																					2						**2**
Eupodotis melanogaster	O	1												**1**				1									**1**
Francolinus sephaena	N																										
Halcyon albiventris												2		**2**													
Halcyon chelicuti						2								**2**													
Indicator indicator									2					**2**													
Lagonosticta rubricata	N		7		11	2			17		17			**54**			2			7							**9**
Lamprotornis nitens									2		2		1	**5**													
Lanius collaris	O															2		8									**10**
Macronyx capensis																											
Macronyx croceus	O														6	8	3	10	4	6	7	6		3		10	**63**
Melaenoris pallidus		1		1							1		4	**7**													

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Species cont...		1n	2n	3n	4n	5n	6n	7n	8n	9n	10n	11n	12n		1o	2o	3o	4o	5o	6o	7o	8o	9o	10o	11o	12o	
Melaenoris pammelaina	N	4	2			2		6		2	2	4	4	**26**													
Meropus pusillus																		1									**1**
Mirafra africana	O															1	4				1		1	4	2	2	**15**
Mirafra sabota								2		2				**4**													
Myioparus plumbeus								1						**1**													
Nectarinia collaris					1									**1**													
Nectarinia talatala							1		1			1		**3**													
Nicator gularis		1												**1**													
Nilaus afer	N			5			2	1	5	4		2	4	**23**													
Numida melaegris																				5							**5**
Oriolus larvatus	N			1		2					1			**4**													
Parus niger	N	6	3	5			1		2	4	2	2	2	**27**													
Petronia superciliaris		3			8		2	5	1	2			6	**27**													
Ploceus ocularis							1							**1**													
Ploceus subaureus											1			**1**													
Prinia subflava	N	3	2		6	7	4		7		6			**35**						1			6			1	**8**
Pycnonotus barbatus	N	13	5	8	7	16	15	14	11	3	4	7	4	**107**	6			5	4								**15**
Rhinopomastus cyanomelas	N	3					1	3	7					**14**													
Saxicola torquata	O														8	3	10	5	6		3						**35**
Schoenicola brevirostris	O														6												**6**
Serinus mozambicus				1	6			4		3				**14**				3			6						**9**
Sigelus silens	O			2			1							**3**													
Streptopelia capicola						4								**4**													
Streptopelia semitorquata								1						**1**													
Sylvietta rufescens	N		1	2	1	1	1	2					1	**9**													
Tchagra australis		1						1						**2**													
Tchagra senegala	N		2	5					7	2	3			**19**												1	**1**
Telophorus sulfureopectus	N							1	3	1				**5**													
Tockus alboterminatus											4			**4**													
Turdus libonyana	N										2		3	**5**													
Turnix sylvatica																										2	**2**
Turtur chalcospilos										2			6	**8**													
Upupa africana													1	**1**													
Uraeginthus angolensis	N	2		1				2					5	**10**				1								2	**3**
Urocolius indicus	N		1		2			5	9		3			**20**													
Vanellus coronatus																		2									**2**
Zosterops pallidus			2	2	6	3	2	5				2		**22**													
Total species		**18**	**17**	**19**	**17**	**14**	**17**	**21**	**21**	**15**	**18**	**12**	**19**	**19**	**8**	**8**	**7**	**13**	**6**	**7**	**9**	**4**	**6**	**5**	**3**	**9**	**26**
Specialist species		**9**	**11**	**13**	**7**	**9**	**9**	**13**	**13**	**10**	**12**	**8**	**14**		**6**	**7**	**6**	**7**	**4**	**3**	**7**	**4**	**3**	**4**	**2**	**3**	