Home range use by Southern Ground-Hornbills (*Bucorvus leadbeateri*) - quantifying seasonal habitat selection and vegetation characteristics

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Abstract:

The habitat of an animal is extremely important as it provides that animal with the necessary resources for fulfilling its life-history requirements (Brennan & Block, 1993; Beyer *et al.* 2010). A habitat is defined as a region in environmental space which comprises of multiple abiotic and biotic variables influencing an animal's location (Krausman, 1999; Beyer *et al.* 2010). Animals tend to utilise discrete areas within a habitat, constituting part of their home range. Home range analysis helps to delineate the area used by an animal habitually and areas of concentrated use (Samuel *et al.* 1985; Seaman & Powell, 1996; Moorcroft *et al.* 1999; Mitchell, 2007; Rodgers & Kie, 2011). Patterns of differential use of space within an animal's home range are the result of competing demands and trade-offs. In this study, a kernel technique was used to determine the home range of four satellite-tracked groups of Southern Ground-Hornbills *Bucorvus leadbeateri* in the Associated Private Nature Reserves (APNR) in the South African lowveld. Satellite data were analysed in ArcGIS® 9.3 to quantify habitat selectivity by groups of ground-hornbills at different times of the year to determine a) favoured habitat types, and b) the resolution with which they perceive their environment. Each of the groups showed variation in the utilisation and extent of their home ranges on a seasonal basis. Home range sizes contracted towards the nest during the summer breeding season (December to March) and expanded during the dry season (April to September). Within the home range of one of the groups the physical characteristics of habitat types (i.e. vegetation types) were sampled at 250 random co-ordinates in order to assess whether habitat preference at the meso-scale can be explained by the physical attributes of that vegetation type. By profiling and quantifying the vegetation of areas in the home range that are used by Southern Ground-Hornbills to differing degrees, this information could be used as a proxy to facilitate re-introduction efforts, by providing a tool to identify optimal landscape configurations.

Keywords: Southern Ground-Hornbill, home range, habitat type, habitat preference, perception

Introduction:

Considerable ambiguity exists regarding the definition of a key concept in wildlife management and practice, the concept of "habitat" (Brennan & Block 1993; Krausman 1999). The term "habitat" is confounded by the subjectivity of its application and the plethora of associated terminology (e.g. microhabitat, macrohabitat, habitat configuration, habitat selection, habitat preference, habitat use; Brennan & Block 1993). Descriptions of an animal's habitat may range from a very broad, landscape-scale vegetation type to the immediate physical environment of an animal, incorporating both a spatial and temporal component, further promoting the ambiguity of the concept (Brennan & Block 1993; Krausman 1999). Furthermore, habitat is sometimes referred to as the "address" of organism: this exacerbates the confusion surrounding the term, as it may not be specified whether the "address" refers to a city, neighbourhood, street, postal code, house, room, or a room within a house (Brennan & Block 1993).

A habitat is defined as a region in environmental space comprising multiple abiotic and biotic features or attributes which influence the location of an animal (Krausman, 1999; Beyer *et al.* 2010). Environmental variables are either mediated directly (e.g. forage quality) or indirectly (e.g. altitude) resulting in a continuum of differential space use by animals (Beyer *et al.* 2010). Largely, the habitat utilized by an animal to maximize its fitness is distributed heterogeneously in space (Brennan & Block, 1993; Beyer *et al.* 2010). Whether finding mates, rearing offspring, acquiring food or defending territories, all require a spatial adjustment in location by the animal (Beyer *et al.* 2010; Kie *et al.* 2010). The advent and use of satellite-based technology in animal tracking allows location data to be collected with an ever-increasing rate and accuracy (Kie *et al.* 2010; Tomkiewicz *et al.* 2010; Urbano *et al.* 2010). These advances have been accompanied by advances in the analytical tools available for describing home ranges and patterns of spatio-temporal use of those ranges (Hebblewhite & Haydon 2010; Kie *et al.* 2010). Burt (1943) defined a home range as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young: occasional sallies outside the area, perhaps exploratory in nature, should not be considered as part of the home range." Burt's definition acknowledges that differential space use arises due to trade-offs in animal behaviour, but fails to provide appropriate empirical criteria as how to delineate home range boundaries and indentify areas that vary in intensity of use within the home range (Kie *et al.* 2010, Rodgers & Kie, 2011).

Home range analysis essentially attempts to delineate the areas used habitually by an animal and the extent to which particular areas are utilized (Samuel *et al.* 1985; Seaman & Powell, 1996; Moorcroft *et al.* 1999; Mitchell, 2007; Rodgers & Kie, 2011). Furthermore, to facilitate an understanding of the behaviour, and by extension the fitness of animals, it is vital to quantify the dynamics of differential space use within a heterogeneous habitat (Beyer *et al.* 2010). The goal is to understand the processes that give rise to patterns of space use within such a habitat, thereby facilitating more informative conservation and management decisions (Beyer *et al.* 2010; Kie *et al.* 2010). Combining knowledge of animal movement and distribution data obtained from satellite tracking with *in situ* measurements of habitat characteristics further allows meaningful interpretations of habitat use (Beyer *et al.* 2010; Hebblewhite & Haydon, 2010). Performing statistical comparisons of habitat use as a function of habitat availability helps to identify whether habitats within a home range are utilized randomly or selectively (Johnson, 1980; Beyer *et al.* 2010). The non-random use of habitat is synonymous with preference, because certain habitats are used disproportionately to their availability (Krausman, 1999; Beyer *et al.* 2010). A habitat that is preferred over another may provide conservation managers with additional scope when seeking to reintroduce or translocate a threatened species, because it provides guidelines for identifying optimal habitat configurations.

Southern Ground-Hornbills (*Bucorvus leadbeateri*) have experienced a significant reduction (65%) in their numbers and area of occupancy over the past century (Kemp and Webster, 2008). With a current global threat listing as *Vulnerable* (IUCN, 2001), they are the focus of many conservation and re-introduction efforts, e.g. the Mabula Ground-Hornbill Project. Previous studies of Southern Ground-Hornbills in the Associated Private Nature Reserves (APNR) revealed social and environmental factors which positively influence their breeding success (Wilson, 2010). Food availability, mediated through rainfall, is the primary environmental variable influencing breeding success (Kemp *et al.* 1989; Wilson, 2010). However, rainfall cannot be managed and from a conservation-management perspective, it is important to consider other environmental variables which may promote breeding success and survival (Wilson 2010). The availability of suitable nest sites for the birds also limits breeding success (Kemp and Begg 1996; Henley and Henley 2005; Wilson, 2010). In response to this, the installation of artificial nest-boxes has been a successful management option, with groups nesting in them contributing 60% of the reproductive output from 2001-2008 in the APNR (Wilson, 2010). The proportion of open woodland surrounding the nest site of ground-hornbills also positively influences breeding success, especially in groups that use natural nests, making bush clearance in the immediate vicinity of the nest a viable management option (Wilson, 2010). Lastly, breeding success is positively linked to group size, with groups comprising more than three individuals being the most successful (Wilson, 2010). Potential management options to date have focused primarily on improving conditions related immediately to the nesting experience of Southern Ground-Hornbills.

This undoubtedly is a key aspect of the birds' behaviour to manage, however nesting activities only span four months of the year. Management options sought in the other eight months of the year could be prove to be equally productive.

Little is known about how Southern Ground-Hornbills utilize and perceive their extensive home ranges. The quality (territory size, food availability, refuges, vegetation types and nest sites) of the home range ultimately dictates the breeding success of the birds, but to quantify these 'quality' factors individually requires long-term data and subsequent integration of these data on applicable scales. In general terms, vegetation characteristics and physiognomy contribute to determining the range of occupancy of a particular species (Rotenberry 1985; Krausman 1999; Beyer *et al.* 2010). Along with other environmental factors, vegetation attributes are likely to have a direct influence on how a Southern Ground-Hornbill perceives its environment. Perception of the landscape is likely to cycle on a seasonal basis, as Southern Ground-Hornbills are subject to competing demands and motivations (Beyer *et al.* 2010). In general, animals move between habitats to satisfy these demands and motivations (Beyer *et al.* 2010; Kie *et al.* 2010; Tomkiewicz *et al.* 2010). For ground-hornbills, identifying and quantifying the seasonal changes in space utilisation within their home ranges is fundamental to developing an understanding of how their home range contributes to fulfilling the diversity of life-history requirements.

Satellite transmitters were fitted on four Southern Ground-Hornbill groups in the APNR in order to quantify how the birds utilise the available habitat types (i.e. vegetation types) within their home range and on the extent to which this may influence a group's success. Preference i.e. (time spent) for specific habitats within a home range would indicate that these sites provide above-average benefits for Southern Ground-Hornbills. These benefits may be resources (food, nest sites) or refuges (escape from heat and predators). Profiling and quantifying the vegetation types within the home range that are favoured by Southern Ground-Hornbills to differing degrees, could provide information that in turn could be used as a proxy to facilitate re-introduction efforts, when it becomes important to identify optimal landscape configurations.

This study aims to quantify seasonal habitat selection and identify those physical characteristics of the vegetation that influence patterns of home range use by Southern Ground-Hornbills in the South African lowveld, using an established study population. Specifically, the project aims to quantify habitat selectivity by groups of ground-hornbills at different times of the year to determine a) favoured habitat types, and b) the resolution with which they perceive their environment. Both of these parameters are important in guiding reintroduction programmes. The study addresses the following key questions:

1.) To what degree do Southern Ground-Hornbills utilise different habitat types within their territories?

2.) Does habitat preference differ between groups and seasons?

3.) To what extent do Southern Ground-Hornbills distinguish between different habitat types – i.e. how many habitat types do they 'recognise' in the landscape?

4.) Can Southern Ground-Hornbills' apparent perception of the landscape be explained by vegetation structure?

Study species, site and methods:

Study species:

Southern Ground-Hornbills are co-operatively breeding birds that live in social groups, with each member contributing to group activities, especially the raising of young (Kemp, 1996; Hockey *et al.* 2005). They exhibit delayed maturity, small clutch size, slow reproductive rate (average 1 chick/group/9 years in the Kruger National Park), large home ranges, prolonged post-fledging dependency and high longevity (Kemp, 1988; Kemp *et al.* 1989). Groups comprise two or more members (max 12) that move around the landscape cohesively (Kemp, 1980; Kemp, 1988). Groups spend *ca* 70% of the day on the ground, often seeking shade or a suitable resting place around midday (Hockey *et al.* 2005). At the end of a day the group flies up to roost in either a large tree or on a rock face, where they spend the night (Hockey *et al.* 2005). Home range size (±100 km^2) is thought to be determined primarily by the availability of suitable nest sites (usually spaced 4-10 km apart) and secondly by food availability during the dry season (April to September - Kemp *et al.* 1989; Wilson, 2010). Southern Ground-Hornbills have a relatively long and narrow binocular field of vision (Martin & Coetzee 2004). The width is restricted by the bill tip projecting into the lower half of the binocular field but allows the bird to view its own bill tip: this type of visual field is commonly associated with birds requiring precision-grasping of prey items (Martin & Coetzee 2004). The birds are strictly carnivorous, eating reptiles, insects, amphibians and small birds and mammals (Vernon, 1986). Southern Ground-

Hornbills also have long lash-like feathers protruding from the upper eye lids, used to shade out sun (Martin & Coetzee 2004). The highest density of Southern Ground-Hornbills in southern Africa (one group per 20 km^2) occurs at Mana Pools, Zimbabwe (Begg 1996 in Kemp and Begg, 1996; Hockey *et al.* 2005). Major threats that have precipitated the decrease in numbers include habitat fragmentation, afforestation and crop farming (Kemp & Webster 2008): secondary factors include poisoning, use in traditional medicinal, Newcastle's disease, electrocution and trade in live birds (Kemp & Webster 2008).

Study site:

The Klaserie Private Nature Reserve is one of four private member reserves of the APNR (Associated Private Nature Reserves) which is situated in the north-eastern lowveld of South Africa, abutting the Kruger National Park (KNP) to the east (Fig. 1). The APNR covers an area of 180 000 ha, making it one of the largest privately owned reserves in the world dedicated to conservation (Greyling *et al.* 2004). It now forms part of the Greater KNP Biosphere Reserve in conjunction with the Sabie-Sand Game Reserve and other Provincial Nature Reserves: fences originally separating these reserves were removed in 1993 (Greyling *et al.* 2004). Land in the APNR is either corporately or privately owned, but is managed collectively and collaboratively with the Scientific Services Section of the KNP (Greyling *et al.* 2004; Van Der Waal, 2010)

The APNR climate is sub-tropical and highly seasonal, with hot, humid summers and dry winters (Venter *et al.* 2003). Eighty percent of rainfall occurs in summer between October and March. Mean annual precipitation ranges from 450 $mm.yr^{-1}$ in the north east, to 600 $mm.yr^{-1}$ in the south west (Van Der Waal, 2010). January is the hottest month, with a mean maximum temperature of 33.6°C. In the coldest month (June), the mean minimum temperature is 9.4°C (Venter *et al.* 2003). Soils in the APNR and western KNP are mainly derived from granite, having a coarse texture and low nutrient (N, P) availability (Venter *et al.* 2003). The landscape is highly heterogeneous, with dominant vegetation types consisting of lowland savanna, open tree savanna, mixed and open woodland, low thicket and shrubveld, varying structurally from open savanna to closed woodland (Fig. 1) (Venter & Gertenbach, 1986; Van Der Waal, 2010). In Klaserie Private Nature Reserve 22 vegetation types have been defined on the basis of the dominant plant species and community composition (Van Rooyen *et al.* 2005; Van Rooyen, 2005).

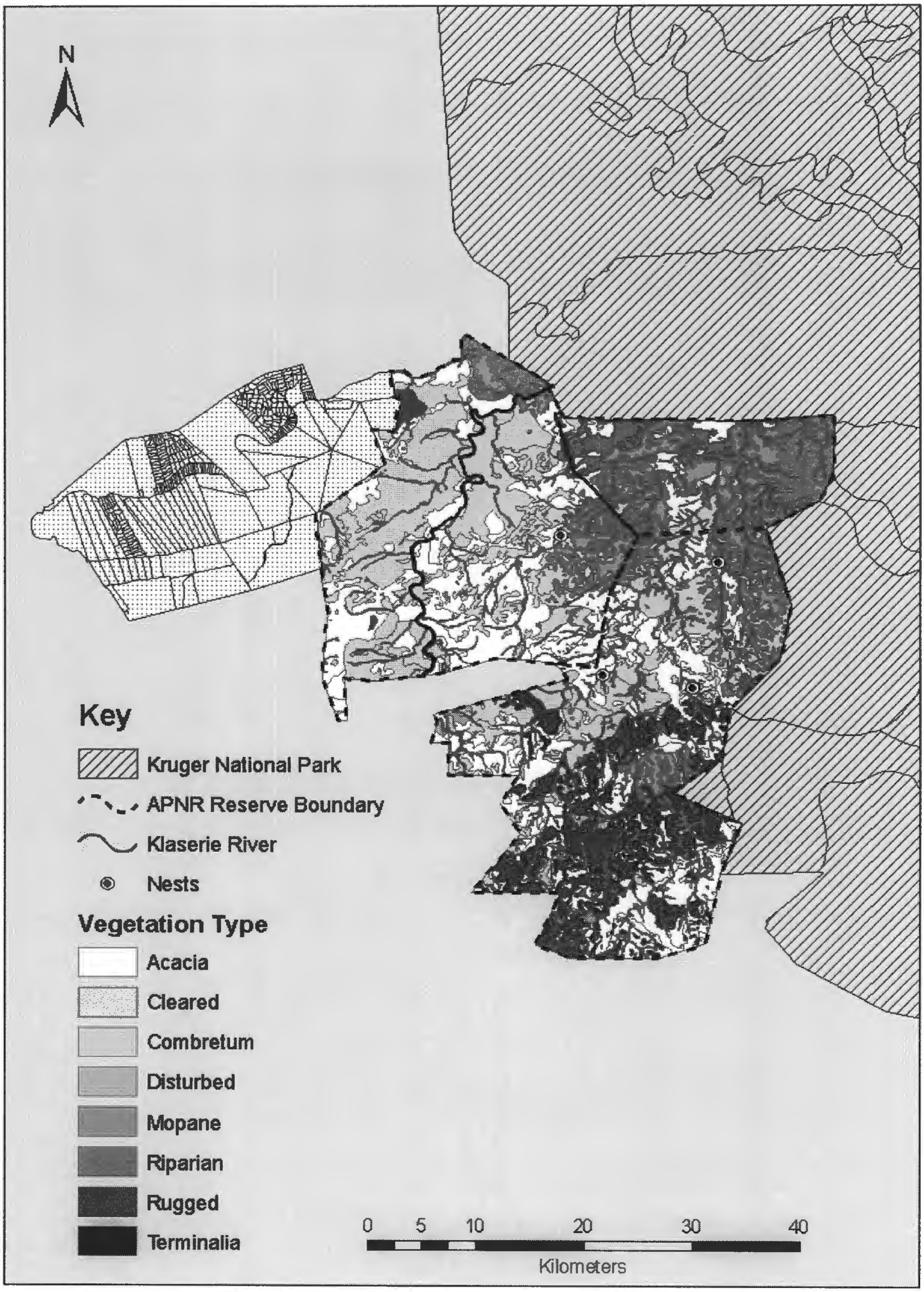

Figure 1: Associated Private Nature Reserves (APNR) (24°2'10"S - 24°33'20"S and 30°48'45"E - 31°28'55"E).

The vegetation of Balule Private Nature Reserve (in the north west) has not yet been mapped

Methods:

The study comprised two main parts: firstly seasonal habitat preferences of Southern Ground-Hornbill groups were determined using satellite telemetry data; secondly the physical vegetation characteristics of one group's home range were quantified during field surveys. The purpose of the vegetation surveys was to gain insight into the birds' perception of different vegetation types and how this perception influences use (i.e. does vegetation physiognomy determine the birds' preferences?). The vegetation map of the APNR is based primarily on floristic contrasts, but it is likely that Southern Ground-Hornbills respond proximally more to the physical structure of the vegetation than to its component plant species (the birds have an exclusively animal diet, and also require large trees in which to nest and suitable shady refuges from high ambient temperatures in summer).

Part one: Home range analysis

The satellite telemetry data obtained for the Keer Keer, Kharan Khaya, Rhino Road and Senelala ground-hornbill groups from July 2010 through to June 2011 were decoded using MTI Argos-GPS Parser software and overlaid on a geo-referenced vegetation map of the APNR using ArcGIS® 9.3. All satellite fixes (i.e. GPS fixes) were projected in UTM36S (Universal Transverse Mercator 36° South) as required by HRT (Home Range Tools) for ArcGIS® 9.3 when computing a Kernel Density Estimate (KDE). A KDE is a commonly employed method for delineating an animal's home range size (Kie *et al.* 2010; Rodgers & Kie 2011). This non-parametric statistical method estimates a probability density from a set of points (satellite fixes) by summing the probability density function of fixed volume (i.e. 'kernel') over each of the individual points using an appropriately scaled reference grid (Rodgers & Kie 2011). This study used a raster grid cell size of 50 m.

The choice of an appropriate smoothing parameter (h) is vital when deriving a KDE (Rodgers & Kie 2011). The smoothing parameter (h) determines the spread of the kernel over a point and the detail of the utilization distribution (UD). The UD becomes extremely variable if it is "under-smoothed" (i.e. using a narrow kernel) and homogenized, losing fine detail, when "over-smoothed" (i.e. using a wide kernel - Rodgers & Kie 2011). A trade-off is sought between the two (Horne & Garton 2006; Rodgers & Kie 2011). An automatically calculated smoothing parameter (h_{ref}) in HRT for ArcGIS® 9.3 was used when computing the KDE for each Southern Ground-Hornbill group. The resulting UD represents the varying degree of space utilization by Southern Ground-Hornbill's within their home range and the probability of locating the group at a single site (Samuel *et al.* 1985; Rodgers & Kie 2011). The UD is composed of regions, containing either high values (many observations, high probability) or low values (fewer observations, low probability). Regions of similar probability are linked using contour lines (isopleths - Rodgers & Kie 2011). The extent of the home range is defined as the 95% isopleth, i.e. the area occupied 95% of the time by a Southern Ground-Hornbill group. A map of the four group's home ranges for each month (from July 2010 to June 2011) was developed in ArcGIS® 9.3 in order to assess if any seasonal displacement of home ranges takes place.

Habitat selectivity:

Habitat selectivity (E_i) of each ground-hornbill group was calculated on a seasonal basis using Jacobs' (1974) modification of Ivlev's Index (Velasquez *et al.* 1991).

$$E_i = (p_i - q_i)/(p_i + q_i - 2p_iq_i)$$

where $p_i = N_i/N_t$ and $q_i = A_i/A_t$, where

N_i = number of satellite fixes per vegetation type *(i)*, N_t = total number of satellite fixes,

A_i = area (ha) of vegetation type *(i)* in home range, and A_t = total area (ha) of home range.

E_i ranges from +1 to -1. Although the index has no statistical properties, values > +0.25 were considered as indicating preference for a vegetation type and values < -0.25 indicating avoidance of a vegetation type. E_i values between +0.25 and -0.25 indicate a neutral attraction for a vegetation type. The number of satellite fixes occurring in a vegetation type were calculated using Hawths Analysis Tools for ArcGIS® 9.3 Version 3.27 (Beyer, 2003), for each of the four seasons, themselves defined on the basis of rainfall seasonality (Early Wet (October - December), Late Wet (January - March), Early Dry (April - June) and Late Dry (July – September). The sizes of Southern Ground-Hornbill groups' home ranges and the extent of each of the vegetation types within each home range were calculated by converting the 95% isopleth into a polygon and intersecting it with the APNR vegetation map. Once all Southern Ground-Hornbill groups' habitat selectivity indices were calculated, the values were used to produce a map (in ArcGIS® 9.3) corresponding to each of the four seasons. A table was compiled in Microsoft® Excel to illustrate whether any of the groups showed similar seasonal shifts in habitat preference.

Part two: Physical vegetation characteristics

In the APNR, the Senelala Southern Ground-Hornbill group was selected as the target group for the study of physical vegetation characteristics. At the time of the study, this group had accumulated more than 7000 satellite 'hits' since the transmitter was fitted on the alpha male in early 2010. The home range can thus be estimated with confidence as can the group's seasonal use of habitats. The following field sampling methods were used as they provided the most time-efficient and effective relative measures of vegetation characteristics during the late dry season (when vegetation sampling took place).

A random stratified sampling protocol was developed for the study of vegetation characteristics using ArcGIS 9.3® software. This made use of two variables required to calculate the habitat selectivity indices, *viz.* home range size and the extent of each vegetation type within the home range. The proportion of each vegetation type relative to the total area was calculated (e.g. area [ha] of vegetation type *n* within the home range/total area [ha] of the home range). In order to avoid under-sampling the home range of the Senalala group, 250 random sample points (GPS co-ordinates) were allocated across vegetation types based on their proportional areas within the home range. This was done by multiplying the proportional area (summing to unity) of a vegetation type by 250. Thus for each vegetation type, the number of sample points were representative of the area occupied by that vegetation type within the home range. Thus, if the area of vegetation type *a* was twice the area of vegetation type *b*, then vegetation type *a* had twice as many sample points. These sample points were then randomly distributed within the corresponding vegetation type using the random point generator tool available in Hawths Analysis Tools for ArcGIS 9.3® Version 3.27 (Beyer 2006). The GPS co-ordinates of the 250 sample points were then extracted and recorded in a table in Microsoft® Excel.

The following physical components of the vegetation were selected for measuring at a single point (GPS co-ordinate) in the home range. Whilst these differ from classical measures as may be made during botanical surveys, they were deemed appropriate surrogates for how Southern Ground-Hornbills might see the habitat around them. The variables measured were: A) Vertical (canopy cover – a proxy for shade) and B) Horizontal (vegetation/stem density, ground cover). Canopy cover was measured using a Canopy Occlusion Meter (COM) which gives an indication of the relative amount of canopy cover in a vegetation type when viewed from the eye height of a ground-hornbill (See Appendix 2.). Twelve measures of canopy cover were taken at a distance of 4 m from the tripod, one every 30°, starting at 0° and then rotating in a clockwise direction until 330°. The amount of occlusion was estimated as the proportion of sky occluded in the mirror (see Appendix 2). Open sky thus yielded a value of 0% (no occlusion), whereas a fully closed canopy was recorded as 100% (total occlusion). Canopy cover is important for Southern Ground-Hornbills in providing shade when daily temperatures increase and they are no longer able to forage (Dickens, 2010). Vegetation density was measured in three ways. The horizontal component of density was measured using a laser range finder (LRF) and Bitterlich's Wedge (BW), respectively providing indexes of vegetation density and stem density. A Bosch® PLR50 laser range finder (LRF) was mounted on the tripod. If the laser beam encountered an object large or dense enough to reflect the beam, the device registered the distance to such an object up to 50 m distance. Twelve readings of horizontal visibility were taken using the LRF, one every 30°, starting at 0° and then rotating the LFR in a clockwise direction until 330°. These readings were made at two heights: first at Southern Ground-Hornbill eye height (600 mm) and then above maximum grass height (1.20 m). The Bitterlich's Wedge, a unitless measure, was used as a supplement to the LRF data, to calculate stem density. This was done by performing a basal sweep and counting all the stems exceeding the 0.5 increment of the wedge. Vegetation density on the ground (i.e. the vegetation through which ground-hornbills walk – mostly grass) was measured using a disc pasture meter (DPM) which provides an indication of grass biomass. Eight DPM readings were taken at a distance of 2 m from the tripod centre, every 45°, rotating in a clockwise direction around the tripod. The former component - horizontal vegetation and stem density - may have implications for predator avoidance and general movement and the latter component – vegetation ground cover density - for food availability and detectability. These three physical components were expected to provide some measure of how ground-hornbills perceive habitat in terms of a) ease of travel and food acquisition, b) predator avoidance and the need for vigilance, and c) potential for shade provision.

On a daily basis, a map of the groups' home range with 15 sample points was produced in ArcGIS 9.3® and collectively uploaded to a Garmin® GPSMAP® 78s unit using DNRGarmin® software. Once arriving at a sample point, the above sampling protocol was followed by placing the tripod on the exact GPS co-ordinate, orientated towards magnetic north, in order to standardize across samples. All data were captured and manipulated in Microsoft® Excel.

Statistical analyses:

A tree cluster analysis was performed in Statistica V.10 using the physical vegetation characteristics data for the dry season. Only favoured or avoided vegetation types (based on the habitat selectivity index) were used, with preference selected as the response variable in the analysis. The output of the tree cluster analysis used complete linkage and Euclidean distance. Variables included in the analysis were, median LRF value (the median at Southern Ground-Hornbill eye height), mean COM value (mean of the 12 readings at a sample point), the square root transformation of the mean DPM value: the mean of eight readings was taken and calibrated using the following equation - kg ha^{-1} = $[31.7176\ (0.3218^{1/x})\ x^{0.2834}]^2$ for mean DPM heights < 260 mm (Zambatis *et al.* 2004). Square root transformation was used to reduce the difference in magnitude of DPM values with the other variables. BW value (a unitless measure) was the final variable included.

Results

Part 1: Home range analysis

The Southern Ground-Hornbill groups in the APNR varied in home range size. The largest home range was occupied by the Senelala group (10 322 ha) and the smallest by the Rhino Road group and (5551 ha - Table 1). All four groups attempted to breed in the 2010-2011 breeding season (December - March) and all showed a contraction in home range size during this period (Table 1). Three of the groups (Keer Keer, Kharan Khaya and Rhino Road) fledged chicks and contracted their home ranges by similar amounts during the breeding season (using only 36%, 24% and 35% of their home ranges, respectively- Table 1). The Senelala group's chick did not survive to fledge and this group used up to 70% (7180 ha) of their home range during the same period. In each season, the home ranges of all four groups' consisted largely of habitats for which the birds showed no strong attraction or avoidance (Table 1). The Rhino Road group was the one group that showed active avoidance of a substantial proportion of their home range (55%) in the late dry season (Table 1). At the same time of year, the other three groups (Keer Keer, Kharan Khaya and Senelala) largely used different habitats in proportion to their relative abundance.

Table 1: Summary of attributes of the four Southern Ground-Hornbill groups used in the study.

	Keer Keer	Kharan Khaya	Rhino Road	Senelala
SGH group attributes				
Group size (n)	4	8	9	8
Nest type	Natural	Artificial	Artificial	Artificial
Breeding attempt (2010-2011)	Yes	Yes	Yes	Yes
Chicks fledged	Yes	Yes	Yes	No
Home range attributes				
Size (ha)	5886	7157	5551	10322
Size during breeding season (Dec-Mar) (ha)	2027 (36%)	1740 (24%)	1952 (35%)	7180 (70%)
Area (ha) and proportion of favoured habitat per season				
Early Wet	1219 (21%)	677 (10%)	646 (12%)	821 (8%)
Late Wet	1270 (22%)	768 (11%)	663 (12%)	1428 (14%)
Early Dry	0	768 (11%)	230 (4%)	40 (0.3%)
Late Dry	47 (0.8%)	1183 (16%)	1199 (22%)	0
Area (ha) and proportion of habitat avoided per season				
Early Wet	1813 (31%)	1798 (25%)	1579 (28%)	1034 (10%)
Late Wet	1761 (30%)	1798 (25%)	1446 (26%)	2231(22%)
Early Dry	859 (15%)	1085 (15%)	230 (4%)	2065 (20%)
Late Dry	1246 (21%)	91 (2%)	3094 (55%)	185 (2%)
Area (ha) and proportion of habitat used in proportion to its availability per season				
Early Wet	2854 (48%)	4682 (65%)	3327 (60%)	8467 (82%)
Late Wet	2854 (48%)	4592 (64%)	3442 (62%)	6663 (64%)
Early Dry	5027 (85%)	5305 (74%)	5092 (92%)	8217 (80%)
Late Dry	4593 (78%)	5884 (82%)	1258 (23%)	10137 (98%)

During the breeding season (early and late wet seasons), all groups displayed a preference for habitat types in the immediate vicinity of the nest (Figs 2-5, Table 2). *Phragmites australis* riverine vegetation occurring in the drainage lines was particularly favoured by three of the groups in the early and late wet season. Once the breeding season ended, groups shifted to other habitat types within their home ranges (Figures 2-5).

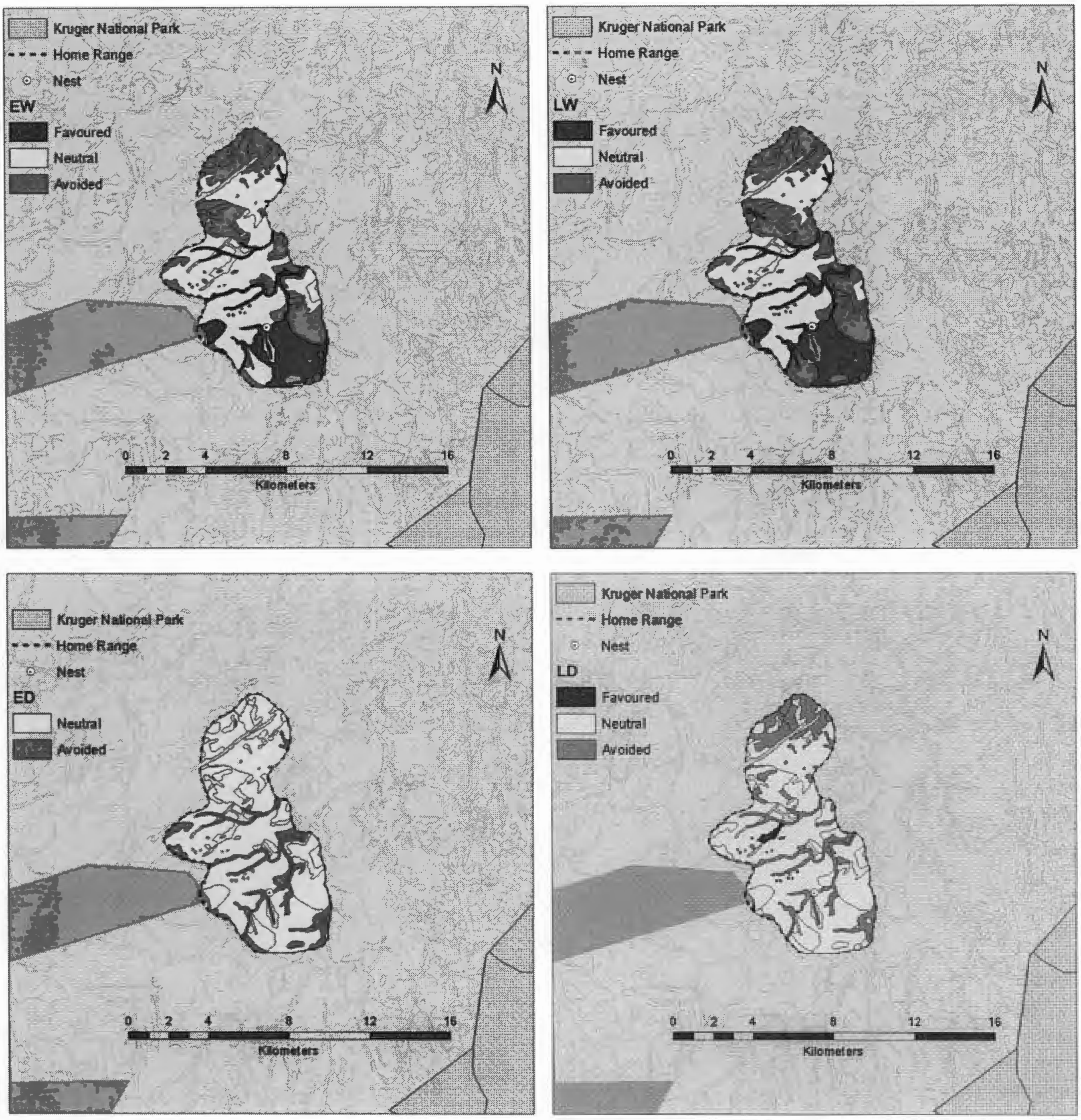

Figure 2: The seasonal habitat selectivity (E_i) of the Keer Keer SGH group within their home range. (E_i) is based on Jacobs' (1974) modification of Ivlev's Index (Favoured: (E_i) > 0.25; Neutral: 0.25> (E_i) > -0.25; Avoided: (E_i) <-0.25). Seasons: EW=Early Wet, LW=Late Wet, ED=Early Dry, LD=Late Dry.

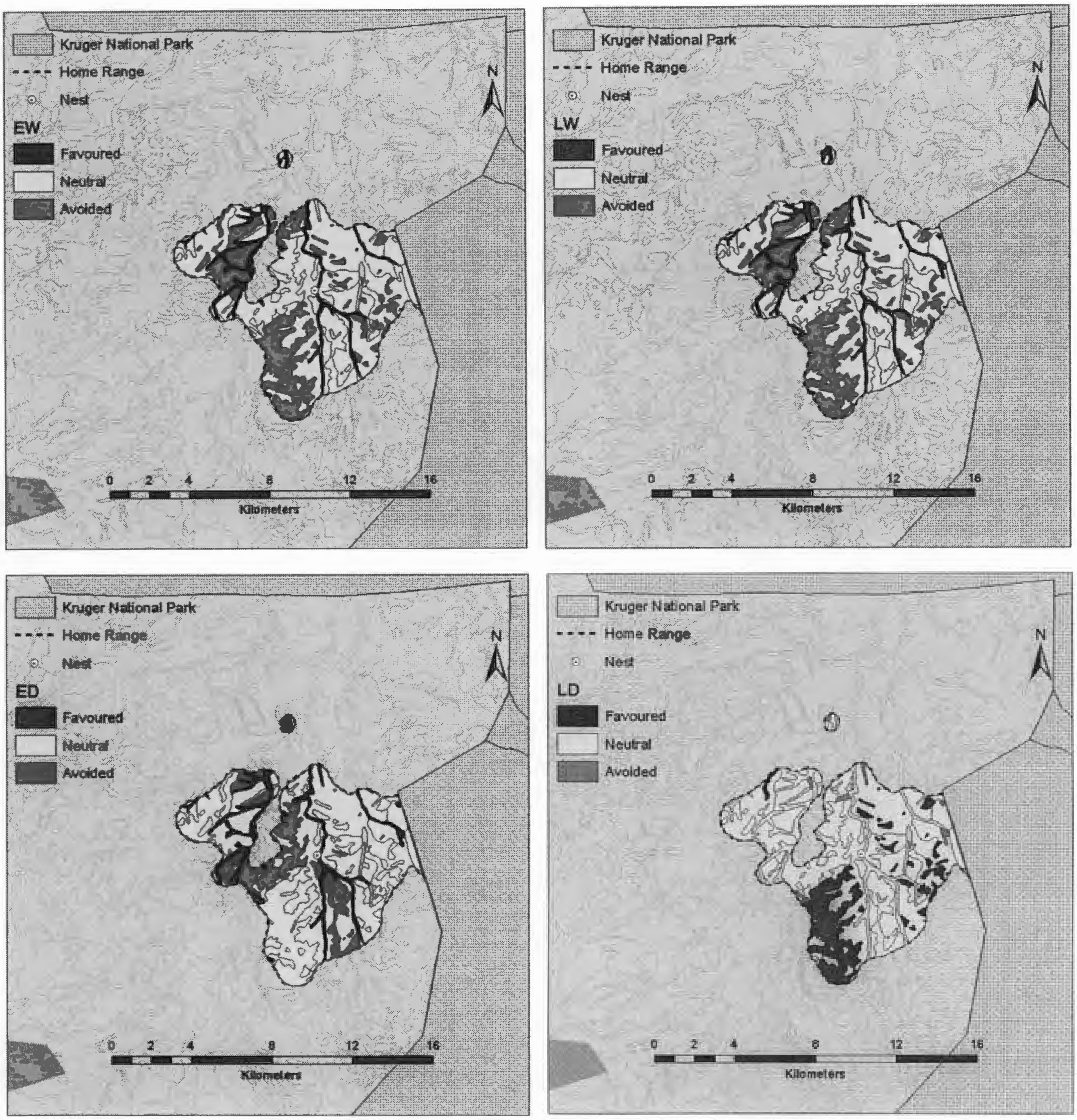

Figure 3: The seasonal habitat selectivity (E_i) of the Kharan Khaya SGH group within their home range. (E_i) is based on Jacobs' (1974) modification of Ivlev's Index (Favoured: (E_i) > 0.25; Neutral: 0.25> (E_i) > -0.25; Avoided: (E_i) <-0.25). Seasons: EW=Early Wet, LW=Late Wet, ED=Early Dry, LD=Late Dry.

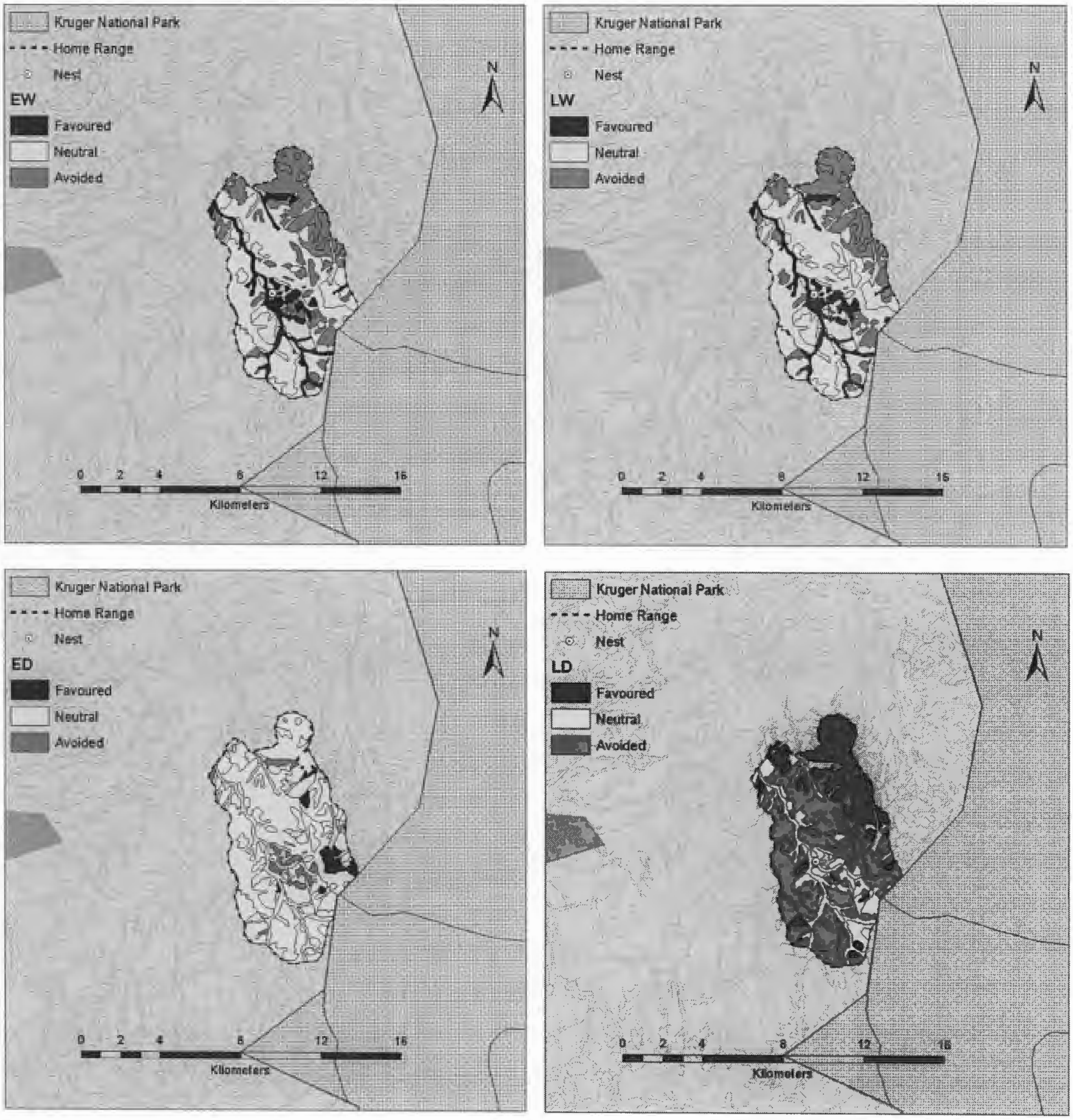

Figure 4: The seasonal habitat selectivity (E_i) of the Rhino Road SGH group within their home range. (E_i) is based on Jacobs' (1974) modification of Ivlev's Index (Favoured: (E_i) > 0.25; Neutral: 0.25> (E_i) > -0.25; Avoided: (E_i) <-0.25). Seasons: EW=Early Wet, LW=Late Wet, ED=Early Dry, LD=Late Dry.

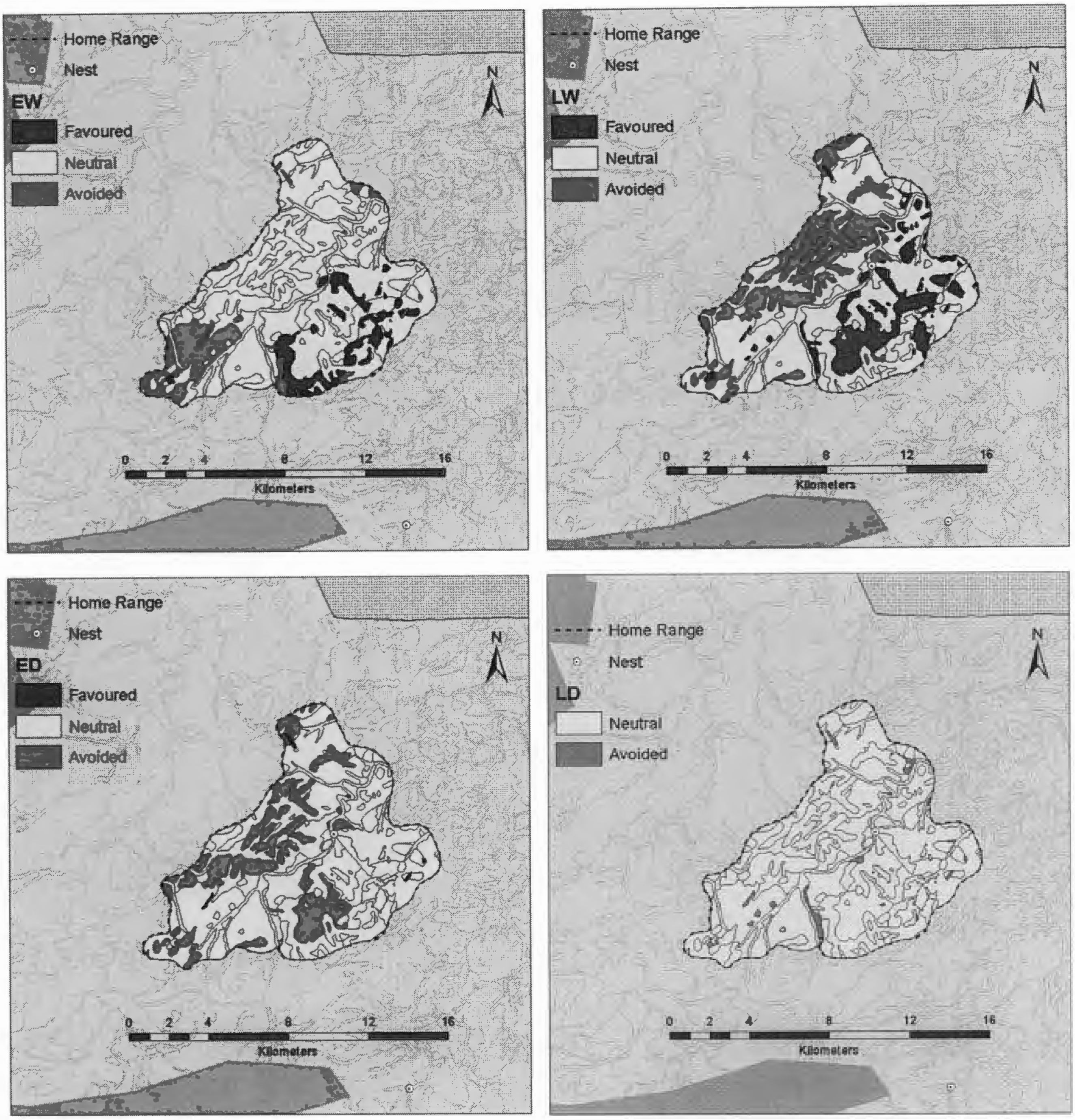

Figure 5: The seasonal habitat selectivity (E_i) of the Senelala SGH group within their home range. (E_i) is based on Jacobs' (1974) modification of Ivlev's Index (Favoured: (E_i) > 0.25; Neutral: 0.25> (E_i) > -0.25; Avoided: (E_i) <-0.25). Seasons: EW=Early Wet, LW=Late Wet, ED=Early Dry, LD=Late Dry.

The Kharan Khaya and Rhino Road groups' home range boundaries were largely determined by habitat types that were favoured at some time during the year (Fig. 6). Home range overlap that occurs between these two groups is due to favoured habitat type located in Kharan Khaya's southern limit and Rhino Road's northern limit. Whether the range boundaries of the Keer Keer and Senelala groups are determined by 'hotspots' distributed along the range edges is less clear. For both groups, the southern limits of their home ranges did coincide with favoured habitats, but the dispersion of such habitats did not explain the northern range boundaries.

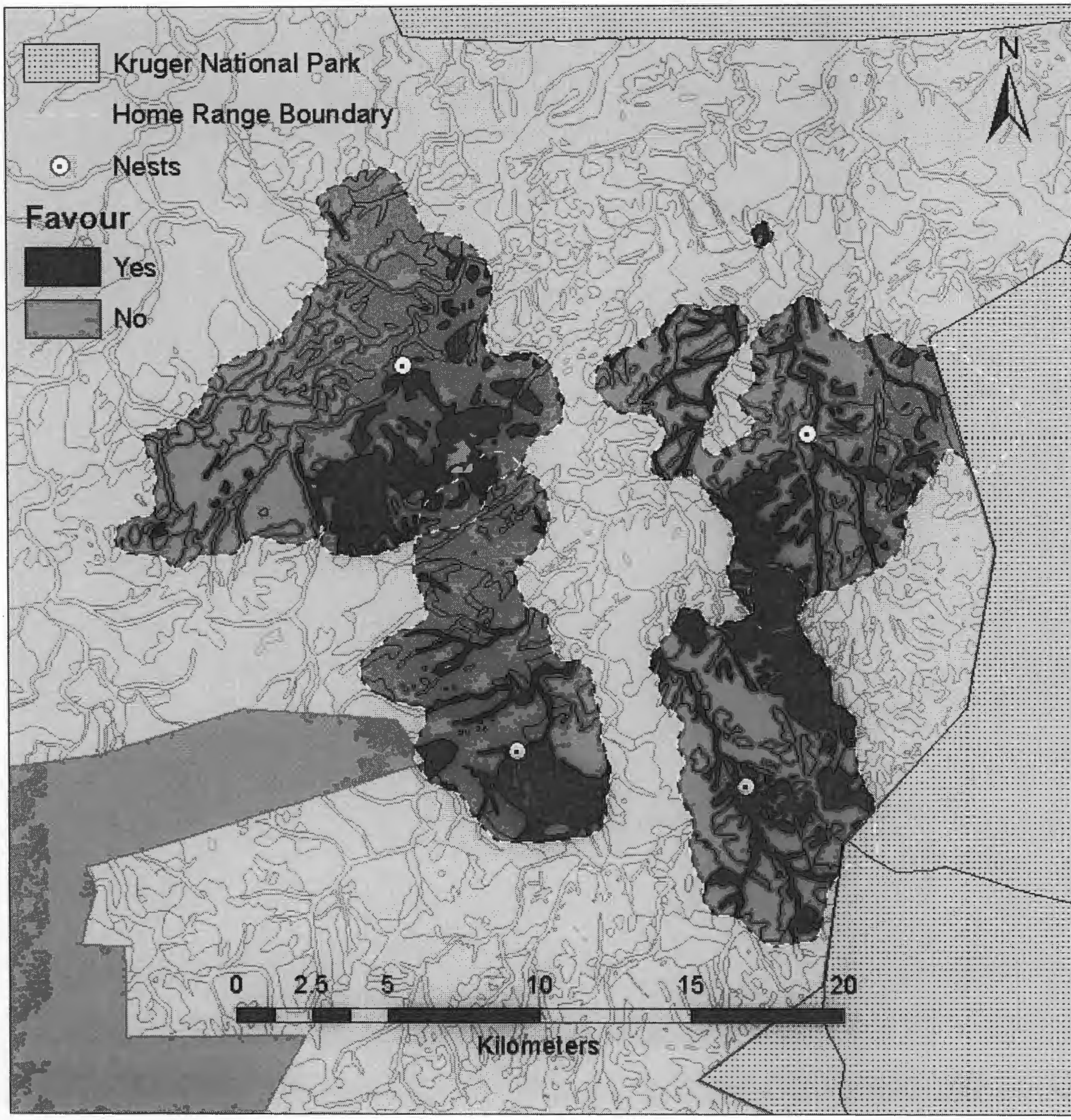

Figure 6: Distribution of favoured habitat types calculated across all seasons in the home ranges of four Southern Ground-Hornbill groups in the APNR. Top left = Senelala; Top Right = Kharan Khaya; Bottom left = Keer Keer; Bottom right = Rhino Road.

Most groups showed similar shifts in habitat selection per season (Table 2). Three of the groups (Keer Keer, Rhino Road and Kharan Khaya) favoured *Phragmites australis* riverine vegetation in the early and late wet season. Interestingly, the Keer Keer group then displayed a complete avoidance of this habitat in the early and late dry season. Disturbed areas were favoured by three groups in the late wet season, with Senelala and Kharan Khaya carrying this preference through into the early dry season, but avoiding this habitat in the late dry season. Within seasons, some habitat types were favoured by one group and avoided by another (Table 2.). For example, Combtreum *Xerophyta retinervis* low thicket was favoured by the Keer Keer group in the early wet season, at which time the Senelala group was neutral towards it and the Kharan Khaya and Rhino Road groups avoided it. In the late wet season, the Senelala group's preference changed, avoiding this vegetation type (as did the Rhino Road and Kharan Khaya groups: by contrast, the Keer Keer group continued to favour the Combretum habitat. In the early dry season the Keer Keer, Kharan Khaya and Rhino Road groups showed no preference for or avoidance of this vegetation type, but it was avoided by the Senelala group. In the late dry season, the Rhino Road group avoided this habitat whilst the other three groups showed no preference or avoidance.

In the late dry season (July to September 2010) home range size expanded outwards from the nest, attaining maximum extent during this period (Fig. 7). During this period all four groups' home ranges partially overlapped, touching at least two of the other groups (in July 2010). Overlapping home ranges remained evident between the Senelala and Keer Keer group until November 2010, whilst the Kharan Khaya group rapidly contract their home range with the onset of the rainy season and egg-laying period. With the arrival of the breeding season (December 2010 – March 2011) all four groups' home ranges contracted in size. This contraction is inwards towards the nest site, evident in each group (Fig 7.). The Kharan Khaya group shows the biggest contraction in home range size during this period closely followed by the Keer Keer group (Fig 7, Table 1.). At the end of the breeding season, the groups started to expand their home ranges outwards from the nest, with home range overlap occurring again in May and June 2011.

Table 2: The seasonal habitat selectivity (E_i) by Southern Ground-Hornbill groups in the APNR: F = favoured; N = neutral association; and A = avoided. Only vegetation types that occurred in two or more groups' home range were used. Group abbreviations used are: KK=Keer Keer; KK=Kharan Khaya; RR=Rhino Road; SN=Senelala. Seasons: EW=Early Wet; LW=Late Wet; ED=Early Dry; LD=Late Dry.

Vegetation Type	EW			LW			ED			LD		
	F	N	A	F	N	A	F	N	A	F	N	A
Acacia nigrescens - Combretum apiculatum mixed woodland	RR	KE, KK	SN	RR	KE, KK, SN	-	-	KE, SN	RR, KK	-	KE, KK, RR, SN	-
Acacia nigrescens - Terminalia prunioides woodland	-	KE, SN	-	-	KE, SN	-	-	KE, SN	-	-	KE, SN	-
Acacia tortilis lowland woodland	-	RR, SN	KE, KK	RR, SN	-	KE, KK	-	RR, SN	KE, KK	-	KE, KK, RR	SN
Cleared *Colophospermun mopane* woodland	SN	-	KE	SN	-	KE	-	KE, SN	-	-	SN	KE
Colophospermum mopane - Combretum apiculatum woodland	-	KE	KK, RR, SN	SN	KK, RR	KE	RR	KE, KK, SN	-	-	KK, SN	KE, RR
Colophospermum mopane dense woodland and shrubveld (thicket)	-	KK, SN	KE, RR	-	KK, SN	KE, RR	-	KE, KK, RR, SN	-	RR	KK, SN	KE
Combretum apiculatum - Grewia bicolor low thicket	-	SN	KE, RR	-	RR	KE, SN	-	RR, SN	KE	-	KE, SN	RR
Combretum apiculatum - Sclerocarya birrea - Strychnos madagascariensis open woodland	SN	-	KE, RR	-	SN	KE, RR	-	KE, RR, SN	-	RR	KE, SN	-
Combretum apiculatum - Sclerocarya birrea open woodland	-	SN	KE, KK	SN	-	KE, KK	-	KE, KK	SN	KK	KE, SN	-
Combretum apiculatum - Xerophyta retinervis low thicket	KE	SN	KK, RR	KE	-	KK, RR, SN	-	KE, KK, RR	SN	-	KE, KK, SN	RR
Disturbed areas (old fields, air fields, habitation)	-	KK	KE, SN	KE, KK, SN	-	-	KK, SN	KE	-	-	KE	KK, SN
Euclea divinorum - Sporobolus ioclados short woodland on saline lowlands and floodplains	RR	-	SN	SN	-	RR	-	RR	SN	-	SN	RR
Phragmites australis river beds	KE, KK, RR	SN	-	KE, KK, RR	SN	-	KK	RR, SN	KE	-	KK, RR, SN	KE

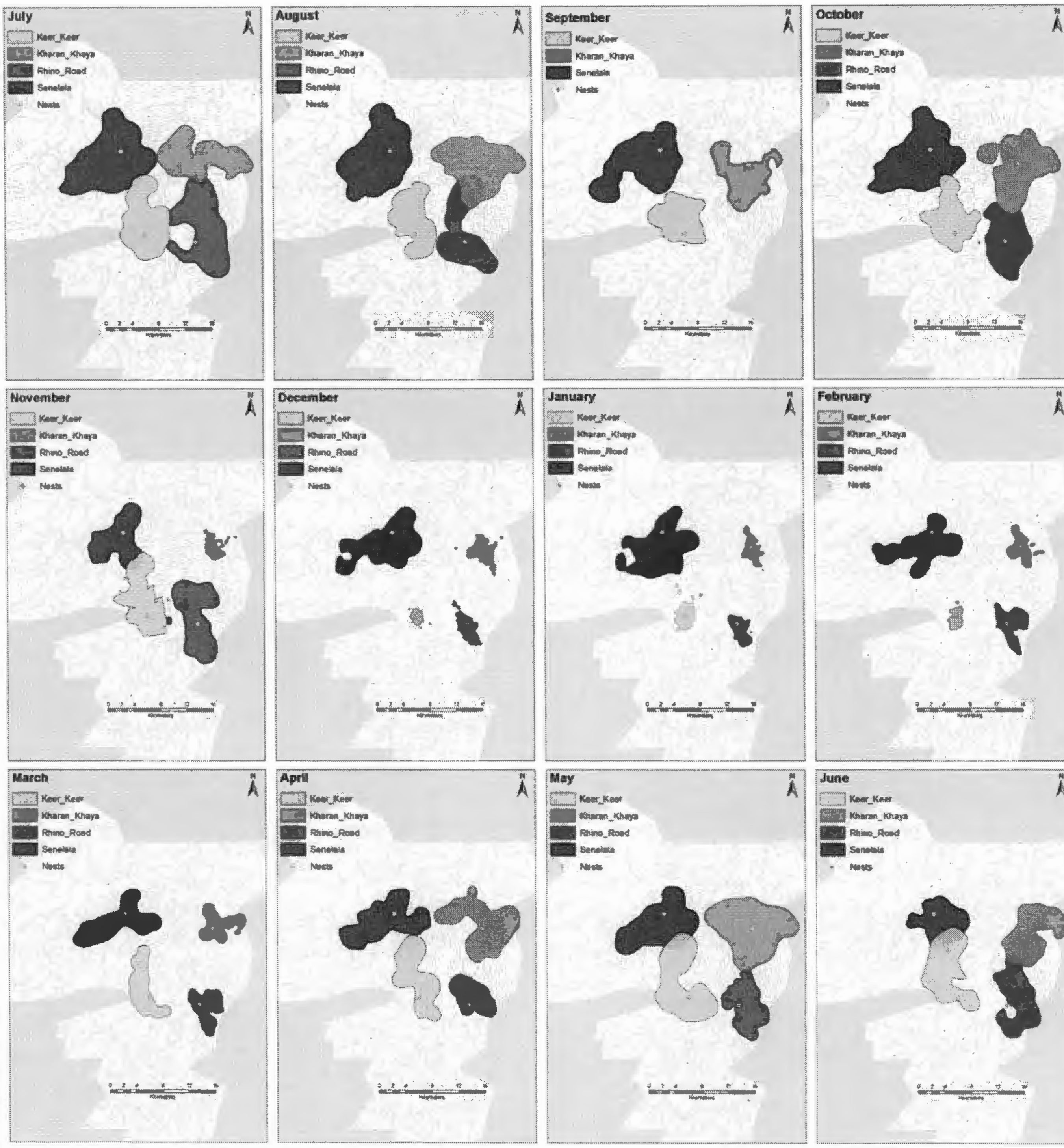

Figure 7: Monthly displacement and change in size of Southern Ground-Hornbill groups' home ranges in the APNR from 1 July 2010 until 30 June 2011. Home ranges were calculated using a Kernel Density Estimate (KDE) in HRT (Home Range Tools) for ArcGIS® 9.3 and plotted at the 95% isopleth. No home range was estimated for the Rhino Road group in September because the satellite transmitter fell off the alpha male and was not reattached until early October.

Part two: Physical vegetation characteristics

Physical vegetation components showed some variation across vegetation types (Fig. 7). Disturbed areas had the highest DPM value of (37 kg.ha^{-1})^2 and cleared *Colophospermum mopane* woodland the lowest (19 kg.ha^{-1})^2. Canopy occlusion did not vary considerably between vegetation types, with *Acacia tortilis* – lowland woodland providing the most potential 'shade' (23% canopy occlusion) whilst *Combretum apiculatum – Sclerocarya birrea* open woodland the lowest (8%). Mean stem density (BW) did not vary greatly between vegetation types, with *Combretum apicluatum – Sclerocarya birrea* open woodland having the highest mean stem density of 11 and disturbed areas having the lowest mean stem density of 3. The LRF data were not included in Figure 7 because the BW measurement was considered the more appropriate and repeatable measure of vegetation/stem density.

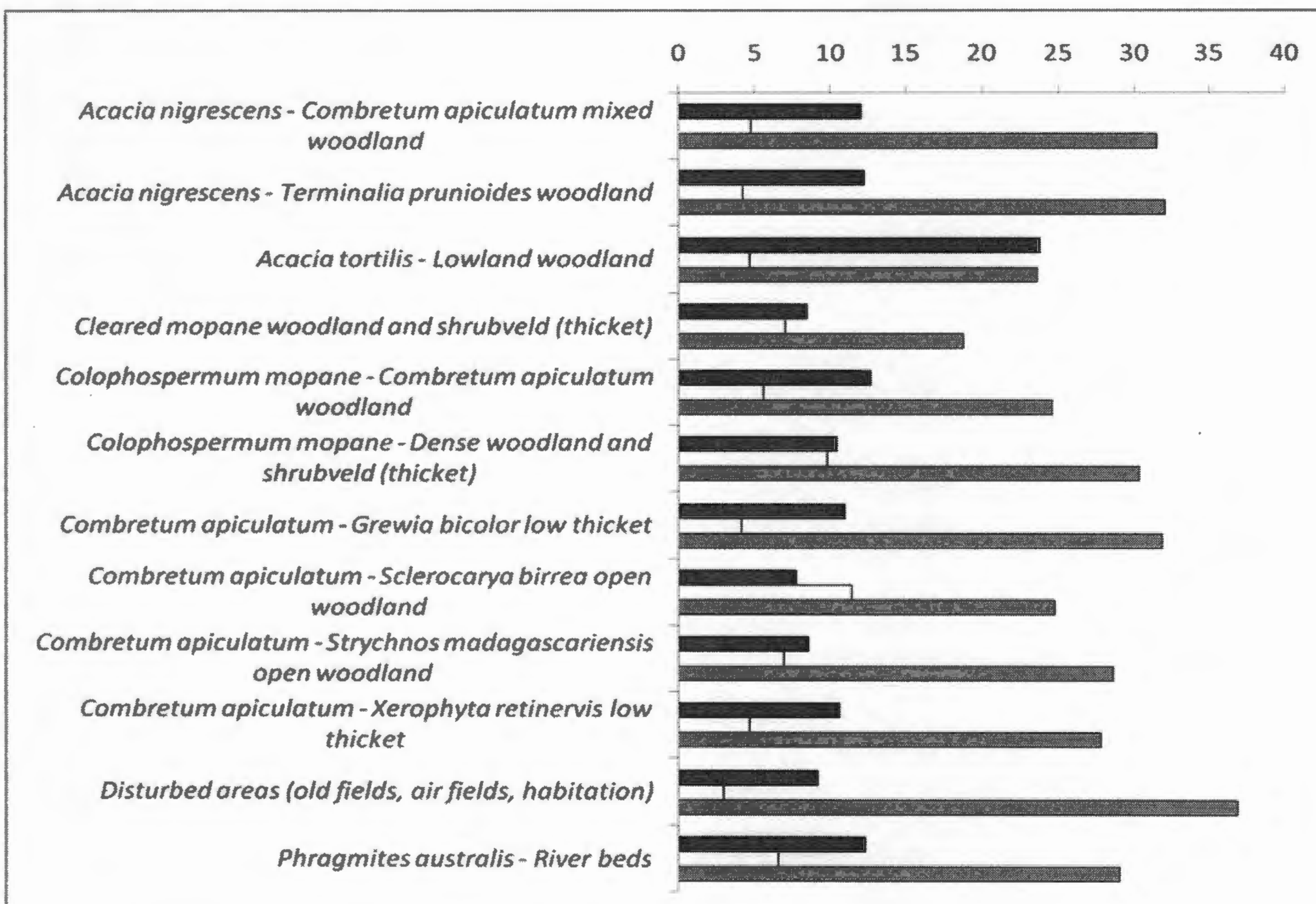

Figure 8: Physical characteristics of the Senelala Southern Ground-Hornbill group's vegetation types (n= 12 in the dry season). Black = Mean Canopy occlusion (%); White = Bitterlich's Wedge; Grey = Disc Pasture Meter (kg.ha^{-1}).

There was no separation of favoured and avoided vegetation types in the tree cluster analysis (Fig. 9). The favoured vegetation type (disturbed areas) did not form a sister group to avoided vegetation types, but rather clustered amongst at a very low linkage distance. Therefore favoured vegetation types (disturbed areas) did not differ greatly from the avoided vegetation types (*Combretum apiculatum xerophyta retinervis* low thicket and *C. apiculatum sclerocarya birrea* open woodland) in physical characteristics during the dry season.

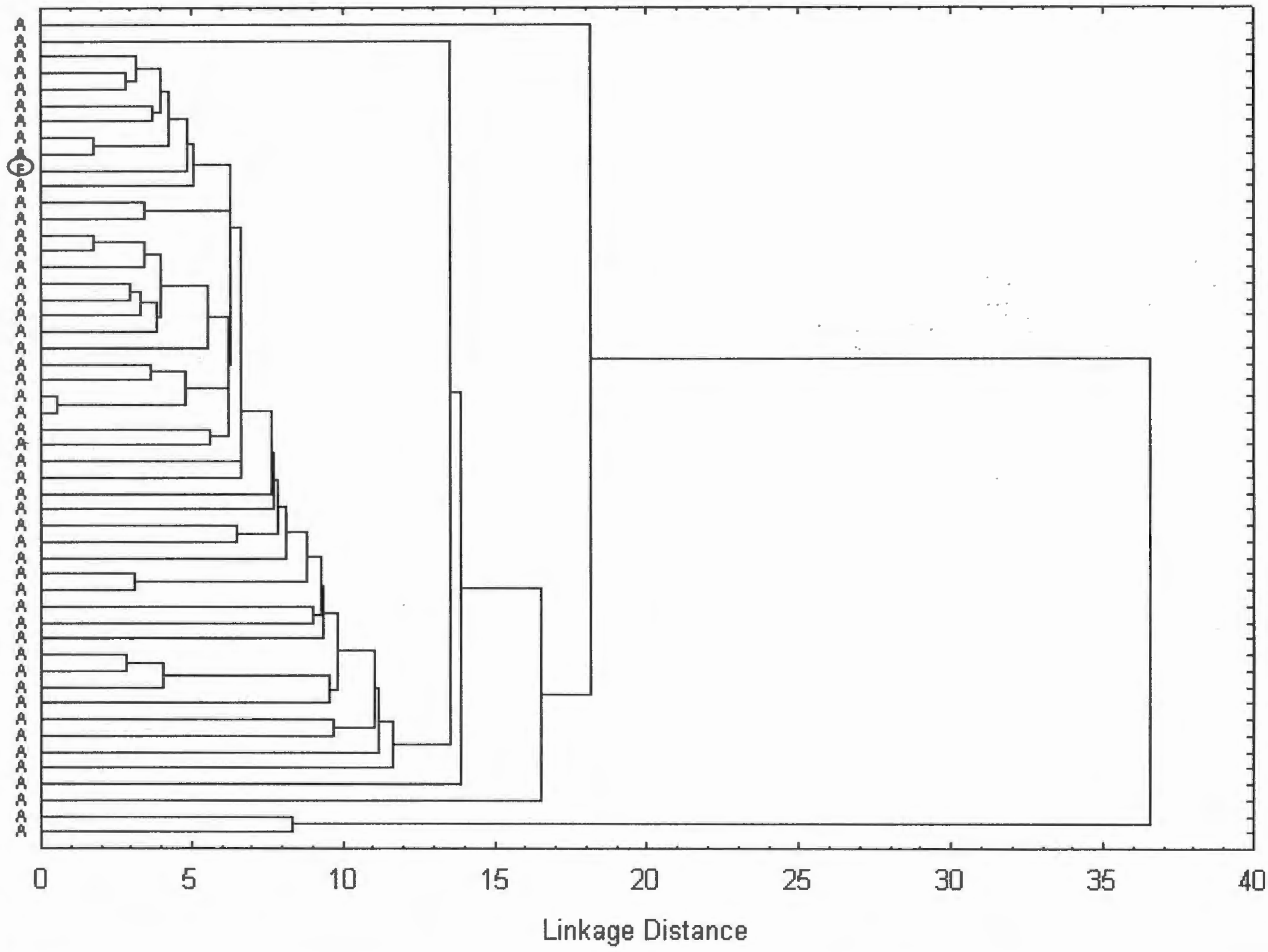

Figure 9: Tree cluster analysis of the Senelala Southern Ground-Hornbill group's favoured (n=1) (disturbed areas) and avoided (n=2) (*C. apiculatum xerophyta retinervis* low thicket and *C. apiculatum sclerocarya birrea* open woodland) vegetation types in the dry season. (F: favoured [circled]; A: avoided).

Discussion:

From previous work done on Southern Ground-Hornbills four main factors have been indentified that determine the reproductive success of the birds. Rainfall over the breeding season is the primary variable affecting breeding success (positively influencing food availability), the interaction of nest type (natural or artificial) with the amount of open woodland in the vicinity of the nest, the availability of an artificial nest and group size (Wilson 2010). Only two of these variables present management options, one of which has been adopted with great success e.g. the installation of artificial nest boxes (Wilson, 2010). Bush clearance in the immediate vicinity of the nest, a second alternative management option (Wilson, 2010), has yet to be actively implemented. For a bird whose conservation status is listed as *Vulnerable* by the IUCN (IUCN, 2001), coupled with great concern regarding its declining range in southern Africa (Kemp and Webster, 2008), other practical management options are required (Wilson, 2010) which require a deeper understanding of how ground-hornbills perceive and utilise the habitats within their home ranges. Therefore this study undertook, for the first time, to analyse satellite telemetry data in an attempt to quantify home range use and to identify favoured habitat types and link these to physical vegetation characteristics. Ultimately, such analyses should improve the efficacy of reintroduction or translocation protocols by allowing identification of optimal landscape mosaics.

Seasonal home range use:

Southern Ground-Hornbills did exhibit seasonal patterns of habitat preference, demonstrating that within-season habitat use is non-random (Figs 2-5; Table 2). Because different habitat types are used non-randomly suggests that Southern Ground-Hornbills distinguish between habitats within their home ranges on the basis of the benefits they derive from different habitats at different times of year. Home range sizes were largest during the dry season months (April to September), when the birds are not breeding and when aridity and low temperatures are likely to reduce food availability (Figs. 2-5 and Fig. 7). Many of the birds' prey items, e.g. insects, reptiles and small mammals, are more abundant during the wet summer period (Rautenbach *et al.* 1988; Linzey and Kesner, 1997). Throughout the year, however, there are habitats that ground-hornbills use in proportion to their availability (i.e. for which they show no attraction or avoidance) (Table 1; Figs. 2-5). Use of such habitats is greatest during the dry season, when groups are not tied to a nest. That said, the Rhino Road group did show an increase in habitat selectivity during the late dry season. This was for *Combretum apiculatum - Sclerocarya birrea - Strychnos madagascariensis* open woodland and *Colophospermun mopane* dense woodland and shrubveld thicket, both of which were completely avoided by the same group during the wet season. Similarly the Senelala group showed a preference for *Combretum apiculatum - Sclerocarya birrea - Strychnos madagascariensis* open woodland only during the early wet season: this is probably because this habitat type occurs in the immediate vicinity of the nest and is therefore likely to be traversed daily.

According to the Resource Dispersion Hypothesis (RDH) (Macdonald, 1983; Johnson *et al.* 2002; Bino *et al.* 2010), if resource "hotspots" are distributed unevenly in space and time, home range size will adjust accordingly. The home range size and shape of Southern Ground-Hornbills is partially but not exclusively determined by the location of these "hotspots" (i.e. there is no obvious concentration of such hotspots at the periphery of the home range), the pattern inconsistent across all four groups. The Keer Keer and Senelala groups show no compelling evidence for their home range size and shape determined by the location of "hotspots" (Fig. 6). In contrast the home range of the Rhino Road and Kharan Khaya groups show more compelling evidence in favour of the RDH, as favoured habitat types are frequently located on the periphery (Fig. 6). The southern extent of the home-range of the Kharan Khaya group coincides with a habitat type that is favoured only during the late dry season: for the rest of the year this habitat type is strongly avoided (Fig. 3). The northern extent of the home range of the Rhino road group is also determined by this same habitat type also favoured only in the late dry season (Fig. 4 and Fig. 6). The seasonal selection of habitat types and the temporal displacement of the home range by the Kharan Khaya (Fig. 3) and Rhino Road (Fig. 4) group is mounting evidence in favour of the RDH in explaining home range size in these two Southern Ground-Hornbill groups.

Across the home ranges of the four groups studied, not all habitat types are shared or occur at equal abundance (Table. 2). The rarity of a habitat type seemingly plays an important role in determining preference by Southern Ground-Hornbills and thus contributes to the diverse patterns of space use arising in the different groups. The Senelala group's home range of 10 322 ha is almost twice the size of the Keer Keer and Rhino Road groups (5886 ha and 5551 ha respectively - Table 1.). This is a substantial difference in home range size, however the extent of favoured habitat within the home range when summed across all seasons (2289 ha - (Table 1, Fig. 6) is similar to the extent of favoured habitats in the home ranges of the other three groups (Keer Keer - 2536 ha; Kharan Khaya – 3396 ha and Rhino Road – 2738 ha). The Senelala group showed strong habitat preference only during the breeding season (when they favoured habitats in the vicinity of the nest), and the same was true of the Keer Keer group (Figs 2, 5.).

During the breeding season, Southern Ground-Hornbills are essentially central place foragers, making limited use of their extensive home ranges, as responsibility is focused on nesting activities (Wilson, 2010). The Keer Keer, Kharan Khaya and Rhino Road groups showed a major contraction in home range size during the breeding season: all three of these groups successfully reared chicks to fledging (Table. 1). The Senelala group, whose breeding attempt failed due to depredation of the chick, did not show the same contraction towards the nest site. The size of the home range during the breeding period is likely determined by the availability of resources in the immediate vicinity of the nest. Therefore nest site location is influenced by the spatial arrangement of favoured habitat types in the vicinity of the nest. As seasonal central place foragers, the birds have two alternatives in order to satisfy the demands of reproduction: 1) spend more time in sub-optimal habitats near to the nest, or 2) travel further and forage in optimal habitat (Bino *et al.* 2010). The birds may be forced to forage over much larger areas and further from the nest during this period if the nest is located in sub-optimal habitat. However, if a group is required to forage over greater distances in the breeding season due to unsuitable nest site location it may potentially compromise the fitness of the chick. This presents yet another management option (nest placement) and may help explain why some groups are more successful than others. As the chick leaves the nest, the groups start to exploit other resources further afield, possibly reflecting resource depletion close to the nest (Fig. 7).

Physical vegetation characteristics:

Savanna landscapes are highly heterogeneous and therefore the habitat types are not always clearly defined (Van Der Waal, 2010). Based on the habitat variables measured in this study, habitats across the home range of the Senalala group were structurally similar to one another. The vegetation data were collected in the late dry season (July), when resources were predicted to be at their most scarce and birds to be at their most selective in terms of habitat, strongly favouring those habitats providing the greatest food rewards. However, analysis of seasonal habitat preference (Fig. 5) revealed exactly the opposite: this was the time of year at which birds used different habitats (as defined botanically) in proportions very similar to their availability, and the proportion of favoured habitat was very small, resulting in only one vegetation sample taken within this habitat. There are three possible interpretations of this result: 1) too few samples were taken in the favoured habitat for analyses to be meaningful; 2) physical differences between habitat types in the late dry season (the least 'leafy' time of year) were too subtle to be detected by the sampling techniques employed (and also too subtle to be detected by the ground-hornbills which largely used habitats in proportion to their availability); or 3) the variables measured were inappropriate (and were also unable to distinguish between avoided and 'neutral' habitats – analysis not presented).

Generally, the degree of habitat selectivity, as derived from satellite data, increased during the wet season. During this time (the breeding season), the concentration of habitat use in the vicinity of the nest could be a result of a) these being the most food-rich habitats at that time of year, or b) these simply being the habitats closest to the nest (such that selectivity is determined by travel costs rather than gross foraging returns).

In the late dry season, the only habitat favoured by the Senalala ground-hornbills was disturbed areas. These sites had the highest mean grass biomass, suggesting that these areas may have provided the best foraging opportunities because grass biomass is assumed to be a surrogate for food availability (Wilson, 2010). Furthermore, low stem density in disturbed areas allows the birds to move around with greater ease. During the wet season, ground-hornbill groups made greater use of riparian vegetation, possibly as a refuge from heat during the middle of the day (Dickens, 2010).

Although this study was unable to provide a mechanistic link between vegetation structure and habitat preference by ground-hornbills, the fact that all groups showed seasonal patterns of habitat preference (strongest in the wet season) suggests that physical vegetation characteristics do influence how the birds perceive the landscape (Table 1.). A comparison of food abundance associated with favoured and avoided habitat types may provide further insight into how perception influences preference on a seasonal basis.

Conclusion:

This study showed that Southern Ground-Hornbills show variation in the utilisation and extent of their home range on a seasonal basis, but these patterns were far from rigidly consistent across groups apart from a repeated pattern of a reduction in home range size during the wet season when birds are breeding. Habitat selectivity also increased considerably during the wet season, but whether this reflects changing food resources or central place foraging constraints is equivocal. Sampling of vegetation attributes during the dry season, when habitat selectivity by birds is at its weakest and the leaf loading of trees at its lowest, was unable to establish a conclusive link between vegetation structure and preference by the birds.

The results of this study point at three immediate priorities for future research: 1) measurement of vegetation structural attributes at other times of year when more trees are in leaf and when habitat selectivity is greatest; 2) more detailed analysis of satellite tracks which should attempt to distinguish between birds in transit and birds that are foraging/resting; and 3) linking patterns of habitat use to reproductive performance and thus provide the rationale for the choice of reintroduction/translocation priorities. The first of these two is relatively easy and should reveal whether the vegetation attributes to which this study predicted ground-hornbills should respond are indeed those to which they do respond at times of year when they are habitat-selective. The second may prove less tractable, because a) satellite data are only collected at hourly intervals, and b) even when foraging, ground-hornbills cover large distances fairly quickly. The success of the third objective largely depends on the resolution achieved in addressing points 1 and 2. The Shangri La would be to link the 'on the ground' data to satellite imagery. If this can be done, the selection of reintroduction/translocation sites would be rendered much more efficient.

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Appendix 1:

Tables (3-7) show the area of vegetation types in each Southern Ground-Hornbills home range. The number of satellite fixes for each vegetation type in each season (EW, LW, ED, LD) are included.

Table 3:

Keer Keer					
Vegetation Type	**Area (ha)**	**EW**	**LW**	**ED**	**LD**
Acacia gerrardii - Euclea divinorum - Sporobolus nitens lowland savanna	47.14	7	17	12	56
Acacia nigrescens - Combretum apiculatum mixed woodland	2313.26	500	481	849	580
Acacia nigrescens - Terminalia prunioides woodland	493.70	85	85	116	138
Acacia tortilis lowland woodland	253.80	19	30	51	37
Cleared areas	27.44	0	0	11	2
Colophospermum mopane - Combretum apiculatum woodland	121.32	1	0	51	10
Colophospermum mopane dense woodland and shrubveld (thicket)	460.31	14	31	206	62
Combretum apiculatum - Grewia bicolor low thicket	42.67	0	0	5	10
Combretum apiculatum - Sclerocarya birrea - Strychnos madagascariensis open woodland	461.19	30	21	195	130
Combretum apiculatum - Sclerocarya birrea open woodland	321.19	29	32	162	89
Combretum apiculatum - Xerophyta retinervis low thicket	655.79	273	309	329	149
Disturbed areas (old fields, air fields, habitation)	51.52	6	20	25	11
Phragmites australis river beds	562.99	351	308	115	52
Spirostachys africana - Euclea undulata mixed alluvial savanna	73.72	1	3	18	9

Table 4:

Kharan Khaya					
Vegetation Type	**Area (ha)**	**EW**	**LW**	**ED**	**LD**
Acacia nigrescens - Combretum apiculatum mixed woodland	1066.67	157	278	170	111
Acacia tortilis lowland woodland	18.68	1	0	0	2
Colophospermum mopane - Combretum apiculatum woodland	1542.08	190	268	340	192
Colophospermum mopane dense woodland and shrubveld (thicket)	1983.32	423	581	599	305
Combretum apiculatum - Sclerocarya birrea - Strychnos madagascariensis open woodland	1183.48	108	87	242	284
Combretum apiculatum - Xerophyta retinervis low thicket	595.90	21	12	126	96
Disturbed areas (old fields, air fields, habitation)	90.71	14	38	108	4
Phragmites australis river beds	677.01	257	386	323	76

Table 5:

Rhino Road					
Vegetation Type	**Area (ha)**	**EW**	**LW**	**ED**	**LD**
Acacia luederitzii - Euclea divinorum lowland woodland	463.82	111	142	61	13
Acacia nigrescens - Combretum apiculatum mixed woodland	229.96	129	129	17	9
Acacia nigrescens - Combretum hereroense open woodland	1772.60	306	304	441	36
Acacia tortilis lowland woodland	31.87	5	13	8	1
Colophospermum mopane - Combretum apiculatum woodland	230.03	33	52	101	3
Colophospermum mopane dense woodland and shrubveld (thicket)	164.77	12	0	26	10
Combretum apiculatum - Grewia bicolor low thicket	247.93	32	83	75	3
Combretum apiculatum - Sclerocarya birrea - Strychnos madagascariensis open woodland	1033.79	97	57	156	95
Combretum apiculatum - Xerophyta retinervis low thicket	115.47	16	4	17	1
Euclea divinorum - Sporobolus ioclados short woodland on saline lowlands and floodplains	14.44	6	5	2	0
Phragmites australis river beds	401.60	318	292	102	11
Terminalia sericea - Combretum zeyheri - Pterocarpus rotundifolius - open woodland	713.08	180	158	91	8
Terminalia sericea - Combretum zeyheri woodland	132.28	4	5	17	3

Table 6:

Senelala					
Vegetation Type	**Area (ha)**	**EW**	**LW**	**ED**	**LD**
Acacia nigrescens - Combretum apiculatum mixed woodland	993.46	35	134	338	92
Acacia nigrescens - Terminalia prunioides woodland	2353.74	262	239	679	403
Acacia tortilis lowland woodland	144.53	16	39	31	12
Cleared areas	222.27	73	99	81	22
Colophospermum mopane - Combretum apiculatum woodland	520.32	85	137	182	103
Colophospermum mopane dense woodland and shrubveld (thicket)	2111.94	348	221	443	229
Combretum apiculatum - Grewia bicolor low thicket	666.38	71	30	140	153
Combretum apiculatum - Sclerocarya birrea - Strychnos madagascariensis open woodland	599.73	134	117	107	73
Combretum apiculatum - Sclerocarya birrea open woodland	500.63	46	112	51	56
Combretum apiculatum - Xerophyta retinervis low thicket	1564.75	217	81	216	320
Disturbed areas (old fields, air fields, habitation)	40.43	2	16	35	2
Phragmites australis river beds	604.40	84	121	164	58

Appendix 2:

How to measure canopy occlusion (%) with the Canopy Occlusion Meter (COM).