MODELING THE SPATIAL ECOLOGY OF LIONS (*Panthera leo*) IN HLUHLUWE-UMFOLOZI PARK.

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ABSTRACT

While many studies have been done on Lions, relatively little work has been conducted on how they interact with local habitats and the factors of importance in determining home ranges and territories. The interactions between predators and patchily distributed resources and the basic tenets of Ideal Free Distribution theory have been used in this study as the basis in explaining how lions distribute themselves in space and why they choose particular areas above others in regards territory location.

The study was conducted in the Hluhluwe-Umfolozi Park, South Africa and involved the use of historical lion sightings data recorded between the years 1973 and 1999 inclusive. A variety of potential explanatory variables including vegetation, topography, rainfall, main river distribution, roads, hyaena den locations and prey were used in developing logistic models which were then used to predict areas most likely to be colonised by lion. Model predictions were tested against independently collected validation data from an introduced pride. Modelling was conducted at a $1km^2$ grid cell size.

In total, seventeen models were formulated for four lion variables, namely cubs, adult females in groups of two or more, adult males seen with adult females and adult males only. All models accounted for a significant amount of deviance ($p<0.001$) except for one cub model ($p=0.003$). Models which performed best in correlations with validation data were those formulated for adult females in groups of two or more and cubs ($p<0.05$). Variables of importance in these models included distance from main rivers and presence/absence of public roads. Preferences for travelling on roads were influenced by vegetation type, with thicket promoting travel on roads and the opposite being true of open woodland, however this was only true for females in groups of two or more. Main rivers represent high quality resource areas for lions in the reserve since they provide water, shelter, cover (hence ease of prey capture) and travel lines.

I hereby declare that these studies represent my original work and have not been submitted in any form for any other degree or diploma to any other tertiary institution. Where use has been made of the work of others it has been acknowledged in the text.

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Chapter 1

Introduction

1.1 Modeling lion spatial ecology

Very little work has been done on the relationships between lions (*Panthera leo*) and their surrounding habitat (Packer, 1997, pers. comm.) and the motivations underlying choices of particular habitats above others, specifically for home ranges and territories, are not well understood. The primary aim of this study is to determine those habitat characteristics which are selected for by lions when choosing particular areas for home range and territory.

Linear models quantify the relationship between environmental variables and known occurrences of a study species, thereby providing descriptors of species ranges (Legendre and Legendre, 1998; Cumming, 2000). Quantitative statistical models can firstly, provide a defined representation of a theory thereby enabling complex dynamics to be examined and, secondly, as a consequence of defining relationships between measurable concepts these models may, following calibration and assessment with data, contribute to the objectivity of the theory upon which they are based (Ford, 2000). Such models are becoming increasingly useful in ecology and can be applied in tests of broad scale ecological hypotheses (Cumming, 2000) with ecologists being in agreement that theory based regression equations provide helpful tools for management (Legendre and Legendre, 1998).

Linear models would therefore provide an effective method whereby habitat characteristics (descriptor variables) favored by lions when selecting territories, can be assessed. Analyses have been conducted at large temporal and spatial scales rather than at the scale of an individual animal over short periods of time. Consequently, general habitat characteristics of an area, which are favored by

lions, have been ascertained. By doing this in a modeling context, predictions of probable territory locations can be made and the accuracy of these predictions tested.

The scale at which an individual observes its surrounding environment influences the individual's perception of the surrounding substrate geometry and also density of resource patches (Ritchie, 1998). If an animal has a large foraging scale, it would perceive an environment as having a few large resource patches. If however, an animal has a small foraging scale it would perceive the same environment as having many small patches of resources, some of which occur in large resource patches (Ritchie, 1998). Animals foraging at a particular scale would also have a minimum patch size that they are able to distinguish, and should a particular patch be smaller than this minimum, the animal would not perceive it (Ritchie, 1998).

Choice of an area in which to locate a home range is likely to be based on scale dependant perceptions of the habitat as are choices of areas to frequent and the influence of scale on such behavioural decisions should not be ignored.

An additional consideration regarding scale is that imposed by an observer on a particular area. In this context (ecological, not geographical), small scale refers to high/fine resolution, while large scale refers to low/coarse resolution (Obeysekera and Rutchey, 1997; Legendre and Legendre, 1998). Scale is of importance since the scale at which variables are measured influences our perceptions of those variables (Obeysekera and Rutchey, 1997; Bellehumeur and Legendre, 1998). If too large a scale is employed in measuring a particular variable, spatial variation occurring at scales finer than that used for sampling, will be lost or ignored (Obeysekera and Rutchey, 1997; Bellehumeur and Legendre, 1998).

Ideally, the scale which an observer should use in making observations (known as the sampling grain (Legendre and Legendre, 1998)) and conducting analyses should be equivalent to the

scale at which the animal under study conducts spatial decision making (Morrison, Marcot and Mannan, 1992). Thus the observer is able to view/perceive the environment in the same spatial context as the animal in question. This is borne out by Levin (1992) who states that in order for a description of environmental variability and predictability to make sense, it is necessary to refer to the range of scales relevant to the organism under study.

The sampling grain referred to above should be larger than an individual animal (unit object) and smaller than the structures (territories in this particular case) resulting from unit processes (Legendre and Legendre, 1998). With regards this project, a sampling grain of $1km^2$ has been used. While this resolution was obligatory since the majority of lion sighting data were collected on a $1km^2$ grid, it does fall within the recommendations stipulated above since lion home ranges in Hluhluwe Umfolozi Park (HUP) generally range in size from approximately $25km^2$ to $120km^2$ (calculated from Maddock *et al.* 1996), with territories being, by definition, somewhat smaller.

Since the principal objective of this study was to ascertain those habitat characteristics which, at a territorial scale, are of importance, the use of a $1km^2$ grid is justified. At this scale, a large amount of environmental data generalisation has already been incurred, as was discussed earlier. By using a scale any coarser than this, however, it is likely that too much variation in environmental variables would be lost. Lions make spatially related decisions at scales far smaller than this and many of the variables used in this study have been included, based on their importance to individual animals and daily decision making (e.g. when and where to hunt) rather than prides and choice of territory location. However, it is probable that small scale decision making influences choices made at both larger spatial (Ritchie, 1998) and temporal scales (i.e choices of territorial areas). Smaller scale studies also promote an understanding of the biological processes under consideration and this must be incorporated into broad scale predictive linear models to improve their reliability (Cumming, 2000).

1.2 Social ecology of lions

The importance of large carnivores such as lions to conservation efforts conducted within enclosed wildlife reserves, specifically those which are small in size, is evident through the effects of predation on herbivore populations (Mills and Shenk, 1992; Hunter, 1998). Interactions between lions and other species of large carnivore such as cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*) and hyaena (*Crocuta crocuta*) are also of importance in such contexts thus it would be of great benefit to both conservation and management to be able to predict where introduced prides of lions are most likely to establish home ranges and territories and therefore where they are most likely to influence resident populations of other animals.

Lions are conspicuously social animals when compared to other members of the Felidae (Packer, 1986). In the past, the main reason underlying sociality in lions was thought to relate to the advantages gained by foraging or hunting in a group (Packer, Scheel and Pusey, 1990). It has been subsequently shown that this is by no means the only reason for sociality occurring in lions although large prey size does allow group foraging to occur (Packer *et al*, 1990).

It has been proposed that sociality in lions has evolved due to a combination of three factors namely a preference for large prey, presence of open habitats and high population density (Packer, 1986). The capture of large prey allows several individuals to feed from a specific carcass. As it is easier to see in open habitats, when a kill is made by a lion, others are attracted to the site of the kill more rapidly than would have happened in a more closed environment. In the case of a high density of lions there is a greater chance of losing substantial amounts of food from kills to conspecifics (Packer, 1986). Thus high population density is one of the reasons for sociality rather than vice versa (Packer, 1986). Since the loss of food to close relatives is preferable to losses to unrelated or distantly related individuals, this may account for the formation of prides consisting of close relatives (Lindström, 1986; Packer, 1986).

Lions form permanent prides which consist of two to eighteen adult related females with all dependant offspring being included in the pride. They are accompanied by a coalition of one to seven males which remain resident for approximately two years, until they are replaced by another male coalition (Packer, Herbst, Pusey, Bygott, Hanby, Cairns and Borgerhoff Mulder, 1988). Prides have been described as fission/fusion social units (Packer *et al*, 1988; Packer, 1986) to which membership is stable, with females forming a number of smaller sub-groups which exist throughout the pride range (Packer *et al*, 1988; Packer, 1986). The size of these sub-groups is related to the size of the original pride, cooperative cub defence and creche formation, group territoriality and female reproductive patterns. The above factors override the benefits of group living derived from food intake (Packer *et al.* 1990).

Schaller (1973) states that although lions have territories, they do not use all areas within these territories equally. Instead they spend most of their time in what he terms the focus of activity, an area of abundant food and water, available even in times of shortage. Current terminology differs slightly from this definition. Home range has been described as an area traversed by an individual, pair, social or family group of animals which is used for gathering food, mating and caring for young (Huggett, 1998). Territory, on the other hand, is described as that part of a home range which is actively defended against conspecifics. Further, defended territories do not usually include peripheral regions of a home range (Huggett, 1998). This definition of territory is synonymous with the area of focus as described by Schaller (1973) and will be used here.

There is no dominance hierarchy displayed within the female pride structure (Packer, 1986; Schaller, 1972). Females do not defend home ranges because these areas are usually too large to defend effectively (Schaller, 1972). They do however defend the areas which, at a particular time, are being occupied by the pride (Schaller, 1972), i.e territories. Most females never move away from the

home range on which they were raised, and even if forced to do so, will still remain on or adjacent to the fringes of their original home range (Packer, 1986). Females will defend their territories against the invasion of other females (Heinsohn and Packer, 1995) and it is also recognised that although kills are sometimes contested, the primary driving force behind territorial defence appears to be related to the long term value of a particular area (Packer *et al.* 1990).

Males, in contrast, place more importance on gaining access to females than on having a territory in which to hunt (Kruuk, 1986; Packer, 1986). They would thus defend their females from other invading males rather than defending the female's, i.e. their own, territory for its inherent value (Heinsohn and Packer, 1995). As a consequence males spend a lot of their time roaming an area until they find a suitable pride to take over, and once evicted from a pride will again travel large distances to find another one. They are not anchored by a specific home range for the duration of their lifetime, as in the manner displayed by their female counterparts. Instead, when males acquire a suitable pride, they either accompany the pride in an effort to discourage other male competitors, or they patrol territory borders and advertise their presence by scent marking and roaring (Funston, Mills, Biggs and Richardson, 1998). Males maintain a specific territory and defend its resources, females and cubs until such time as they are evicted from that pride, or move off.

When assessing areas of optimum habitation for lions i.e areas where they would be likely to establish a territory, it may be misleading to consider the distribution of males as being of equal importance to the distribution of females, in terms of resource location. It would appear that females are the ones responsible for selecting home range areas since males are governed more by the distribution or presence of females than by the distribution of resources. It has been stated that the distribution of hunting areas may play only an indirect role in affecting male lions and this through range size of females (Kruuk and Macdonald, 1985; Kruuk, 1986). More emphasis should therefore

be placed on the distribution of females, since they are distributed according to available resources such as safe denning sites and good hunting areas (Packer, 1986). This does not mean that males are unaffected by resource availability, but simply that female distribution may be an overriding factor in determining where males choose to locate themselves. Another distinction must be made between nomadic females and pride females since single nomadic females are not capable of maintaining territories on their own (Heinsohn and Packer, 1995).

The importance of having a territory lies mainly in the fact that successful breeding is almost impossible without one (Packer *et al.* 1990; Heinsohn and Packer, 1995). One of the main reasons underlying communal cub rearing and defence (creche formation) and lion sociality in general, is related to defence against the threat of attack (Heinsohn and Packer, 1995; Packer *et al.* 1990) either by males or conspecific females. Long term resource value of an area is however thought to be the primary driving force behind territorial defence (Packer *et al.* 1990), as has already been alluded to.

Finding and maintaining a suitable territory is therefore of importance to pride females with the underlying assumption being that lions can and do search for areas which will provide them with the best possible resource set they can find. This scenario has been observed in several game reserves where lions have been re-introduced. When released, the pride stays close to its holding pen but after a while the lions will explore the entire reserve before choosing an area to settle down and form a clearly marked home-range (Packer, 1997, pers. comm.).

It appears also that lions consistently favour particular landscape features, with these features playing an important role in home range selection (Packer, 1997, pers. comm.). The choice of an optimal home range/territory needs now to be considered in the light of current theoretical background under the assumption that resources are patchily (rather than uniformly) distributed in space.

1.3 Ideal free distribution theory

The ideal free distribution (IFD) model was proposed by Fretwell and Lucas (1970) as a possible mechanism explaining the distribution of animals in patchy habitats. The general model appears to be fairly robust and thus applicable to a wide range of organisms (Milinski and Parker, 1991).

There are several assumptions underlying the model and these are as follows: 1) the habitat in question contains individuals which all have the same competitive ability; 2) there are a number of resource patches differing in fitness value which are available; 3) competitors are free to move between patches and there is no cost associated with this movement. Competitors will move to the patch which is expected to yield the highest gain; 4) the fitness value of a particular patch declines as more and more individuals (competitors) move onto the patch (Milinski and Parker, 1991). Animals are thus "ideal" (in terms of the Ideal Free Distribution theory) in that they have perfect information with regards their surrounding environment, and "free", because they are able to enter or leave any patch depending on where gains will be maximised (Abrahams, 1986; Gotceitas and Colgan, 1991; Gray and Kennedy, 1994; Moody, Houston and McNamara, 1996; Kohlman and Risenhoover, 1997).

At equilibrium it is predicted, by IFD, that all animals in all patches experience equal gains (Milinski and Parker, 1991; Gray and Kennedy, 1994). This is shown by the equation:

$$N1/N2 = R1/R2$$

where N1 and N2 are the number of animals in patch 1 and patch 2 and R1 and R2 are the amounts of resources in patch 1 and patch 2, thus the ratio of animals between two patches equals the ratio of resources between those two patches at equilibrium (Gray and Kennedy, 1994).

The higher the number of required resources in combination, the more suitable a particular

habitat should be. There is however a perceptual limit to the number of different resources which an animal can take into account (Abrahams, 1986). The larger the number of different resource items which an animal must take into account, the larger the deviation from IFD predictions (Abrahams, 1986). It is not known what limits lions have in terms of their perception of available resources. They do seem to search for optimal areas in which to locate home ranges, but what factors they take into account and the hierarchy of those factors is not fully understood.

IFD theory may be applicable to lions in terms of where they are likely to locate a home range. It is not valid when describing grouping patterns however (Pusey and Packer, 1987; Packer *et al*, 1990). The main reason for this is that the social interactions that occur among lions, and which are the primary driving force behind grouping patterns, confound grouping patterns based on optimal foraging alone, as proposed by IFD (Pusey and Packer, 1987; Packer *et al.* 1990). Thus, within home ranges, lions of the same pride probably do not distribute themselves according to IFD. While lions may still, as a group, choose optimum areas in which to remain, the number of lions in the group is determined more by social interactions such as co-operative cub defence (Packer *et al.* 1988) than by the quantity and quality of resources, specifically prey (Packer, 1986). When observing distribution patterns over a constant patch size, the number of lions frequenting any given patch may not be a reliable indication of patch quality. Rather, the frequency with which lions visit a patch (within a particular home range) may be a more reliable indicator of preference.

It should be noted, also, that food is not the only resource which must be taken into consideration when attempting to determine habitat preferences.

At a larger scale, it is also likely that IFD is not adequate in describing home range patterns and related pride sizes for a given area or reserve in which a number of prides, comprising a population, exist. The reason for this is that IFD may be violated if the animals in question are

territorial in nature, since territoriality violates the assumption that animals are free to move between patches (Milinski and Parker, 1991). However, although individuals from outside a pride are often prevented from joining a pride, the pride is still able to increase in size over time as cubs are born. Thus, one would assume that over a period of time, an upper limit on pride size may be determined by the quality of resources within that particular home range. Once again there are a number of social factors which may confound this, one of these being sub-adult emigration (Bertram, 1973). Van Orsdol *et al.* (1985), however, found that there was a significant correlation between the number of adult females in a pride and lean season food availability. The study was conducted over ten different habitats and suggests that while recruitment or emigration of subadult females is governed by social factors, these factors may be influenced by ecological variation, which would thus influence the number of adult pride females (Van Orsdol *et al.* 1985). Interestingly, Van Orsdol *et al.* (1985) found no relationship between group size and lean season food availability, which is consistent with the findings of Packer (1990).

There are a number of factors which affect sub-adult emigration two of which are probably not related in any way to the quality of the environment. These include eviction (of females too young to conceive) by new resident males, following a male takeover, and voluntary dispersal in order to avoid mating with fathers (Pusey and Packer, 1987; Hanby and Bygott, 1987). In the second instance, females most often return to the pride range once they have mated (Pusey and Packer, 1987). The third possible reason for subadult female emigration relates to a decline in reproductive success when prides become too large (>10), with the result that large cohorts of females may benefit by leaving their natal territory (Pusey and Packer, 1987). Small cohorts (1-2 females) leave even when pride size would have been less than ten had they stayed, probably because they are less able to resist eviction than large cohorts (Pusey and Packer, 1987). This third reason may be subject to ecological

variability, as stated by Van Orsdol *et al.* (1985).

The use of IFD in predicting pride sizes is not thought to be useful, or possible, owing to the complexity of social factors displayed by female lions (Pusey and Packer, 1987). The data presented by Van Orsdol *et al.* (1985) suggest, however, that pride size (when measured as the number of adult females within a pride) may be limited by lean season food abundance. While this finding does not advocate the use of IFD it does suggest that ecological variation plays a role in determining pride size. Thus, prides having high quality home ranges and territories may, as a result, be larger (or reproductively fitter) than prides which exist on home ranges/territories having a lower resource quality even though the exact numbers and ratios involved don't conform closely to IFD predictions. Since there is an upper limit on group size which is set by pride size (Packer *et al.* 1990) the issues illustrated above should not be overlooked as they may also have an effect on distribution and grouping patterns of lions within their home ranges.

It is likely that prides will locate their home ranges in areas which they perceive to be optimal, provided they are not part of other pride ranges. New prides experience considerable aggression from neighbouring prides when attempting to establish a home range (Pusey and Packer, 1987) thus optimality should be assessed on the basis of available areas, with ranges that are occupied and defended, being largely unavailable. The scarcity and distribution of resources and competition from other animals affects the degree to which individuals are willing to fight for their resources (Davies and Houston, 1984). Even when outnumbered, female lions under such conditions may still fight intruders because of the threat of losing essential territory (Heinsohn, 1997). The consequences of failing to respond to territorial challenges will result in eventual extinction of the pride due to aggression from other prides, as has happened in the Serengeti (Heinsohn, 1997).

There are a number of other factors which need to be considered when using IFD. These

include the influences of resource depletion on distribution patterns and this may have an effect on the point at which an equilibrium, in terms of resource value, is able to occur. In the Phinda Resource Reserve (South Africa), lions had such a strong preference for wildebeest (*Connochaetes taurinus*) that they induced a pronounced population decline in these animals. Therefore the effect of lions on prey populations can be particularly important in small reserves (Hunter, 1998). It is also likely that lions will not relocate their territories once they have been established, should prey depletion occur. This was stated by Packer *et al.* (1990) who found that even when lions in the Serengeti had almost no prey available within their territory, and were forced, as a result, to walk large distances to find the migratory herds of prey, they always returned to their original home ranges. Initial selection of areas for home ranges is unlikely to be affected by prey depletion since decisions would be made on the basis of current status of resources.

Based on the above discussion of optimal patch choice the following general hypothesis has been formulated: large scale habitat quality determines where lions choose to locate territories and home ranges. Within an area, the more resources present in combination with one another, the more suitable or optimal a particular habitat will be. This thesis will attempt to quantify and qualify what resources make up a suitable habitat for lions, using different modelling techniques.

A brief overview describing the structure of this thesis reads as follows:

Chapter Two describes data set generation. Firstly, this chapter introduces the lion data which have been used in the study and the manner in which they were collected. Response variables have been identified and these choices justified. Manipulations of the data have also been described and justified. Secondly, those environmental variables hypothesized to be of importance to lion spatial ecology have been identified. Descriptions of all manipulations occurring within the Geographic Information System (GIS) have been provided.

Chapter Three complements Chapter Two by providing additional information both regarding habitat and lion socio-ecology within the reserve. Grouping patterns among the five management sections comprising HUP have been compared and descriptions of potential underlying environmental mechanisms have been described. The primary aim of this chapter is to provide a general comparative overview of lion biology within the reserve. It thus fulfils a descriptive rather than hypothesis testing role.

Chapter Four describes the methodology and results of the modeling process. It is in this chapter that hypotheses formulated in Chapter Two are evaluated. In addition to this, the validity of the models themselves has also been evaluated. Details of the validation data set and methods whereby validation was conducted have been provided.

Chapter Five provides a general discussion regarding the use of ecological models in general, and more specifically, modeling the spatial ecology of lions in HUP.

Chapter Two

Data Generation

2.1 Introduction

All lion data which have been used formed part of an ongoing lion monitoring program, the details of which are given in: Anderson (1974, 1975, 1977, 1981); Venter & Whateley (1983, 1985); Sandwith & Whateley (1987); Venter (1991); Maddock (1994); Balfour, Howison & van Zyl (1997).

Environmental data variables included: food, shelter (cover), water, topography, local infrastructure, mainly in the form of roads and other (possibly competing) carnivores, in this case, hyaenas.

Geographic Information Systems (GIS) are integral to this study and provide a useful tool for preparing and manipulating datasets in a spatially explicit manner. The study area has been split up into 819 contiguous 1km by 1km grid cells, with each grid cell having associated data on the environmental variables and lion sightings which have been recorded therein. The manner in which each variable was prepared will be described as well as all relevant computer manipulations conducted within the GIS framework.

The aim of the current chapter is thus to produce datasets for lion sightings and for those environmental variables which are of possible importance in explaining lion spatial ecology.

Objectives regarding lion data were to firstly produce digital maps for all lion sightings, secondly, to reduce these data to four age/sex categories which provided the best description of pride animals and thirdly to produce databases, one for each study period, giving a per grid cell representation of each of these age/sex categories, which were then used in analyses.

In terms of environmental data , the objectives were threefold: important variables were

firstly identified from other studies involving lions and/or large carnivores. These variables were then captured and/or manipulated using a GIS to produce a number of spatially explicit maps of the variables in question. Thirdly, a database detailing environmental conditions for each 1km x 1km grid cell within the reserve, will be produced for each of the two study periods in question, namely 1973 - 1984 and 1985 - 1999.

2.2 Study Area

Hluhluwe-Umfolozi Park (HUP) is located in Northern KwaZulu-Natal, South Africa (between 28°00' and 28°26' S. And 31°43' and 32°09' E). The reserve has an area of 96 453 ha (Watson, 1995) and was originally made up of three separate regions, namely Hluhluwe Game Reserve (HGR), Umfolozi Game Reserve (UGR) and the Corridor which connects the two (Brooks & Macdonald, 1983). The Corridor, although managed as part of the game reserve since the early 1950's, was only officially handed to the then Natal Parks Board in 1982, and the combined unit (Fig. 2.1) became known as HUP (Brooks & Macdonald, 1983).

HUP is comprised of five management sections, namely: Manzibomvu, Nqumeni, Masinda, Mbuzane and Makhamisa (Fig. 2.2). The three major rivers in the area are the Black Umfolozi, White Umfolozi and the Hluhluwe (Fig. 2.1).

Topography is hilly, this being more pronounced in the northern sections than in the South, and altitudes range from 40 - 560 m above sea level. More detail on topography, rainfall, vegetation and water distribution is provided at a later stage within the current chapter.
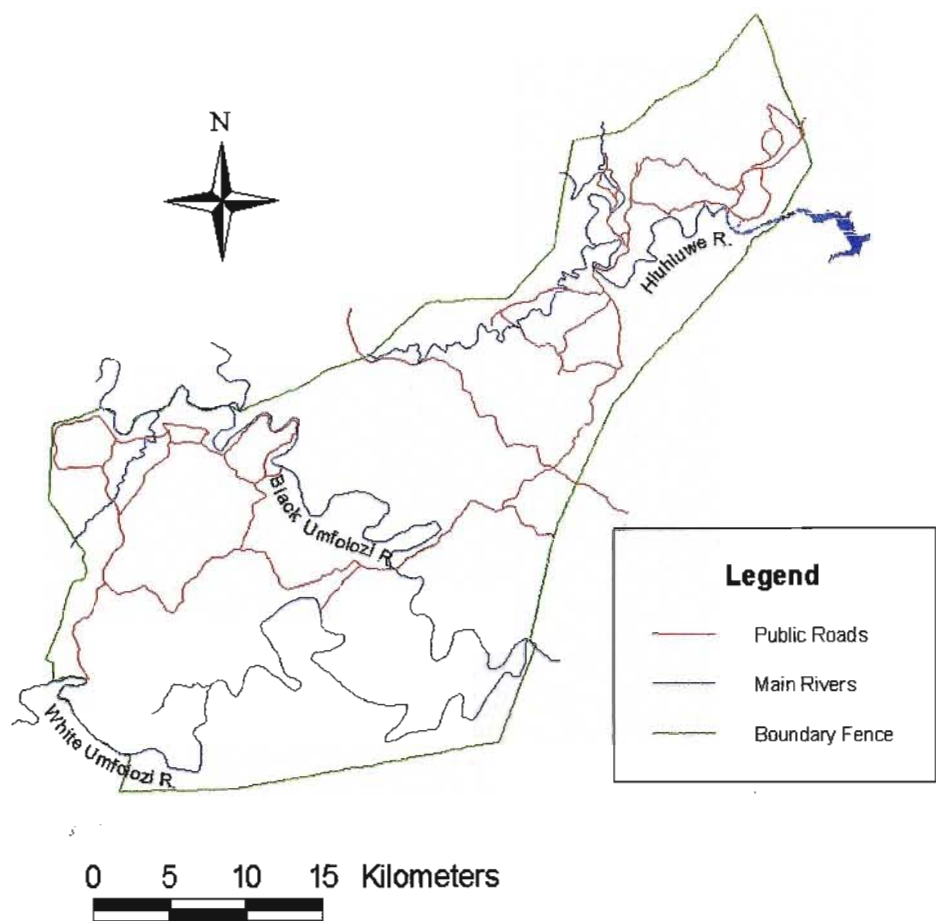
Figure 2.1: Hluhluwe-Umfolozi Park, showing main river systems and public roads.
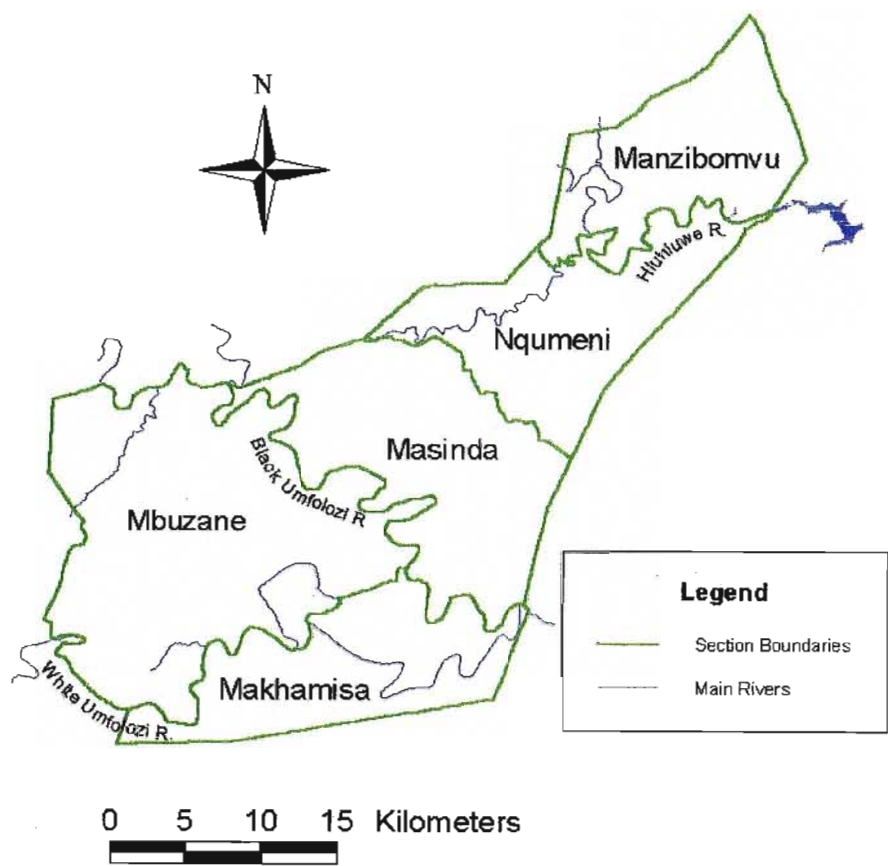
Figure 2.2: Management sections within HUP.

2.3 Materials and Methods

2.3.1 Lion data set generation

GIS programs which were used include: Idrisi 32, Cartalinx 1.2 and ArcView 3.1. All final data sets are at 1km x 1km resolution. All initial data were obtained from the Kwa-Zulu Natal Nature Conservation Services (KZNNCS).

Lion data are based on incidental staff sightings of all lions from 1973 onward. An attempt has been made to exclude tourist sightings from the database as the quality of these data may not be of an adequate standard. No call-up data have been used as call-up's represent an artificial situation and would not give an accurate idea of lion distribution.

Carnivore sighting forms gave the following relevant information: date on which the sighting occurred, age/sex make-up and relevant number of animals in each category, location of sighting (marked on an A4 size map of the reserve). The latitude and longitude of each position was subsequently calculated using 1:50 000 topographical maps of the area. These data were then entered into spreadsheets, with a new spreadsheet for each year. From 1984 onwards, locations of sightings were no longer marked on a map, but were given as a grid reference. A 1km grid system is used in the park, and the reference co-ordinates refer to the center points of these grid cells. As a result, all data, post 1984, can only be analysed at a 1km (or greater) scale.

All sightings data were imported into Cartalinx 1.2, a spatial data building program, in order to obtain a vector point map of sighting locations and their associated information. Two maps were made, one for all data from 1973 to 1983 which had a latitude/longitude reference system, and one for data from 1984 onwards which used an LO co-ordinate system (metres south of the equator and metres east of longitude 31, see Appendix 2). These data were then exported to Arcview 3.1 and all latitude/longitude data were re-projected to the LO31 system. The two maps were then merged

(using the Xtools module and the merge theme command in ArcView 3.1) so as to obtain one map containing all sightings. In order to promote model accuracy, it was decided to split the dataset in half, the reason being that certain environmental data either had changed from 1973 to 1999 (as in the case of vegetation) or were only available for the latter half of the study (as in the case of prey and hyaena dens). The first half of the data set refers to the period from 1973 to 1984 and the second half from 1985 to 1999.

Point data were then all converted to raster format, at a 1km scale, for all relevant lion variables to be used in the analyses. These variables included: number of sightings of adult females in groups of two or more, number of sightings of adult males, number of sightings of cubs and number of sightings of males accompanied by females.

Only females in groups of two or more were used as it was assumed that these approximated pride females better than sightings of lone (and possibly nomadic) females. The minimum number of females required by definition, for a pride to exist, is two. Prides have, however, also been described as fission/fusion social units which comprise a number of sub-groups existing throughout the pride range (Packer *et al*. 1988). By using sightings of females in groups of two or more, both complete prides and their constituent sub-groups have been catered for. Cub sightings should also provide an indication of territory since it is highly unlikely that cubs would ever be seen outside a territorial boundary, given the fact that the reason for having a territory is related to successful breeding (Packer *et al*. 1990). Males seen with females should also provide an indication of pride and hence territory location. The inclusion of a category for sightings of adult males, while probably not indicating pride and territory location, will nevertheless provide a means of comparison between two different aspects of lion spatial socio-ecology since male distribution is primarily determined by the presence or absence of females in an area, whereas territories and prides are distributed according to available

resources.

Following a critical evaluation of all sightings data, it was decided that the lion variables described above be reduced to a binary (presence/absence) scale in view of the fact that actual counts within grid cells were of questionable accuracy. There are a number of potential sources of error which may have contributed to these inaccuracies: Oversampling (and undersampling) in particular grid cells almost certainly occurred with the result that particular cells could have been under or over-emphasized in analyses of counts. Two sets of data were generated, each comprising the four aforementioned variables. Where the number of sightings in a grid cell was one or more (for each of the four lion variables), these values were assigned a 1, and grid cells with no sightings were assigned a 0 (henceforth termed Sighting Category one). In order to cater for repeat visits to grid cells (as discussed in Chapter One) and thus identify and model predictor variables for which a marked preference was shown, a second set of data were generated as follows: where the number of sightings was two or more (henceforth termed Sighting Category two), these values were assigned a 1 and cells containing one or no sightings were assigned a zero. In doing this, "presence" values contained in the data sets for each of the variables were dramatically reduced (see the discussion in Chapter 4). The histograms in Fig. 2.3 illustrate why this occurred: the majority of the data sets are comprised of single sightings per grid cell, hence reducing these to zero values resulted in a decrease in the newly calculated (Sighting Category Two) "presence" values.

2.3.2 Environmental data generation

See Appendices 1 & 2 for descriptions of Idrisi modules and other GIS details (index image production, image definitions and reference systems). A summary has been compiled on some of the problems experienced with the data and the potential solutions to these problems (Appendix 3). There
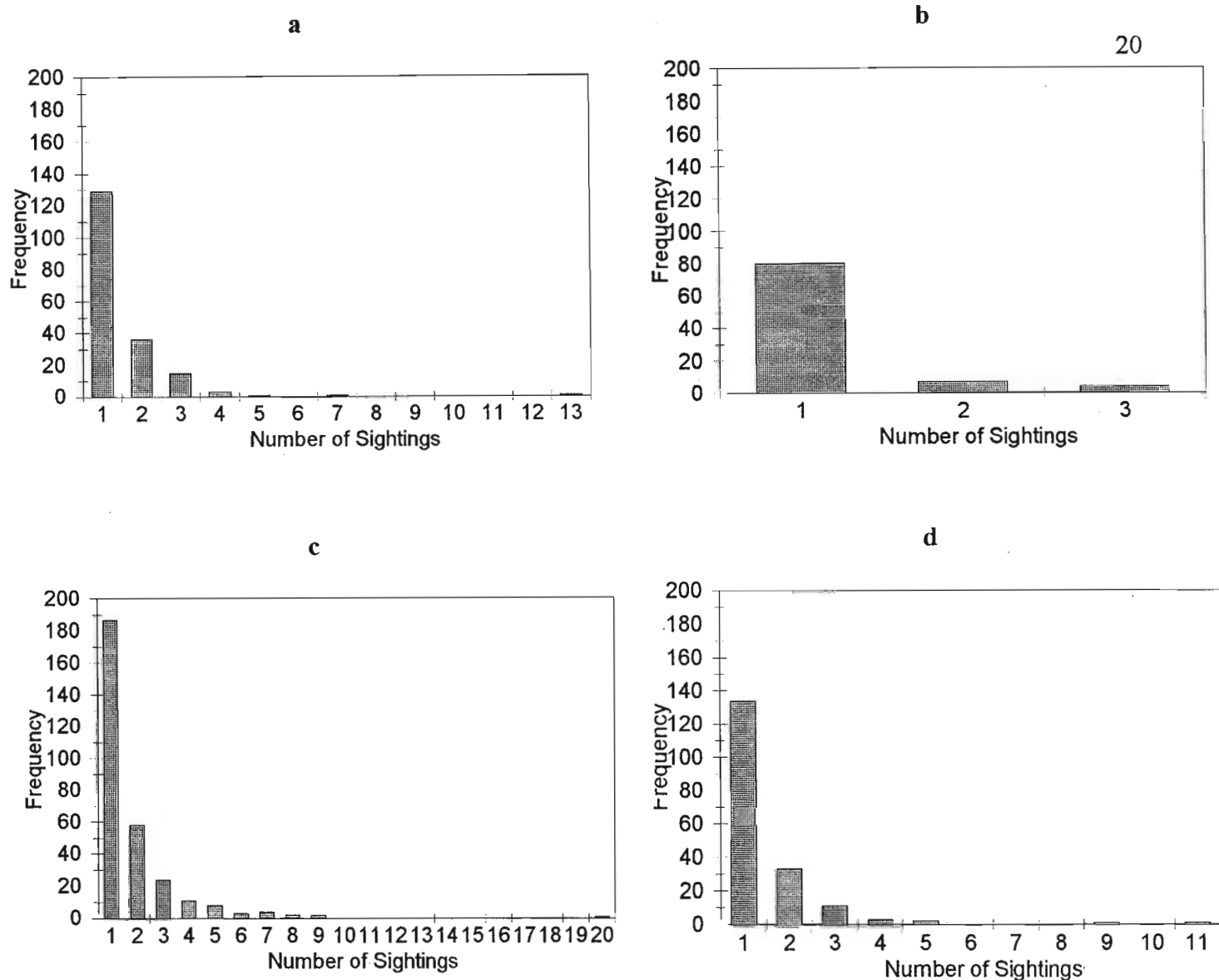
Figure 2.3(a-d): Comparisons, within each age/sex category, of sightings data used in modeling for the two time periods in question. Note the high frequency of single sightings per grid cell and the fact that fewer sightings were recorded during the 1985 - 1999 period. Frequency distributions show the number of sightings per grid cell for: (a) cubs:1973-1984; (b) cubs:1985-1999; (c) adult females:1973-1984; (d) adult females:1985-1999. Frequencies of cells with zero sightings have been excluded. Abnormally high numbers of sightings can be identified e.g. twenty sightings in one grid cell (Fig. 2.3h).

e

f

g

h
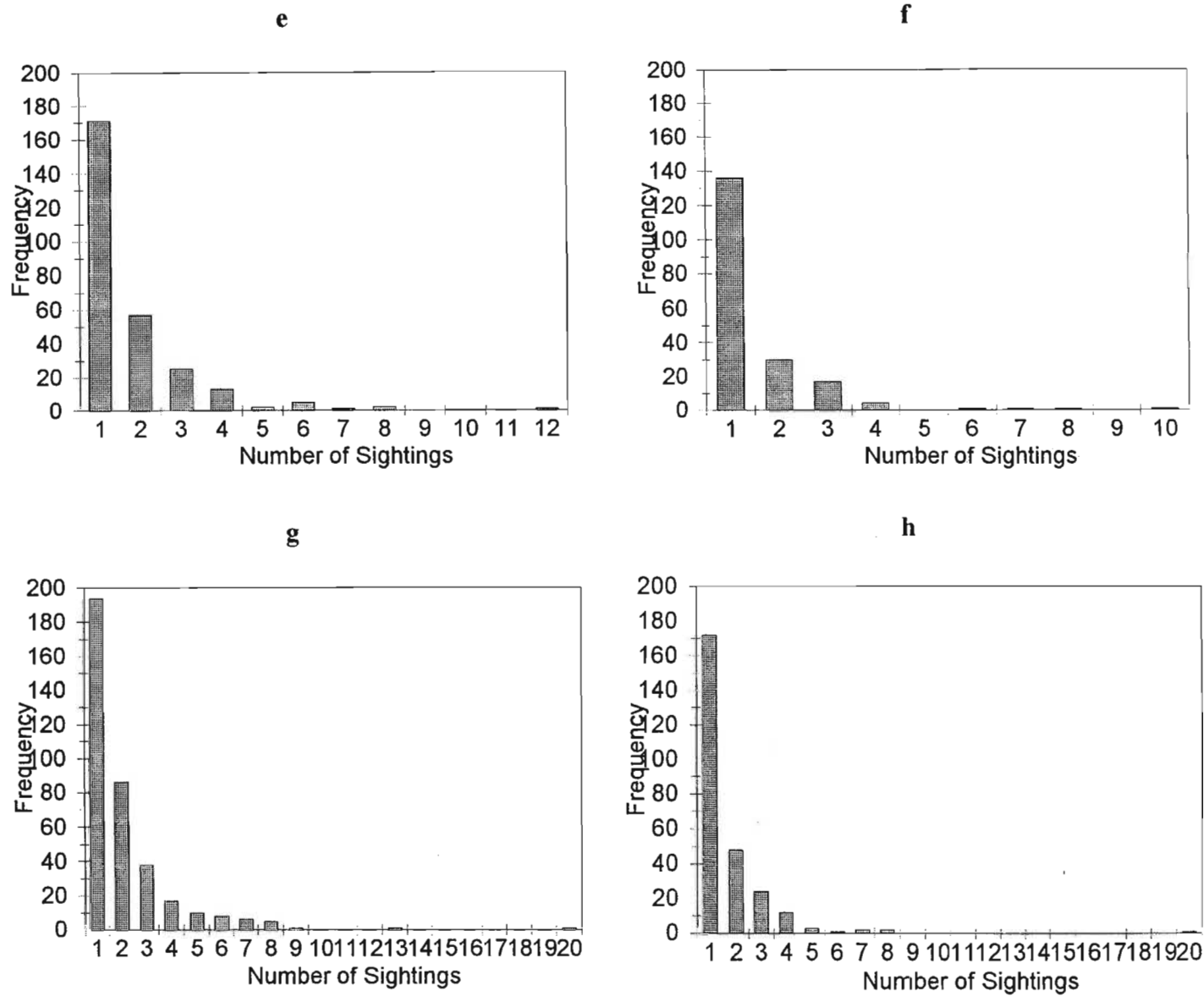
Figure 2.3(e-h): Comparisons, within each age/sex category, of sightings data used in modeling for the two time periods in question. Note the high frequency of single sightings per grid cell and the fact that fewer sightings were recorded during the 1985 - 1999 period. Frequency distributions show the number of sightings per grid cell for: (e) males seen with females: 1973-1984; (f) males seen with females: 1985-1999; (g) adult males: 1973-1984 and (h) adult males: 1985-1999. Frequencies of cells with zero sightings have been excluded. Abnormally high numbers of sightings can be identified e.g. twenty sightings in one grid cell (Fig. 2.3h).

now follow brief descriptions of the procedures utilized in calculating each environmental variable included in the study.

Regarding topography and altitude, the hypotheses that 1) altitude and 2) slope steepness are determining factors in home range and territory location will be tested.

A Digital Elevation Model (DEM) of the reserve was obtained from KZNNCS at 50m resolution. This image was then contracted (by aggregating pixels) by a factor of 20, to give an altitude map at 1km resolution.

Using the DEM obtained from the KZNNCS and the SURFACE ANALYSIS module in Idrisi32 slope (as a percentage) and aspect (in degrees) were calculated. In order to arrive at the required scale, the CONTRACT module (with pixel aggregation) was used for slope, since it was calculated from the original 50m resolution DEM. Due to the problem of averaging aspect (calculating a mean would give a spurious result e.g the mean of the following two aspects (in degrees) [270 + 90]/2 = 180, i.e the average of West + East is South) this variable was excluded from analyses. Pixel thinning was also attempted but it was decided that the inaccuracies incurred by using this method were too large to warrant inclusion.

In this study, only major rivers and their larger tributaries were included in the analysis. The reason for this is that these rivers alone contain water through most, if not all, of the dry season (D. Balfour pers. comm.). Since there are no artificial bore-holes in the reserve, they (major rivers) are effectively the only sources of water during the winter months. Main river systems in HUP were obtained from the KZNNCS in a digitized map format. All minor tributaries were deleted (for the reasons explained above) from this coverage using Cartalinx (a vector based spatial data building and editing program). The edited map was then exported to Idrisi, where it was rasterized at a 25m pixel scale. Rasterization refers to the process whereby lines (vectors) are converted to raster (pixel/cell)

format. The DISTANCE module was then used in order to calculate distances, in metres, from rivers. Once again, CONTRACT was used to obtain an image for distances from rivers at a 1km scale.

With regards rainfall, which, in the park, is unimodal and peaks in mid summer (Brooks and Macdonald, 1983) a linear equation (derived by D. Balfour, KZNNCS) modeling the relationship between rainfall and altitude was used to calculate values per 50m pixel. The equation was based on rainfall records for nine stations within the reserve, with each station having not less than 9 years of associated monthly rainfall data, and reads:

Rainfall (mm) $= 462.7 + 1.164*$Altitude(m) ($R^2 = 0.94$, 7d.f)

A quadratic term was added to the model, but as it only increased the coefficient of determination by three percent, it was excluded.

The IMAGE CALCULATOR was used to apply the rainfall model to the DEM (50m resolution), thus giving a map of rainfall throughout the park. As described previously, CONTRACT was used to derive a map at the 1km grid scale.

With regards the influence of vegetation on lion spatial ecology, the hypotheses to be tested are: firstly, vegetation structure influences choices of home range and territory location and secondly, vegetation complexity or heterogeneity is important in determining territory and home range location.

A 1975 vegetation map was obtained from the KZNNCS in digital format at 50m resolution. This map was produced from aerial photographs and extensive field work was conducted to delimit boundaries for the various plant communities (Whateley and Porter, 1983). The 36 original classes were reduced (using Idrisi's RECLASS module) to the basic physiognomic classification of Phillips (1973) to give the following classes (Table 2.1): forest, woodland, open woodland, thicket and grassland (Whateley and Porter, 1983). The proportion of each vegetation class within each grid cell was then calculated in the Database Workshop.

A 1996 vegetation map was compiled using satellite imagery in combination with ground truthing (Meyer, 1996). The map was produced at 25m resolution and the 19 different vegetation categories were condensed to the five physiognomic classes used in this study (Table 2.2). Once again, the percentage of each vegetation class in each grid cell was calculated.

A further vegetation variable was calculated to gain some index of structural heterogeneity within a 1km grid cell. The PATTERN ANALYSIS module in Idrisi was used to calculate the number of different vegetation classes in a 5x5 pixel moving window. This was performed for both reclassified vegetation maps, at their original cell sizes, namely 25m for the 1996 classification map and 50m for the 1975 classification map.

The theory that prey type and density may influence where lions locate territories and home ranges will need to be tested. To do this, line transect data that have been collected for the years 1996 and 1998 were used to generate maps of prey biomass (kg/km^2) distribution for the seven most frequently eaten prey types thought to be important sources of food for lions in HUP (Maddock *et al*, 1996). These included buffalo, zebra, wildebeest, nyala (*Tragelaphus angasii*), impala, warthog (*Phacochoerus aethiopicus*) and kudu (*Tragelaphus strepsiceros*). 1996 and 1998 are the only two years for which there are accurate herbivore data available. Data collected during previous years is unreliable and of poor quality (O. Howison, pers. comm.), hence no other prey data were incorporated.

There are 26 line transects, of varying lengths, in the reserve (Fig. 2.4). Each transect is associated with a number of observations of animals, where each observation has a tag number, transect bearing, sighting bearing and distance(from the transect) to animal observed. Tags occur every 100m along the transect, and it was necessary to calculate locations for every tag on every transect. To do this, the minimum requirement for straight transects is a start and end point location.

Table 2.1: Assignment of original species specific vegetation classes (as designated in Whateley and Porter's (1983) vegetation map of HUP) to broad physiognomic categories.

Original Vegetation Category	New Category
H*: GRASSLAND (PM, CT)**	Grassland
H: GRASSLAND (TT)	Grassland
U: GRASSLAND (TT)	Grassland
U: GRASS(FLOODPLAIN) (CT)	Grassland
H: TH INDUCED (DC, AK)	Thicket
H: TH (ED)	Thicket
H: TH (AK)	Thicket
U: TH/WOODED GRASS (AK, DC)	Thicket
H: TH (AC)	Thicket
U: TH/WOODED GRASS (AC)	Thicket
U: TH (ED)	Thicket
U: TH/WOODED GRASS (AK)	Thicket
U: O. WDLND (AT: 2 - 4M)	Open Woodland
U: O. WDLND (AB)	Open Woodland
U: O. WDLND (ANi, AG)	Open Woodland
U: O. WDLND (AT)	Open Woodland
U: O. WDLND (CM)	Open Woodland
U: O. WDLND (ANg)	Open Woodland
U: O. WDLND (CA)	Open Woodland
U: O. WDLND (AK)	Open Woodland
H: WDLND (AB)	Woodland
H: WDLND (SA)	Woodland
U: C. WDLND (AG, SA)	Woodland
U: C. WDLND (AB, AV)	Woodland
U: C. WDLND (ANi)	Woodland
H: WDLND (AK)	Woodland
H: WDLND (ANi)	Woodland
U: C. WDLND (ED)	Woodland
H: WDLND (CM)	Woodland
U: C. WDLND (OA, SA)	Woodland
H: FOREST (HK)	Forest
U: RIV. FOREST (SA)	Forest
H: RIV. FOREST (SA, E)	Forest
U: RIV. FOREST (AR, FS)	Forest
H: RIV. FOREST (AR, FS)	Forest
U: FOREST (CH)	Forest

* The Letters H and U refer to Hluhluwe and Umfolozi respectively and give a general idea as to the location of a vegetation class within the reserve.
TH=thicket; WOODED GRASS=Wooded Grassland; WDLND=Woodland
O.WDLND=Open Woodland; C.WDLND=Closed Wooodland; RIV.FOREST= Riverine Forest.
**Capital letters enclosed in brackets refer to species prevalent within a particular vegetation class. These can be ignored as they were not considered when placing vegetation classes into broad physiognomic categories. They have been included simply for illustrative purposes.

Table 2.2: Assignment of original vegetation classes (as designated by Meyer's (1996) vegetation classification of HUP) to the five broad physiognomic classes used in this study.

| Original Vegetation Category	New Category
dry grassland	Grassland
grazing lawn	Grassland
grassland with encroachment, shrubland savannna (sparse)	Thicket
very dense vital grassland	Thicket
grassland with encroachment, shrubland savanna	Thicket
dense grassland with encroachment (vital)	Thicket
grassland with encroachment (dry)	Thicket
very dense grassland with encroachment (vital)	Thicket
reed	Thicket
savanna parkland	Open Woodland
unspecified woodland (influenced by shadow)	Woodland
dense woodland (mixed leaved)	Woodland
closed woodland, *Acacia nilotica*	Woodland
dense woodland, *A. burkei*	Woodland
forest, riverine forest, very dense woodland	Forest
riverine forest, forest, closed woodland (broadleaved)	Forest
dense woodland (broad leaved)	Forest
closed to very dense woodland (broadleaved), riverine woodland	Forest
open forest, closed to very dense woodland (broadleaved)	Forest
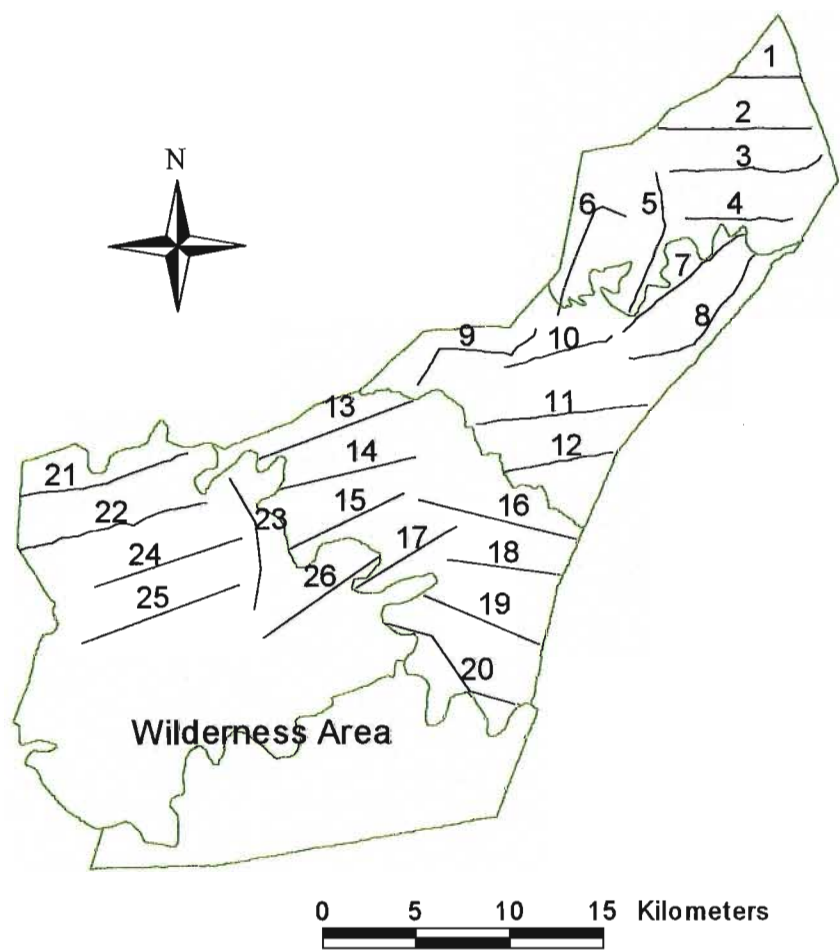
Figure 2.4: Map of line transects (1 - 26) in HUP.

Where not available (i.e. for transects 6,13,14,15,16,17,18,19,20,24,25,26) these were read from a map supplied by the KZNNCS. For non-straight transects, locations of turns and their associated tags were recorded. A macro (written in Microsoft Excel) was then used to calculate the mid-point location of every tag on a transect.

The transect bearing, sighting bearing and sighting distance (mentioned above) were subsequently used to calculate (using trigonometry) a horizontal and vertical distance component of animal locations from transects. These data, along with the tag location data were combined and manipulated to give a positional location for every observation.

A vector image was then produced for the combined 1996 and 1998 data using Cartalinx. This was exported to Arcview, where grid interpolations were performed using the inverse distance weighted option in the INTERPOLATE GRID module. Six nearest neighbor control points were used. Grids estimating the number of animals per prey species per 25 m grid cell were thus obtained. These grids were exported to Idrisi and were multiplied by the average mass per individual (of that prey species) in a population (Table 2.3) to get the average biomass of meat ("on the hoof") available per grid cell. All individual prey maps were summed to give a total meat availability. These were then converted to a 1km^2 resolution using the RESAMPLE module in Idrisi.

Table 2.3: Mean individual mass of prey species found in HUP (after Bothma, 1996).

Animal	Mean mass in kg per individual
Blue wildebeest (*Connochaetes taurinus*)	181.8
Buffalo (*Syncerus caffer*)	495
Burchell's zebra (*Equus burchelli*)	216
Impala (*Aepyceros melampus*)	40.9
Kudu (*Tragelaphus strepsiceros*)	136.4
Nyala (*Tragelaphus angasii*)	72.7
Warthog (*Phacochoerus aethiopicus*)	29.6

In order to quantify the effect of roads on sighting frequency in this study, a non-linear regression analysis was conducted in which the total number of sightings per distance category (0-100 m, 100-200 m, 200-300 m etc up to 2000 m) was regressed against distance from roads [both public and management]. All sightings data from 1984 onwards were excluded from this analysis, as they were recorded on a 1km² grid which precluded them from being placed into 100 m distance categories.

It is hypothesized that lions will show a preference for areas in which public roads are present, with this preference being most pronounced in areas where vegetation is thickest.

Three indices for roads have been used. These include presence/absence of roads (with a differentiation between public and management roads), presence/absence of road intersections and distance from roads in meters.

Vector images of management and public roads were rasterized at a 1km grid scale in order to obtain presence/absence images of these two variables.

Road intersections were digitized (on screen) in Idrisi, and this point image was converted to a 1km raster image. Management and public roads were then combined in the same vector map. This image was converted to raster at 25m pixel scale and the DISTANCE module was used to calculate distances, in meters, from roads. CONTRACT was used to derive a map at a 1km scale. A distinction was made between management and public roads as it was thought that differences could exist in the utilization of these roads by lions. The underlying reason for this decision was that public roads are not only more heavily utilized by cars, but they are also far more open (clear of vegetation) and easy to travel on, whereas management tracks are often overgrown and do not represent as convenient lines of travel.

A final point of consideration concerns the effect of competition from other carnivores, in this

case hyaenas, and the impact this has on lion spatial ecology. The hypothesis to be tested is that hyaenas do have an effect on lion territory location. In order to test this hypothesis effectively, spatially explicit systematic surveys of the hyaena population in HUP would need to be conducted to assess those areas in which high hyaena densities occur. Since no data of this nature are available for the reserve, the following approach was adopted to test the aforementioned hypothesis.

To gain some index of hyaena occupancy throughout the reserve, all hyaena dens known by park staff to be in existence within the reserve were visited and their positions recorded using a Garmin 12 G.P.S. Two variables were calculated, the distance to dens and the presence or absence of dens per grid cell. Dens were given a "use" rating based on the observed frequency of recent activity as perceived by an accompanying game guard. Two very old dens have been excluded from the distance analysis. It is likely that some dens, especially the older ones, have not been recorded because their locations are unknown to the reserve staff. Den records are thus biased toward those currently in use.

2.4 Results and Discussion

2.4.1 Lion data

Maps illustrating the distribution (and frequency) of sightings of each age/sex group (defined previously in the Materials and Methods section) have been compiled for the 1973 - 1984 (Fig. 2.5) and 1985 - 1999 (Fig. 2.6) periods.

With regards the reduction of data to a binary scale, the assumption of absences (zero values) in particular grid cells is a potential problem since lions may have been present, but simply were not seen or recorded. While this is true for lions in general, it may not hold for pride presence/absence. It is highly likely that during the 1973 - 1984 time period, in which intensive lion monitoring

occurred, most if not all pride areas were known and observations of these prides recorded. It follows that areas where no prides existed were also known, and while absences were not recorded as such, they can be reasonably assumed. During the 1985 - 1999 period however, monitoring of the lion population was neither as intensive nor as organised as the previous time period in question. Firstly, there is a period from 1989 to 1993 (inclusive) for which no data are available. Secondly, these data were collected from a different source, namely a set of computer print-outs which were found whilst searching, in the HUP Research Center archives, for original records. The print-outs make provision for different types of lion sightings (eg: incidental staff, bait station, tourist etc.) and also give a group age/sex structure breakdown. As the original records were not able to be found, however, the reliability of these data is questionable, even though only incidental sightings were included and all possible duplicate and/or auto-correlated records were deleted. This meant that where sightings on the same day occurred in close proximity to one another (within 5km as determined by grid co-ordinate locations) one of the sightings was omitted from the data set.

Certain grid cells have possible abnormalities associated with the number of sightings recorded within them. These cells have been indicated in the maps (Fig.'s 2.5 and 2.6) and were identified from the histograms showing the frequency distribution of sightings per grid cell (Fig. 2.3). Once again, however, these anomalies have been avoided by reducing the data set to binary values.

There are a number of factors which may affect the quality and, in certain cases quantity, of sightings data. Firstly, the problem of subjectivity in the classification of lions into various age categories should be mentioned. In particular, the designation of sub-adult females and adult females has proved to be problematic, with most female lions being classified as adult, rather than sub-adult (Anderson, 1974). This problem was again highlighted in the HUP lion monitoring program for 1984 to 1986, where there appeared to be a tendency for field observers to classify sub-adult females as
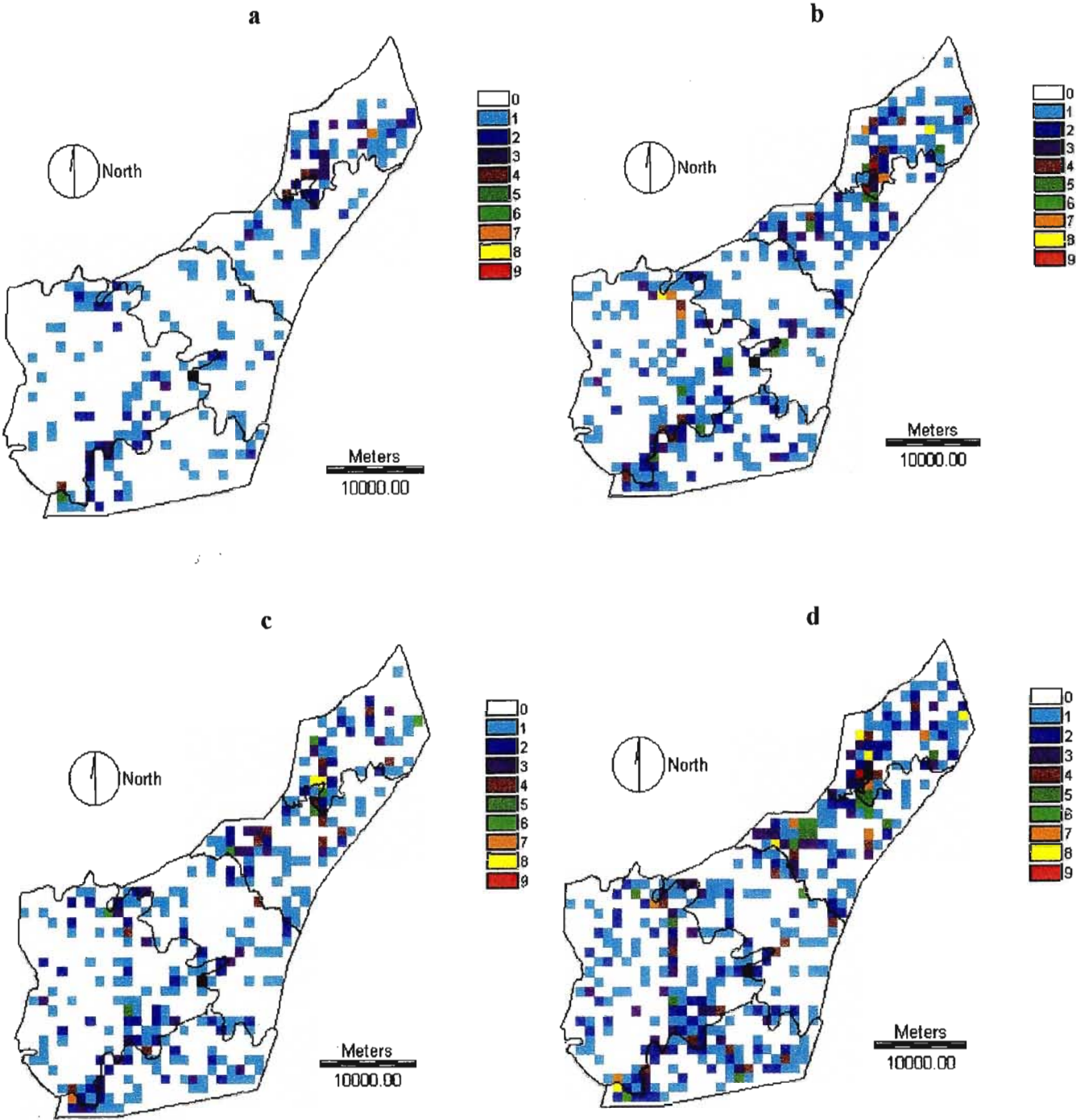
Figure 2.5: Spatial representation of lion sightings data (shown as number of sightings per grid cell) for the period 1973 - 1984. Grid cells which have received two or more sightings may be more accurate indicators of pride areas. Each map indicates a different variable. Number of sightings of: (a) cubs; (b) adult females; (c) males seen with females; (d) adult males. Cells colored black have an abnormally high number of sightings associated with them and should be viewed with caution.

Figure 2.6: Spatial representation of lion sightings data (shown as number of sightings per grid cell) for the period 1985 - 1999. Grid cells which have received two or more sightings may be more accurate indicators of pride areas. Each map indicates a different variable. Number of sightings of: (a) cubs; (b) adult females; (c) males seen with females; (d) adult males. Cells colored black have an abnormally high number of sightings associated with them and should be viewed with caution.

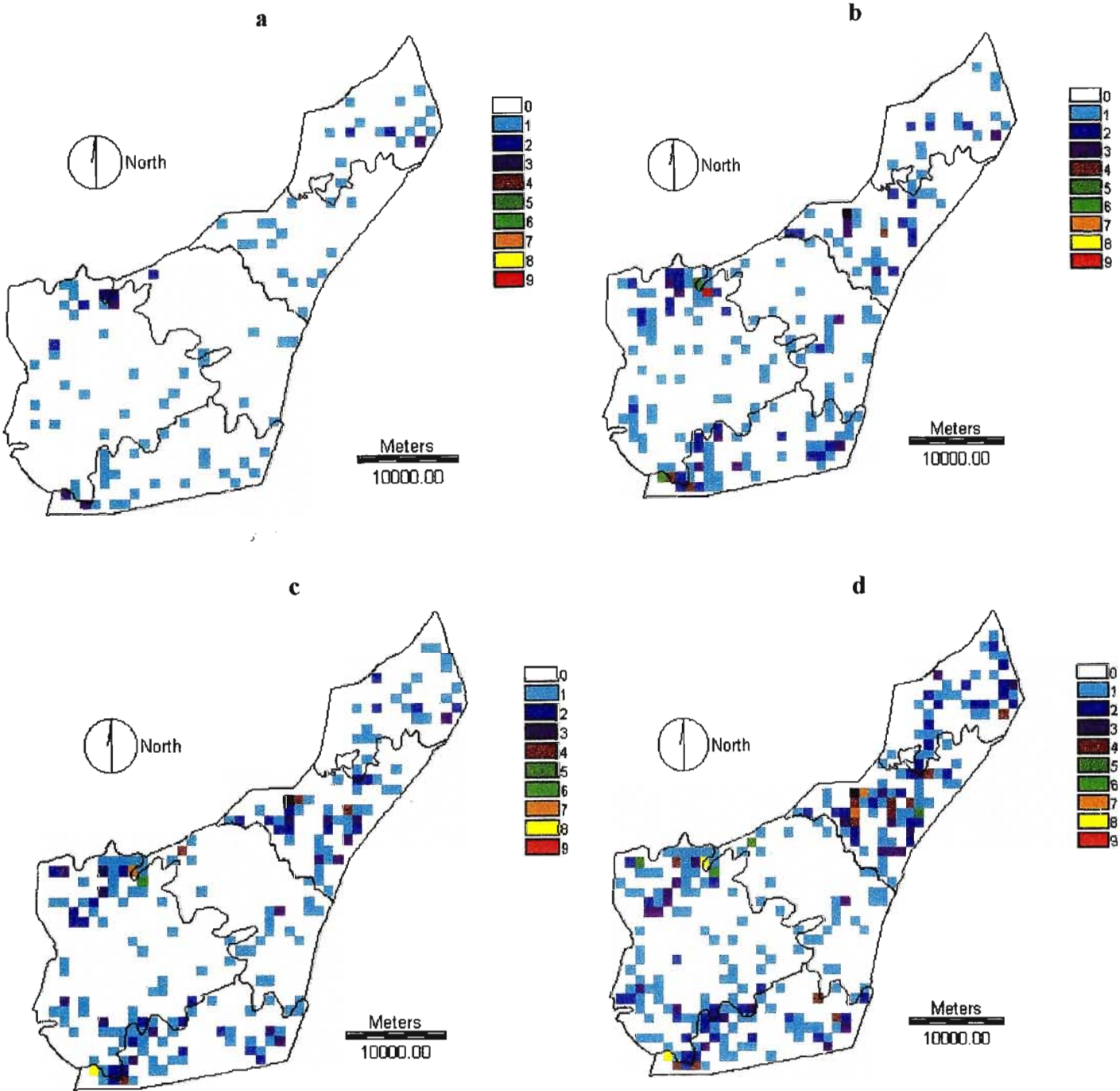adults (Sandwith and Whateley, 1987). A similar problem has been described by other workers in different reserves who mention the difficulties in determining differences between young sub-adult male lions and adult females (M. G. L. Mills, pers. comm.). This may have introduced a certain amount of error into all observations used in this project. To what extent this error may influence analyses is uncertain. Classification of sub-adult females as adult is not a serious problem since most sub-adult females will remain in the same pride (and occupy the same territory) for the duration of their life span. Classification of sub-adult males as adult females, whilst it is recognised as being a problem, is not quantifiable and cannot be rectified. Sighting records do take uncertainty into account with the inclusion of a category for "unknowns" (where observers were uncertain of an animal's sex and age) and these sightings have been excluded from analyses.

A second factor affecting the data is a result of a situation which arose in northern HUP where large numbers of introduced herbivores were being killed by lion because they were not accustomed to predators (Maddock *et al.* 1996). As a result, all lions (except one female, her cub and a sub-adult) in the area were shot during the period from 1988 to 1992 (Maddock *et al.* 1996). No lions have since been resident in the area until recently, when six lions were introduced into Hluhluwe section in 1999. This situation has affected the sighting records for the northern area of the reserve and may introduce error to the analysis. In order to circumvent this all grid cells occurring in the affected area were omitted from analyses involving the 1984 - 1999 data set. The first 139 grid cells were thus excluded, leaving 680 grid cells upon which the models for this period are based.

Thirdly, observational data of this nature (incidental lion sightings) may have a number of adherent statistical "faults". For example observations may not be independent of one another. Sightings data include no identification of specific animals. As a result there is never certainty, for observations temporally and spatially in close proximity to one another, that the same animal or group

of animals is not being recorded more than once. An attempt has, nevertheless, been made to reduce the problem of temporal auto-correlation by excluding all observations occurring in the same vicinity (approximately 5km radius as read from the 1km^2 grid co-ordinate system), which were made on the same day. The major criterion for independence is that each observation of an animal represents an independent choice of the suite of available habitats (Arthur, Manly, McDonald & Garner, 1996). The time interval between observations must, therefore, be long enough for the animal to have moved between any two points in the area (Arthur *et al.* 1996). If an animal's choice of habitat is limited to it's home range, however, the problem may not occur since animals are able to travel throughout their home ranges in short periods of time (Arthur *et al.* 1996). This, combined with the fact that lions are highly mobile and the assumption that pride animals for the most part restrict their movements to their home ranges, may lessen the problem of auto-correlation. The time to independence (of observations) for large highly mobile animals such as lions may be as low as a day. This can be qualified by the fact that two of the male lions introduced to HUP in 1999 moved approximately ten kilometers in one day. A time of 5 days was used by Packer *et al.* (1990), however this was for telemetry data where observations were made of known individuals in a far more extensive system namely the Serengeti.

The thick bush and hilly terrain characteristic of HUP also makes viewing animals fairly difficult, and in some instances, for example, one out of three animals may be seen because the other two are concealed from the observer by grass or bush. Reducing variables to a binary scale will lessen this error somewhat since all data are effectively generalised and exact detail becomes redundant. Generation of a data set which makes use of repeat observations in a grid cell (as explained above) would also aid in reducing this error.

Another issue of importance is the accuracy with which positional locations of lion observations have been recorded. It is highly likely that inaccuracies of up to 250 m (radius) about

recorded points have been incurred. Recording observations at a grid scale as fine as 250 m would therefore be subject to large amounts of positional error which would ultimately affect the fit of the models derived from such a data set. By using a 1km^2 grid, positional inaccuracies are to a large extent nullified (some observations lying on cell boundaries may still be assigned to the incorrect cell, however such instances will occur far less frequently).

2.4.2 Environmental data

A Digital Elevation Model (DEM) in which altitude throughout the reserve is shown at 1km resolution (Fig. 2.7) and a map showing slope steepness (Fig. 2.8), also at 1km resolution, have been calculated. The effect of local topographical conditions in the form of slope, aspect and altitude on lion spatial ecology is not well known. Reserve size, configuration and topography have, however, been found to be likely influences on pride range size (Van Orsdol, Hanby and Bygott, 1985) and thus would probably affect range location. The combination of slope (steepness) and estimated snow shoe hare (*Lepus americanus*) density (prey) was found to explain 50% of the variation in metabolic home range sizes of bobcats (*Felis rufus*) (Litviatis, Sherburne and Bissonette, 1986), indicating that topography should not be ignored.

Water distribution could affect the distribution of lions, or more specifically where they locate their home ranges. Maps illustrating the distance from main rivers (Fig. 2.9) and mean annual rainfall (Fig. 2.10) have been compiled.

The period when drinking water is most important occurs during the hot summer months when evaporative demand is at its highest (Green, Anderson and Whateley, 1984). It was found that lions derived up to 50% of their water requirements from drinking (the remainder of the drinking requirement is made up through the consumption of prey) during the summer months (data from two
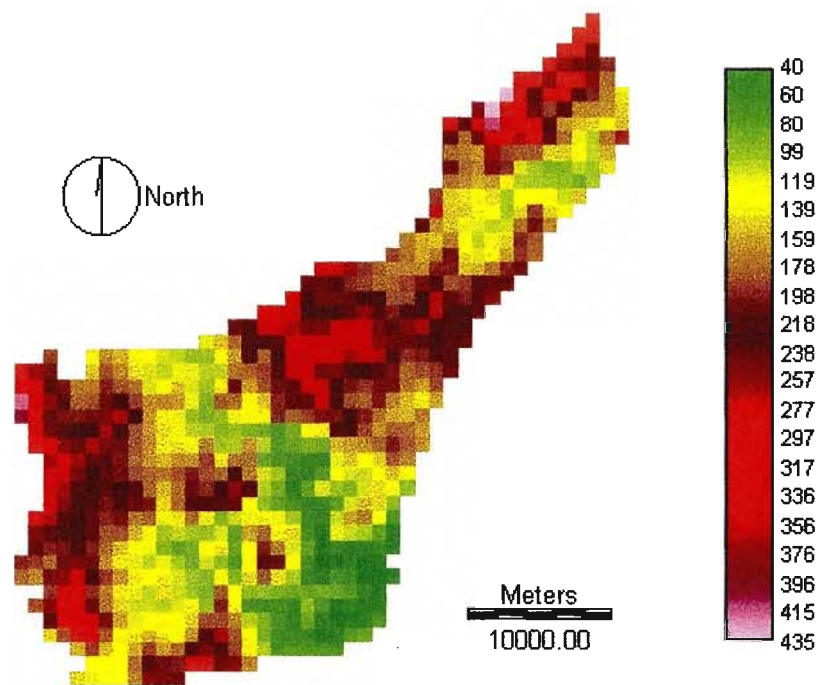
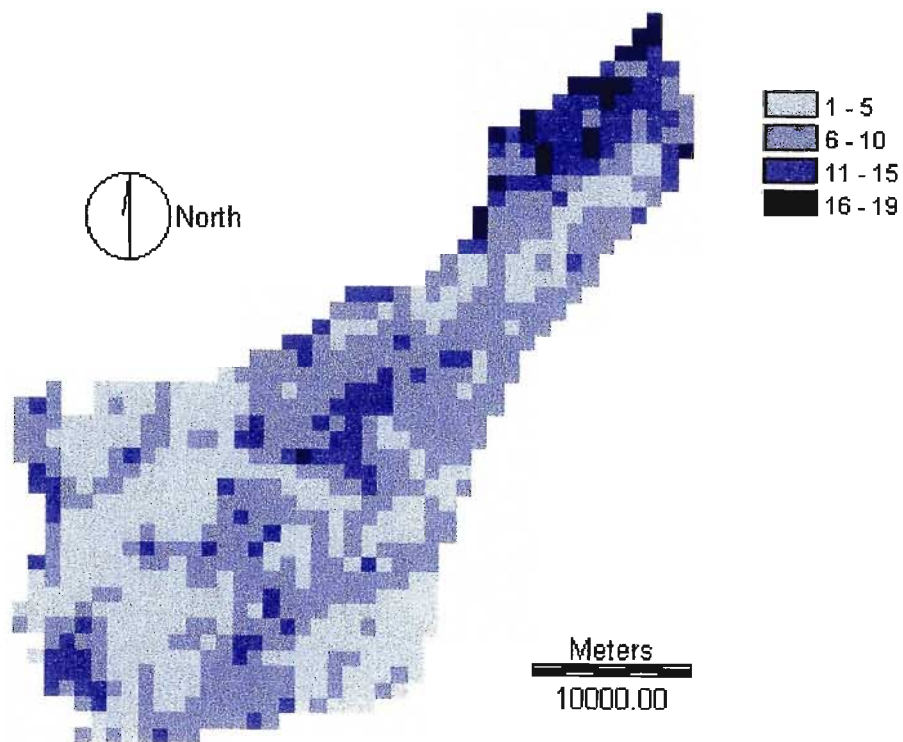Figure 2.7: Altitudes of HUP in meters above sea level

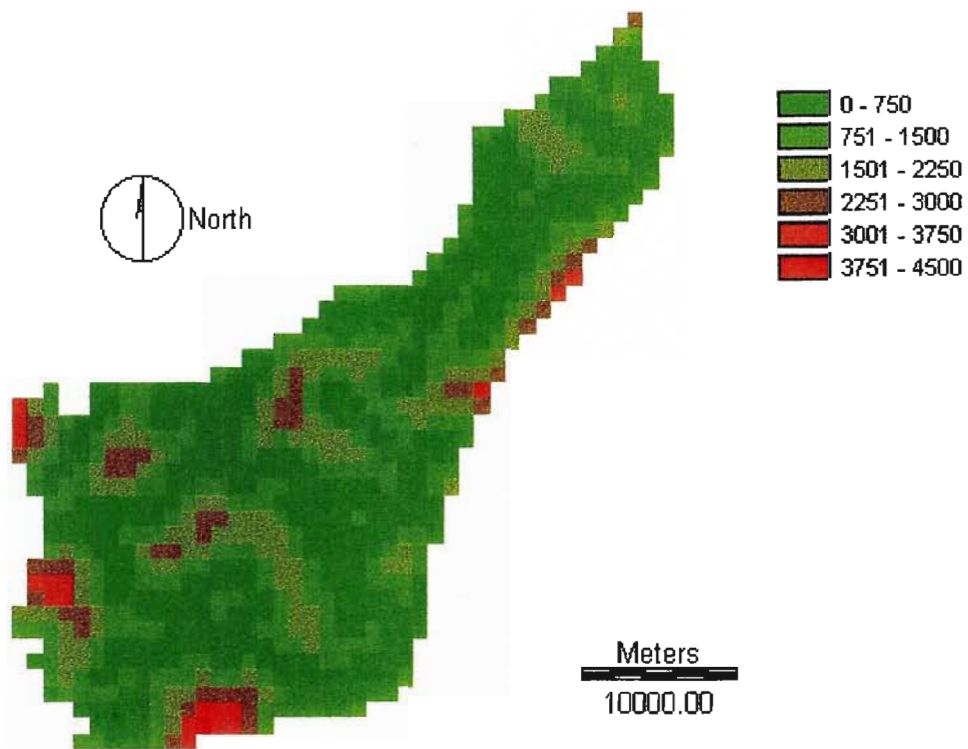Figure 2.8: Slope steepness, as a percentage, in HUP.

Figure 2.9: Distance (in meters) to main rivers in HUP.
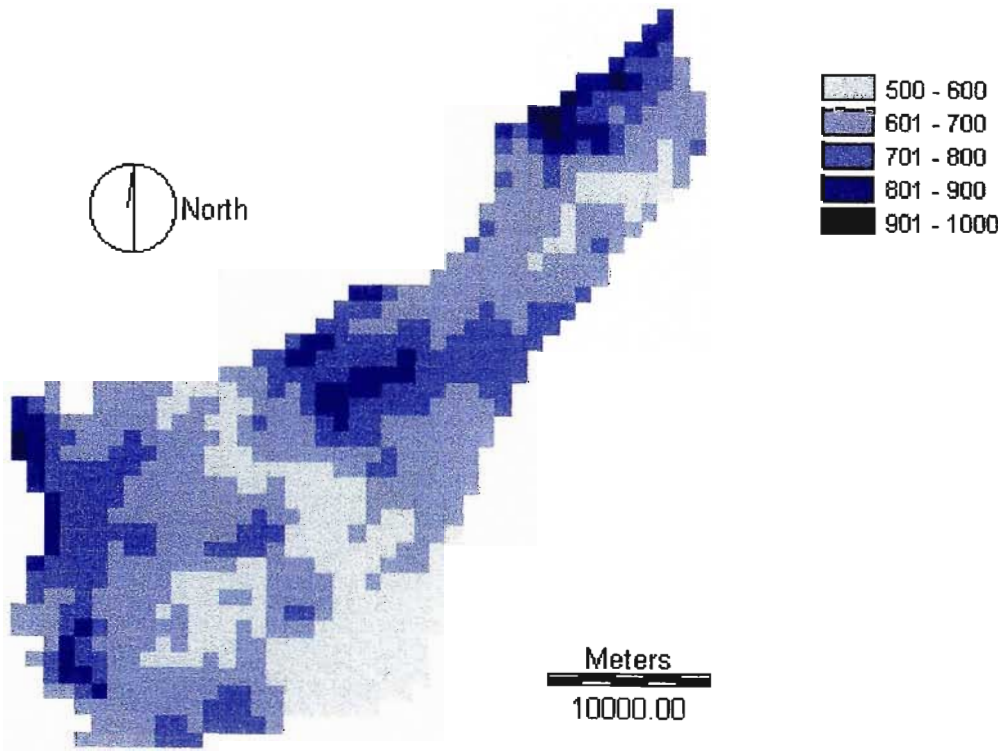

Figure 2.10: Rainfall (in mm) in HUP.

lions), but during the winter months there was no significant contribution by drinking to water requirements (data from three lions) (Green *et al.* 1984). These results should however be viewed with caution owing to the small sample sizes which were used (Green *et al.* 1984).

In areas (such as HUP) which receive most of their rainfall during mid-summer, water is abundant during the months when lions have a high drinking water requirement. Since lions have only a minor drinking water requirement during the period when water is at it's least abundant, i.e the winter months, the distribution of permanent water sources may not have a significant impact on their distribution. Owing to the inconclusiveness of the data from which this argument was based on, the possible importance of drinking water should not, however, be ignored. The presence of available drinking water may have an indirect effect through it's influence on herbivore distributions. As a consequence lions may frequent areas with a more permanent water supply, especially during the dry season, because their prey inhabit these areas(Heinsohn, 1997). This was found to occur in the Phinda Resource Reserve (South Africa) where one particular pride centred its activity around a water hole for six months during the dry winter season, and subsequently dispersed with the arrival of the summer rains (Hunter, 1998). Such within-year seasonal range fluctuations have not been addressed in the current study, since the focus has been on long term patterns of resource use. It is clear, however, that water could play an important role in territory location and it is probable that lions would select territories/home ranges which have a suitable water supply.

Vegetation maps for 1975 (Fig. 2.11) and 1996 (Fig. 2.12) have been compiled as have 2 maps describing the structural heterogeneity of vegetation in the reserve for these two periods (Fig. 2.13).

Figure 2.11: Vegetation composition in HUP for the year 1975. Five different physiognomic classes are shown (a) Forest; (b) Thicket; (c) Woodland; (d) Open Woodland; (e) Grassland. Values are given as percentage cover per 1km² grid cell.

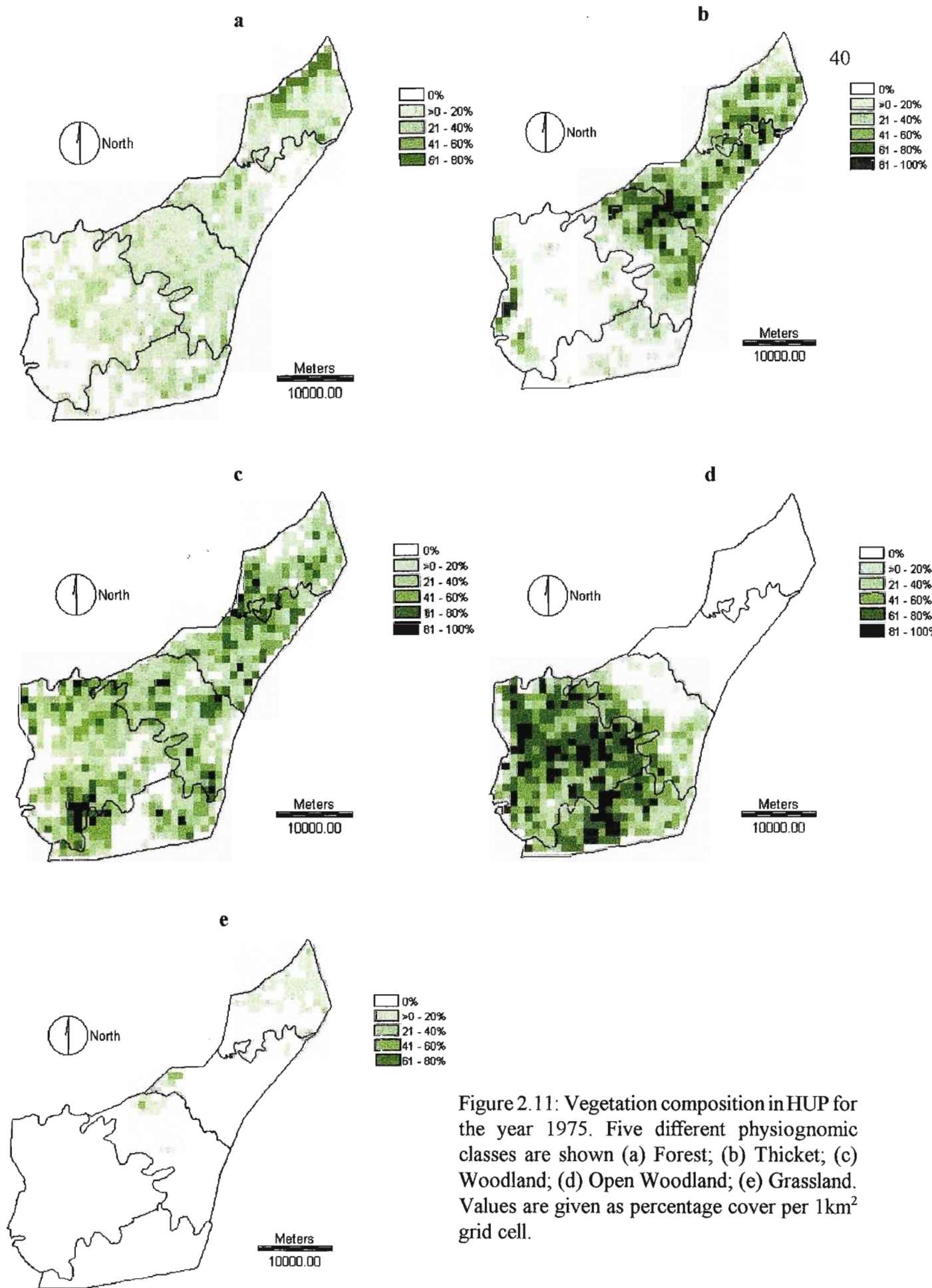Figure 2.12: Vegetation composition in HUP for the year 1996. Five different physiognomic classes are shown (a) Forest; (b) Thicket; (c) Woodland; (d) Open Woodland; (e) Grassland. Values are given as percentage cover per 1km² grid cell.
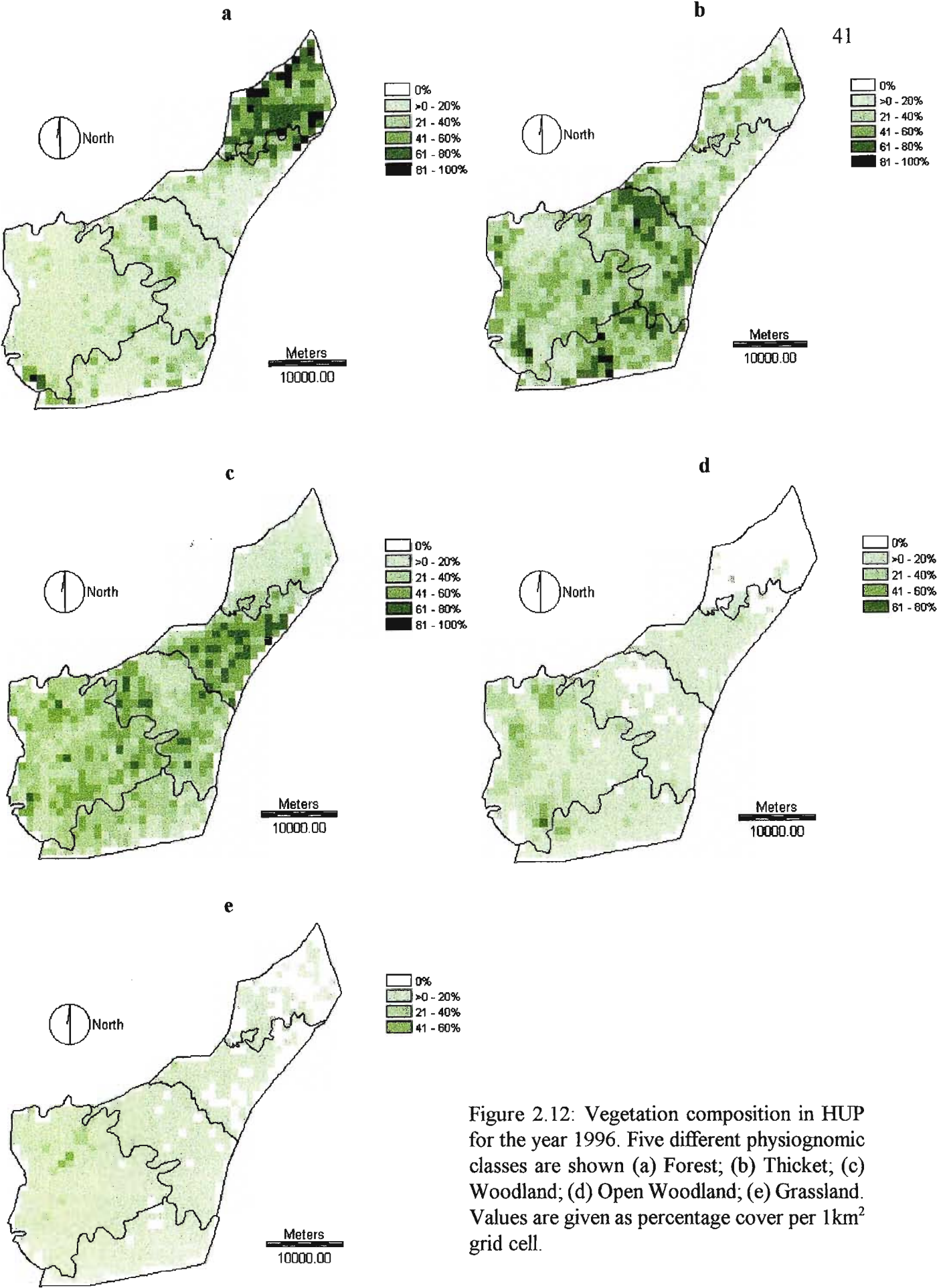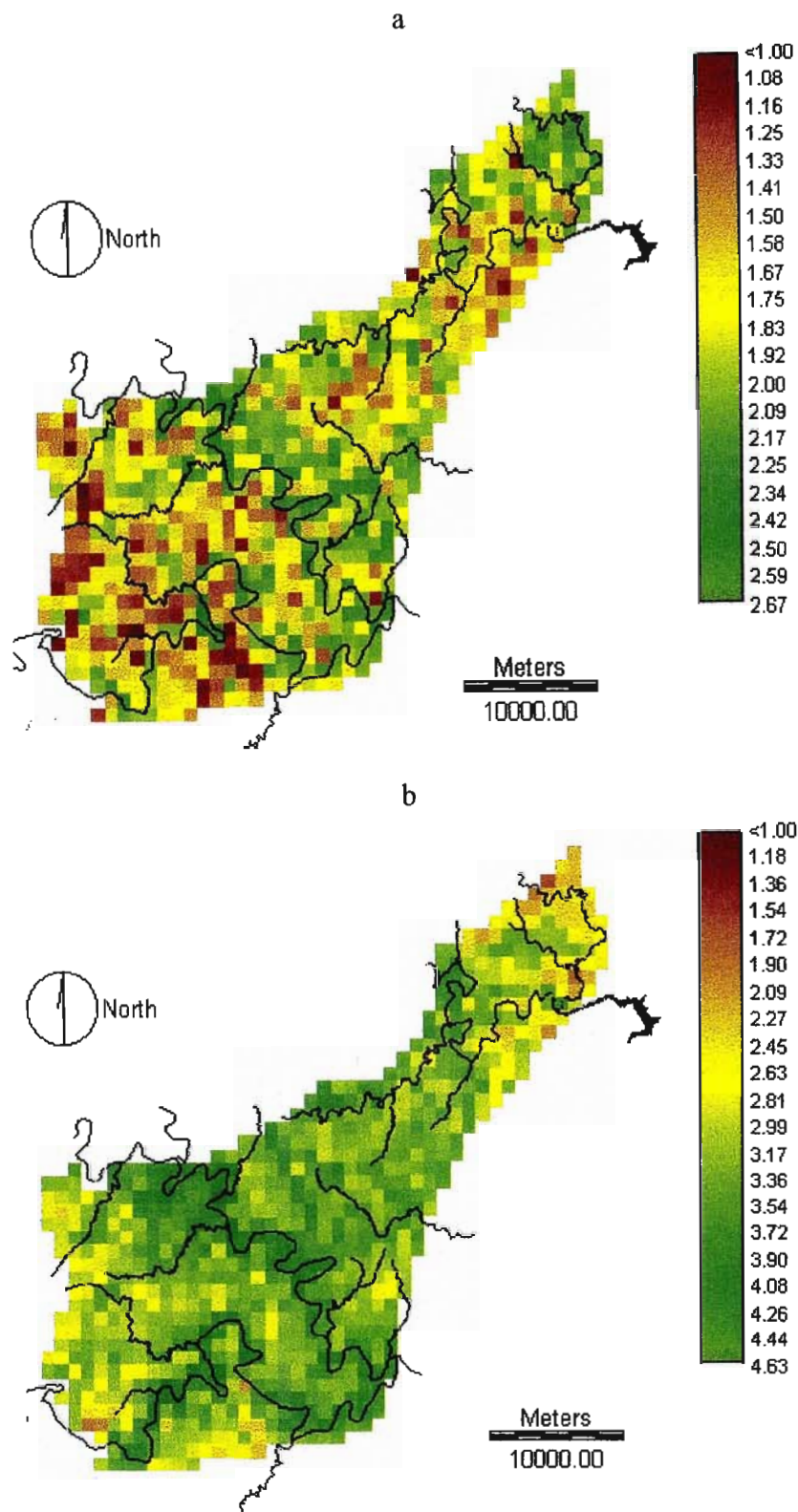
Figure 2.13: Average number of different vegetation classes per 1km² grid cell derived from a: the 1975 vegetation map and b: the 1996 vegetation map. Main river systems are shown in black.

Owing to the nature in which lions catch their prey, ie stalking followed by a rush, it is necessary that they utilize any cover available to them in order to get close to their quarry (Kruuk, 1986; Sunquist and Sunquist, 1989). The closer a lion is able to get to its prey without being seen, the more likely it is to have success in capturing the prey (Van Orsdol, 1984; Prins and Iason, 1989; Sunquist and Sunquist, 1989). There are various aspects relating to cover, namely bush/shrub cover/density, grass length and brokenness of terrain (Funston, Mills and Biggs, 1999; Van Orsdol, 1984; Prins and Iason, 1989). With regards grass length, in very short grassland areas it is difficult for lions to approach their prey under cover (Van Orsdol, 1984; Schaller, 1972). Very long grass (>1.5 m in height) may have a similar effect on hunting success mainly because of a lack of visibility. In addition to this few herbivores, including bulk grazers who favor grazing in tall grass areas, are found in grasslands characterized by a very tall (>1.5 m) sward as has been noted in HUP (D. Balfour, pers. comm.).

In the KNP it was found that male lions had better hunting success in moderate to dense woody vegetation and in medium to long grass, than they did in the open or short grass areas, while female hunting success was significantly affected by grass height but not by shrub cover (Funston, Mills and Biggs, 1999). Similarly, Prins and Iason (1989) found that lion hunting success greatly increased in the ecotone between open grassland and woodlands/thickets. They speculated that in the evenings, lions, under cover of the bush associated with woodlands/thickets wait for buffalo (*Syncerus caffer*) to move from the open short grassland areas to the woodland areas.

In the Queen Elizabeth National Park (Uganda) it was found that both increasing grass height (up to 0.8 m) and bush cover improved hunting success, with bush cover being of greatest importance in uniformly short grass areas (van Orsdol, 1984).

Schaller (1972) observed similar influences of bush density and grass length on hunting

success in the Serengeti. In addition to this, extremely dense bush areas could be less suitable for hunting than areas with moderate bush density (Prins and Iason, 1989), although as stated by Prins and Iason (1989), their conclusions should be viewed tentatively. No data on grass length or bush density within the reserve exist which precludes testing the hypotheses that grass length and bush density affect choices of suitable areas for territory and home range establishment.

The above discussion has served to illustrate that vegetation structure plays an important role in lion ecology and could influence where lions choose to locate territories. Classifications of vegetation, in this study, have been based on Phillips' (1973) general physiognomic classification which is explained below. As such there is a distinction between open and closed woodland, but there is no differentiation between dense thicket and open thicket for instance. The objective was however to arrive at a simple, informative and comparable vegetation classification. This has largely been achieved and should provide a platform from which general habitat preferences can be ascertained.

The use of cover is also of importance to lionesses who conceal their newly born cubs until they are at least one month (four to six weeks) old (Packer *et al.* 1990). However, in the context of HUP, with large portions of the reserve comprising thick bush and abundant cover for denning sites, it was decided to exclude shelter from the study.

It is recognised that the simplification of both vegetation maps to the same five basic categories (at a 1km grid scale) will result in some degree of error and loss of information (Bellehumeur and Legendre, 1998). This is largely unavoidable, although by calculating the percentage cover of each vegetation type per 1km^2 grid cell, as opposed to calculating a mean or median vegetation value per grid cell, decreases the error associated with such areal generalization. Error may have occurred in the process of re-classifying Meyer's (1996) vegetation map to a set of independent physiognomic classes which, while they formed the basis of the 1975 vegetation

classification, were not used at all in the 1996 classification. A comparison of the two maps (Fig. 2.14) shows a distinct change in the amounts of thicket (increased) and open woodland (declined). There has also been an increase in the proportion of forest although this is not as pronounced as that shown by thicket.

This appears to be consistent with the general trend, as a result of bush encroachment, toward closed woodland and forest which has been recorded in the reserve (Watson, 1995). These findings suggest that the vegetation status depicted in the present study may be reasonably accurate, even though classifications were generalized.

Prey distribution in HUP has been illustrated (Fig. 2.15). Food is arguably the most important environmental factor in determining lion habitat preferences (Mills and Gorman, 1997). There are a number of aspects to take into account namely: prey density, spatial and temporal distribution, prey quality, size and defences, all of which affect predator-prey interactions and the ease with which lions are able to catch their quarry (Sunquist and Sunquist, 1989). In general the preferred prey species appear to be buffalo, zebra (*Equus burchelli*) and wildebeest (Maddock *et al.*, 1996; Mills and Gorman, 1997). It is well known, also, that lions, particularly females in groups and adult males, show a preference for large, or medium to large, prey species (Rudnai, 1974; Packer, 1986; Ruggiero, 1991; Funston *et al.*, 1998). The reasons why females in groups capture larger prey could be related to two factors, firstly, the more lions there are in a hunt the less chance of injury there is, particularly when catching larger animals (Packer, 1986). Secondly, a larger carcass is able to feed more lions, thus it would not benefit females in groups to catch smaller prey since each lion would not obtain enough meat (Caraco and Wolf, 1975; Packer, 1986; Sunquist and Sunquist, 1989). It must be stressed, however, that although female lions prefer larger prey, the abundance of such prey may affect whether or not they are hunted frequently (Rudnai, 1974; Prins and Iason, 1989; Sunquist and
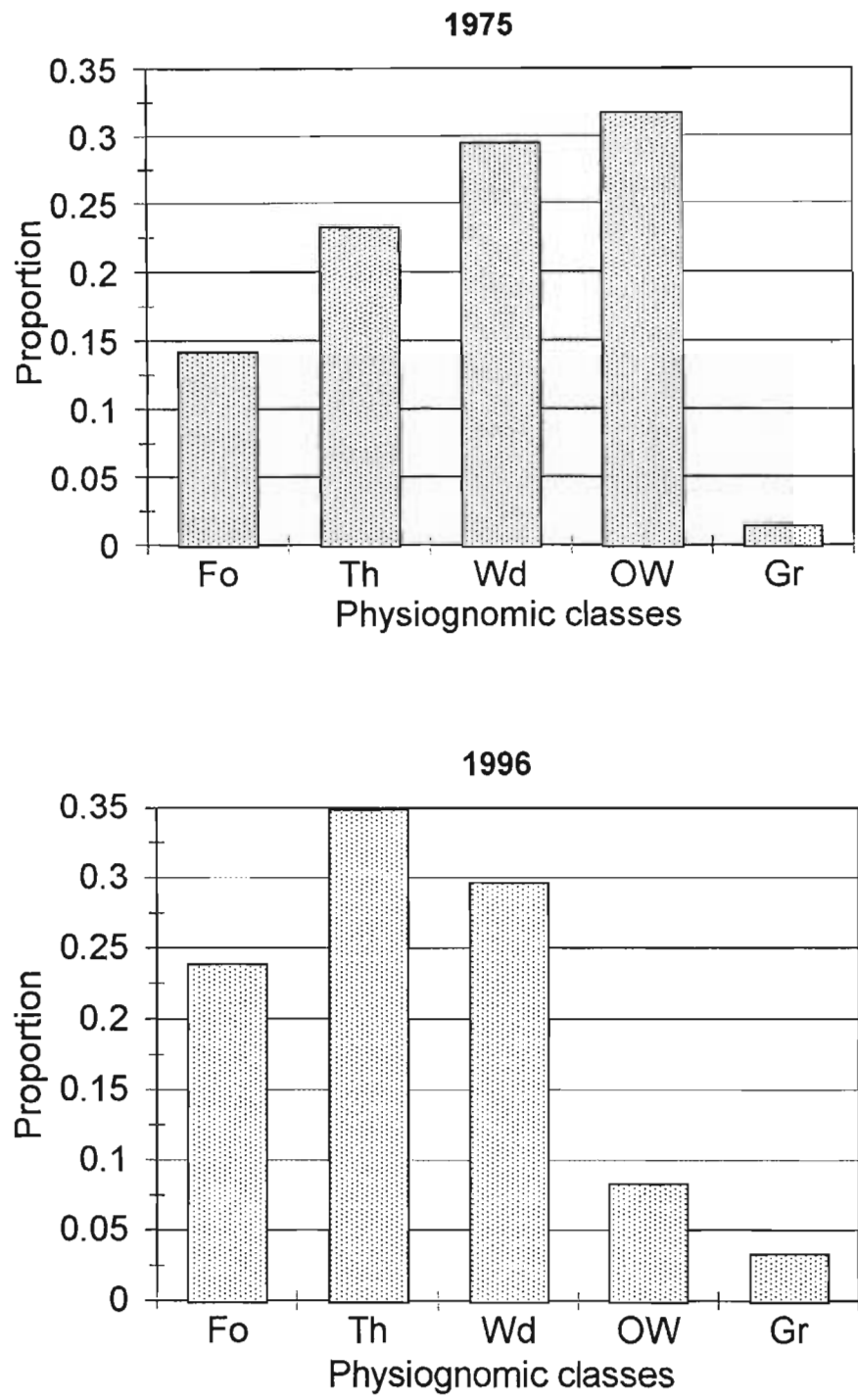
1975

1996

Figure 2.14: Comparison of two histograms showing the physiognomic composition of vegetation in HUP for 1975 and 1996 respectively. (Abbreviations are described as follows : Fo = forest, Th = thicket, Wd = woodland, OW = open woodland, Gr = grassland.)
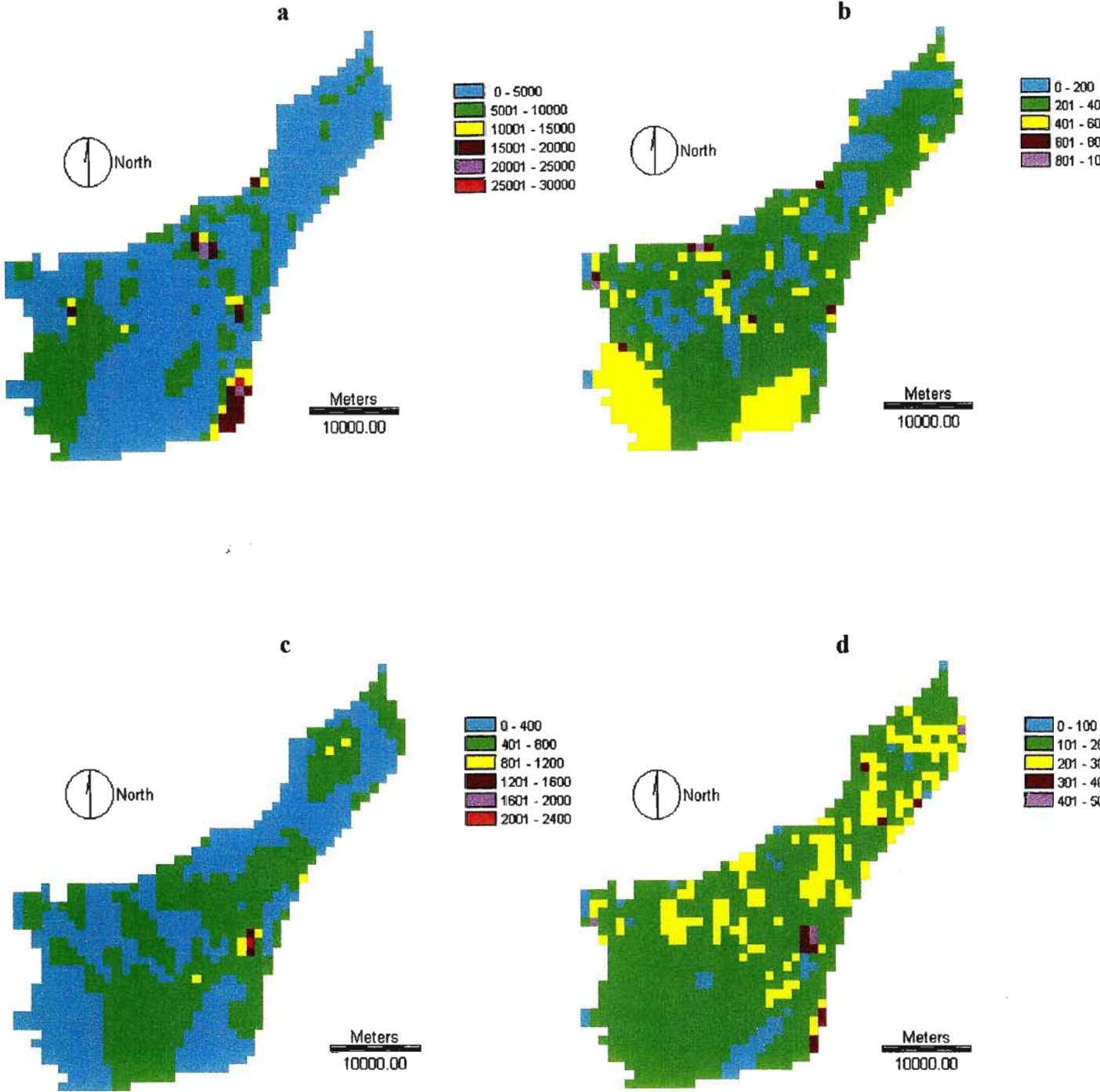
Figure 2.15 (a-d): Prey available to lions expressed as kg of meat per grid cell (kg/km^2) for each of seven different preferred prey species: (a) Buffalo; (b) Impala; (c) Kudu; (d) Nyala. Continued overleaf.

e

Legend (e):
- 0 - 30
- 31 - 60
- 61 - 90
- 91 - 120
- 121 - 150
- 151 - 180

f

Legend (f):
- 0 - 700
- 701 - 1400
- 1401 - 210
- 2101 - 280
- 2801 - 350
- 3501 - 420

g

Legend (g):
- 0 - 1000
- 1001 - 2000
- 2001 - 3000
- 3001 - 4000
- 4001 - 5000
- 5001 - 6000

h

Legend (h):
- 0 - 5000
- 5001 - 1
- 10001 - 1
- 15001 - 2
- 20001 - 2
- 25001 - 3

Meters 10000.00

Figure 2.15 (e-h): Prey available to lions expressed as kg of meat per grid cell (kg/km^2) for each of seven different preferred prey species: (e) Warthog; (f) Wildebeest; (g) Zebra; (h) Total. Total prey available represents the sum of values per grid cell of all seven species.

Sunquist, 1989). Lions as a consequence hunt the more numerically abundant larger prey species (Sunquist and Sunquist, 1989). This preference for larger prey could therefore influence where female lions locate their home ranges (Mills and Gorman, 1997).

The situation may be somewhat different with regards males. In a study conducted in the Kruger National Park (KNP) it was found that territorial males encountered impala (*Aepyceros melampus*) more often and in thicker bush, 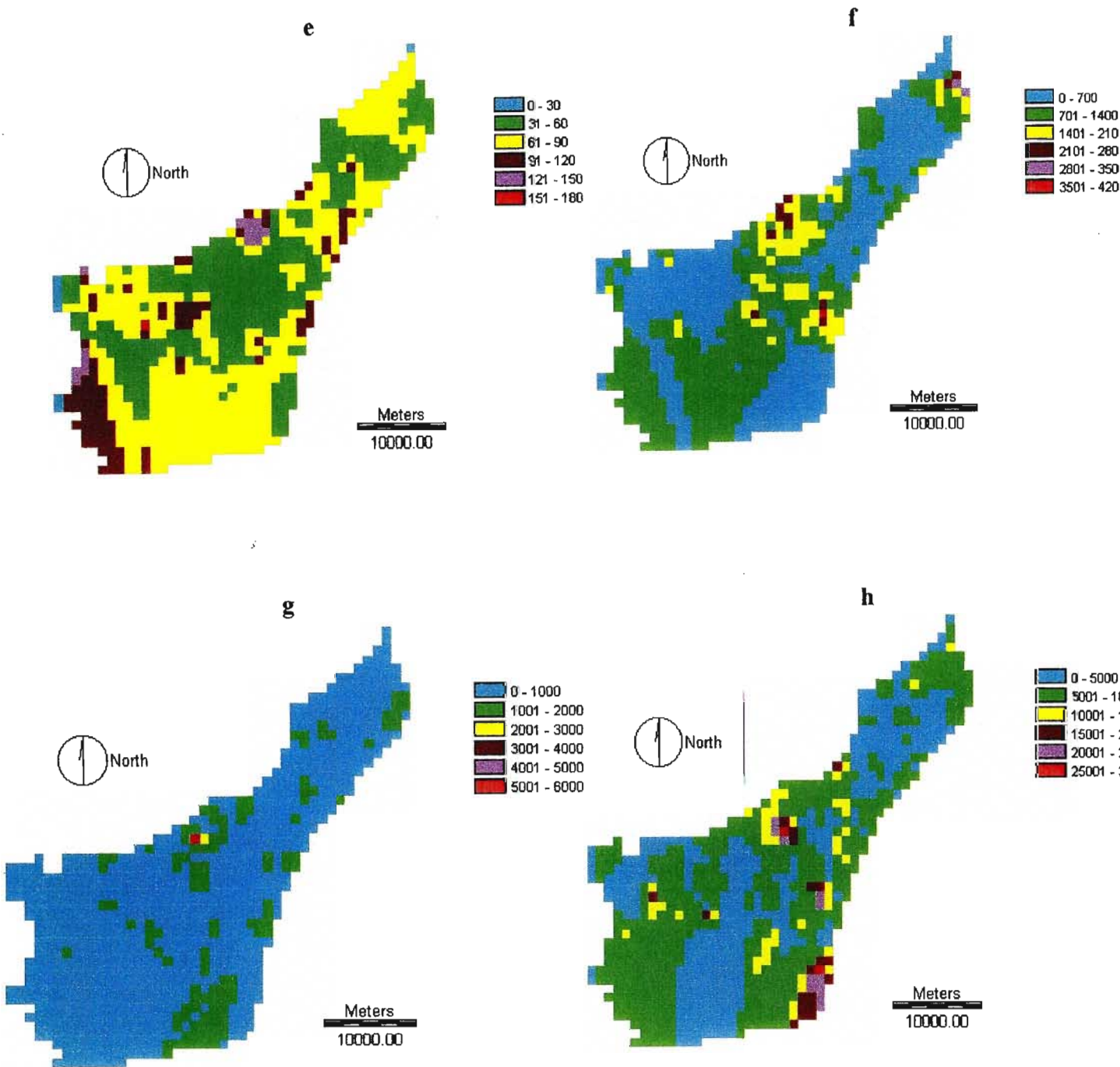simply because in the course of walking territory boundaries they passed through a great number of different habitats (Funston *et al.* 1998). As a result of territorial maintenance these males spent more time in dense bush than either pride females or non-territorial males and they encountered impala by chance rather than by selecting habitats where appropriate prey was located (Funston *et al.* 1998). Once again, the differences in behaviour of pride females and territorial males may be important when considering and determining possible optimal home range areas and habitat selection.

In a study conducted in the KNP it was found that vulnerability rather than abundance may have been the more important factor in terms of predation (Mills, Biggs and Whyte, 1995). Vulnerability relates primarily to prey defences against predation. Van Orsdol (1984) found that prey which occur either in very large groups or on their own are vulnerable to predation, certain prey types may be more vulnerable to predation with prey vigilance (watching for predators) also having a possible impact. Of these, however, only prey group size was found to be significant in terms of increasing predation risk (Van Orsdol, 1984). Examples of the importance of vulnerability include: buffalo are weakened under drought conditions and are, as a consequence, more easily caught at these times, while wildebeest, during wet seasons, experience fragmentation of their herds (Mills *et al.* 1995). This, coupled with an increase in grass cover, makes them more vulnerable to predation during the wet season (Mills *et al.* 1995).

It seems that should there be a particular herbivore that is present in high abundance, which is vulnerable to predation, and is medium to large in size, then these animals would tend to be preyed upon by lions. Current predation theory includes the concept of density dependant predation which describes the manner in which predators differentially select the common prey species and may then switch to other more common species (Endler, 1986). Part of this process may involve an increase in searching efficiency such that predators learn to search for specific prey items (learning a searching image) while overlooking other, less abundant prey types, with the result that the more common prey type comprises a larger part of the diet than would be expected on the basis of availability (Curio, 1976; Taylor, 1984). These approaches complement the primary consideration in this thesis which is that animals make choices regarding the perceived profitability of a particular area. Switching between prey species, therefore, will occur due to a rational choice of a "best" patch being made (Taylor, 1984). Such choices are based on prey density and type which provide measurable and testable components of prey profitability. Choices of most profitable patches and/or prey types occur on a continual basis and such choices should be applicable at greater scales of both space and time. It is therefore possible that lions will select territories on the basis of perceived prey profitability status, and while they do not switch territories, they may switch between patches within a particular territory or home range.

In terms of data collection (line transects), there are a number of stages at which errors in the locations of observations could occur. One example is that a transect which is drawn straight on a map, is almost certainly not straight on the ground. Such occurrences may at times introduce fairly substantial error, however since analyses are being conducted at a $1km^2$ resolution, it is likely that these differences will be negated.

Spatially explicit prey data are also only available for the years 1996 and 1998. While prey

within the reserve are non-migratory, and fairly evenly distributed (owing to the even distribution of water) (Anderson, 1981), it is highly probable that species distributions at present are not the same as they were 25 years ago. The tendency for succession in the reserve to result in woody plant communities has resulted in a decline in population of several ungulate species (Brooks & Macdonald, 1983). It is also probable the these vegetation changes have altered the distribution of herbivores. As a result, it is not possible to use the existing prey data for the period 1973 to 1984.

Another fault with the transect data is that no data exist for the wilderness area located in the South-Eastern corner of the reserve (Fig. 2.4). Interpolated values are, as a consequence, not representative of the actual prey occurring in the area.

The distribution and density of roads and other local infrastructural factors may affect selection of home range areas. It was found in South Texas that coyotes (*Canis latrans*) and bobcats were not adversely affected by roads and fence lines but in fact used these features as travel lines and hunting areas in their newly established home ranges (Bradley and Fagre, 1988).

Maps showing the presence/absence of public and management roads (Fig. 2.16), presence/absence of road intersections (Fig. 2.17) and distance from roads (Fig. 2.18) have been calculated.

It is apparent that roads have a definite effect on the frequency with which lions are seen as is illustrated by the preliminary analysis which was conducted (Fig. 2.19).

The increase in the number of sightings as distance from roads declines is attributable to the following: 1) an increase in areal proportion of the distance categories closer to roads as shown in Fig. 2.19; 2) observers travel more often on roads, even though data were obtained via ranger foot patrols which were not limited to roads; 3) lions exhibit a genuine preference for traveling on roads.
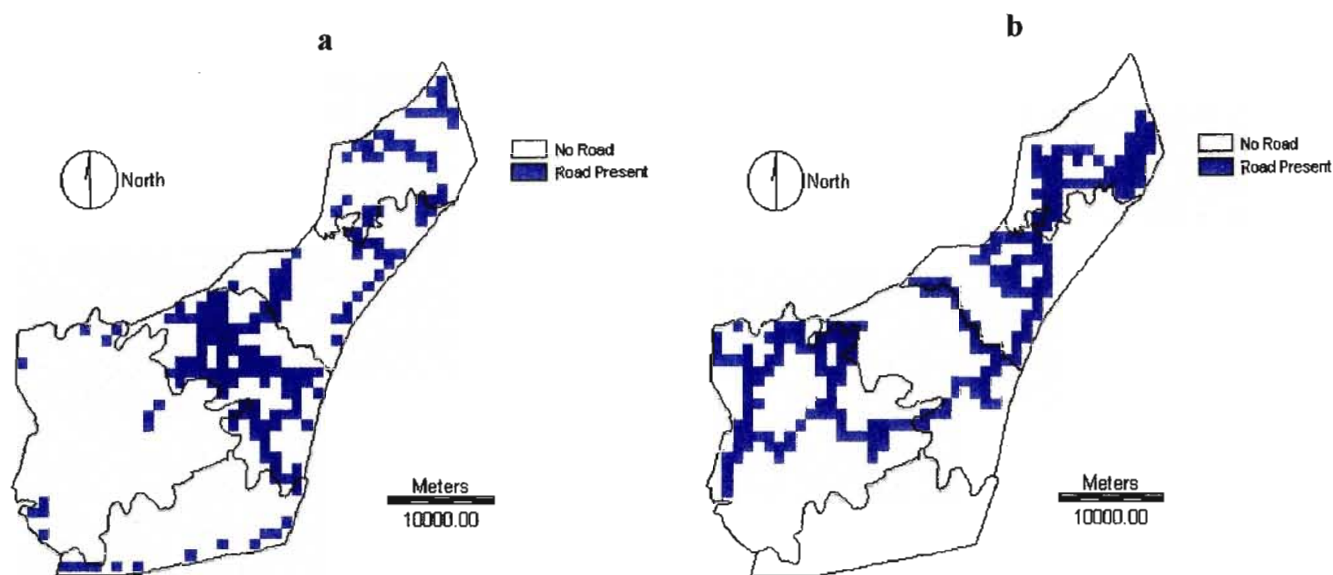
Figure 2.16: Presence/absence of (a) management and (b) public roads (per grid cell) in HUP. (Gaps between grid cells containing roads occur due to the fact that, on the boundary, cells which fell only partially within the reserve were deleted, as explained previously in the chapter)
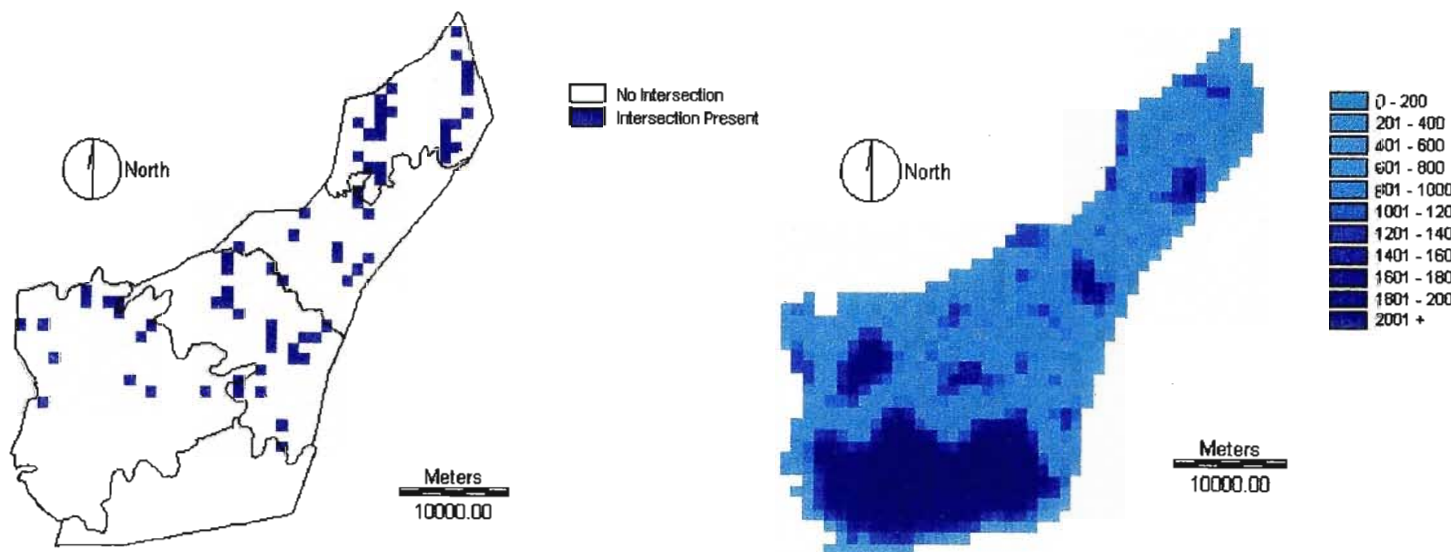
Figure 2.17: Presence/absence of road intersections per grid cell in HUP. (Intersections of management tracks with public roads have been included.)

Figure 2.18: Distance (m) from roads in HUP.
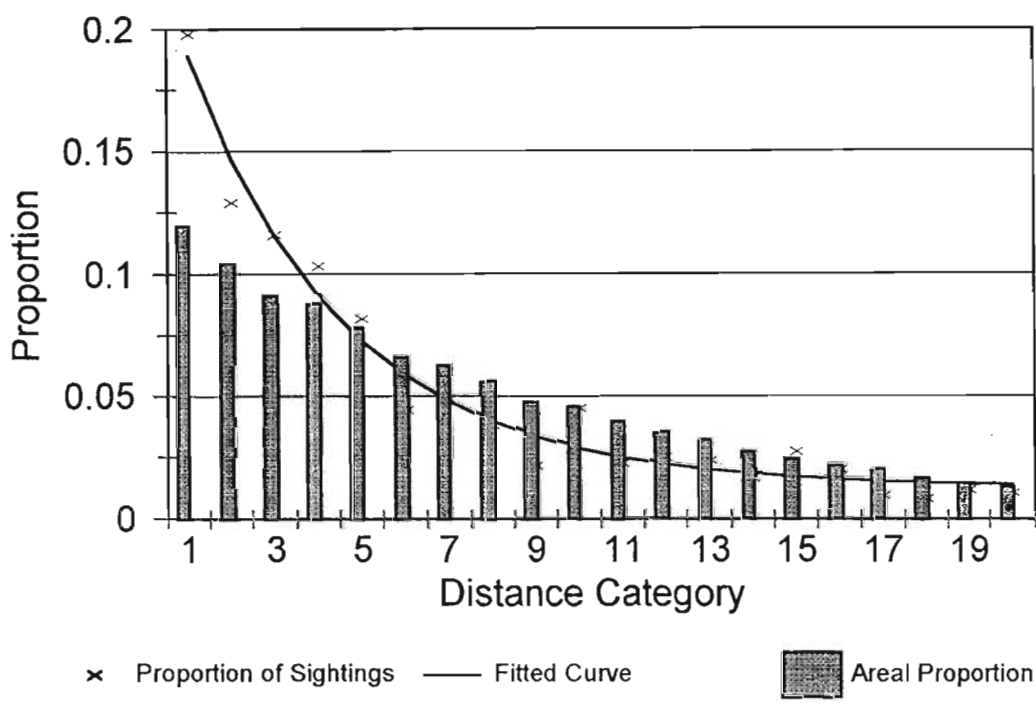
Figure 2.19: Graph showing the relationship between proportion of sightings (per distance category) and distance from roads as a category (1=1-100m, 2=100-200m etc). The proportion of area within the reserve comprising each distance category class has been illustrated. [the fitted curve equation reads as follows: $y = 11.03 + 194.9*0.7626^x$ and accounts for 96.5% of the variation in the data]

It is not possible to ascertain what proportion of lion sightings were made on foot or alternatively, from a vehicle hence the extent of the bias toward sightings made on or from roads cannot be established.

A preference for traveling on roads, particularly in Hluhluwe, has previously been alluded to, when it was noted during a lion monitoring programme that following seasons of high rainfall and consequent bush thickening, lions were seen more often on roads than was previously the case (Venter & Whateley, 1985).

Thus far, competition only from other conspecifics has been mentioned. However, there is a considerable amount of animosity displayed between lions and hyaenas, although it is rare for hyaenas to win a contest for a kill (Packer, 1986; Packer *et al.* 1990). Cooper (1991) has suggested that hyaenas have often been ignored as a factor affecting lion home ranges because they are thought to

play only a minor role in lion behavioural ecology. This may be true when considering prides with males in attendance however in terms of small groups of nomadic lions or females it has been found that when lions are outnumbered, four (or more) hyaenas to one lion, hyaenas were able to drive lions off a kill (Cooper, 1991).

This situation is thought to be aggravated in more open habitats where kills are easily observed (Funston et al. 1998). The density of spotted hyaenas relative to lions may have important consequences relating to the defence of kills and as a result may cause males to be associated more often with their pride females (Funston, et al. 1998). The presence of a high density of hyaenas is also thought to affect lion grouping patterns (Cooper, 1991). Since hyaenas do have some affect on lions it may not be unreasonable to assume that these animals could influence lion distribution, specifically home range and territory location. It would therefore be expected that lions would not locate their home ranges/territories close to the den sites of hyaenas, especially as they (lions) use their home ranges/territories for reproduction and hence cub rearing (Heinsohn and Packer, 1995). It is known that hyaenas will kill and eat lion cubs (and even adults), should they get the opportunity (Schaller, 1972).

Maps showing the distance to hyaena dens (Fig. 2.20) and presence/absence of hyaena dens (Fig. 2.21) have been compiled.

The use of current den location data in testing hypotheses applicable to long term processes may be problematic. The mean period of den occupancy in HUP is unclear. It has been reported that the mean period of occupancy of dens is only 1.5 months for spotted hyaena's in the Kalahari, with den sites seldom being used more than once (Mills, 1990). Exceptions occur with favorite den sites, one of which was used six times in nine years (Mills, 1990). In the Kruger National Park spotted hyaena may remain at a particular den for over six months, if not several years (Mills, 1990). Kruuk
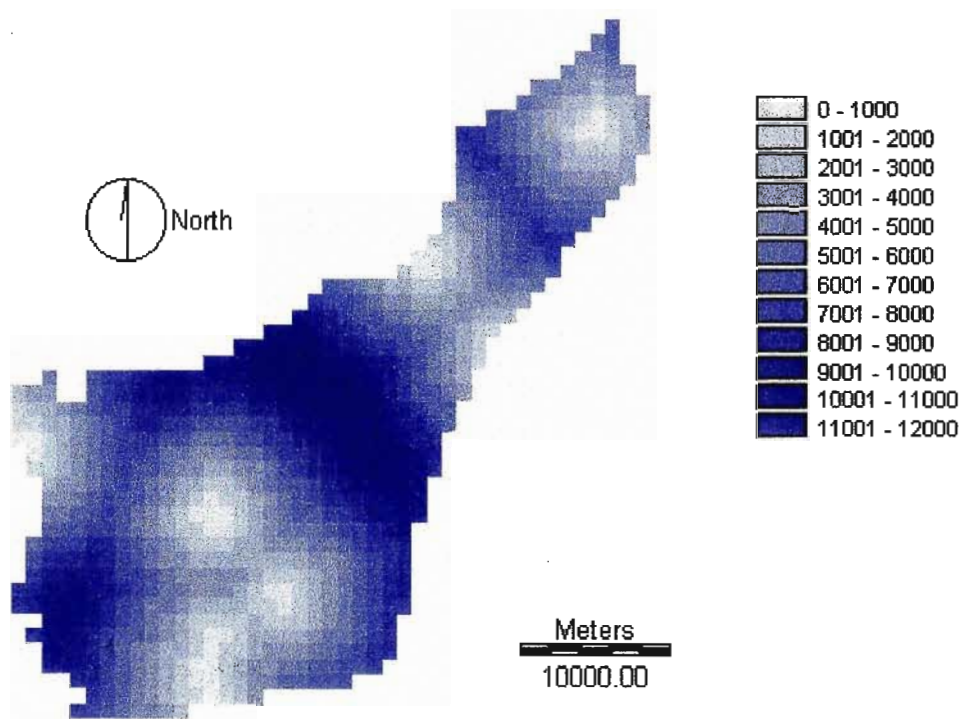
Figure 2.20: Distance (in meters) from hyaena dens in HUP.

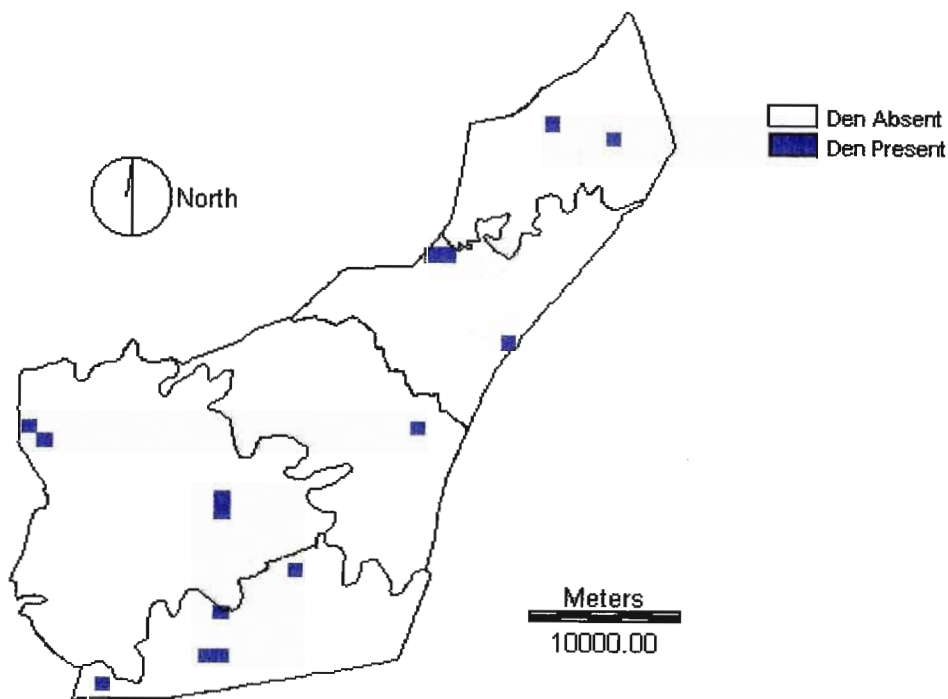Figure 2.21: Presence/absence of Hyaena dens per grid cell in HUP.

(1972) states that, in the Serengeti and Ngorongoro Crater, large dens may remain in use for several years while small dens are only used temporarily. In conclusion, current hyaena den data in HUP should only be used in analyses of the 1985-1999 lion data and it must be remembered that these (hyaena) data are of questionable quality.

Chapter 3

General Lion Spatial Socio-Ecology in HUP

3.1 Introduction

Before commencing with the modelling process, it is necessary to first gain a better understanding of lion biology within the reserve given the associated variation (in lion biology) which exists within HUP. In doing this, a more complete overview of both lion and environmental data used in generating models, will be achieved. The purpose of this chapter is thus observational and descriptive in nature.

Lions were first introduced to HUP (the then Umfolozi Game Reserve) in 1965 when two females and three cubs were re-located to the reserve (Steele, 1970). In addition to these animals, a lone male was also resident in the reserve at the time, having appeared some years prior to this re-introduction (Steele, 1970). In 1974 a lion project was started and by September 1974, it was established that the population had increased to a minimum of 128 animals, with 67 of these being less than two years old (Anderson, 1974). It was at this stage that the need to address lion break outs and consequent stock killings was initiated. Culling was aimed primarily at those animals thought most likely to exhibit tendencies for moving out of the reserve namely sub-adult males and to a lesser extent sub-adult females. Between the years 1974 and 1994, the lion population size in HUP has exhibited large fluctuations (between 64 and 142 (Maddock *et al.*, 1996)) with the accuracy of the mark-recapture techniques used to determine population size being questioned (Sandwith and Whateley, 1987). The lion population in HUP for the monitoring period 1996/7 was calculated to be approximately 85 animals (Balfour, Howison and van Zyl, 1997).

Throughout the entire study period (i.e. from 1973 to 1999) while the number of prides in the reserve has fluctuated, pride areas have remained largely constant and have almost always

been centred on one or several of the main rivers, which was first noted by Anderson (1975). It was further noted that in areas where there were no major rivers (hence no permanent water) no resident prides were present, as was the case in the central corridor region (southern Nqumeni and northern Masinda sections) (Anderson, 1975). In addition to this, it appears that colonisation of the northern areas of Hluhluwe has been very slow in taking place, both in the past (Anderson, 1974, 1975) and in recent times, and has also been affected by the culling of almost all lion in this area during the late eighties and early nineties (Maddock *et al.*, 1996). The lion population of HUP, while it has been actively managed and selectively (culling sub-adults) restricted in size, nevertheless does seem to exhibit preferences for particular areas within the reserve. Given the dramatic vegetational and topographical differences between the five management sections, comparisons of grouping patterns among these sections will be both useful and informative in providing a general description of lion spatial socio-ecology within the reserve and some of the possible environmental mechanisms underlying these dynamics. It should be remembered that grouping patterns in lions are affected by a number of different social factors, as discussed in Chapter One, and are certainly not the result of environmental factors alone (van Orsdol *et al.* 1985; Packer *et al.* 1990). In addition to this, the differential culling which has taken place in HUP may also have affected grouping patterns in this particular context.

The previous two chapters have served to outline the two major components of this project namely the environmental factors under consideration and the lion variables, and manipulations thereof, which are required for the modelling process to take place. The primary objective of the current chapter is to report a basic description of historical lion spatial socio-ecology within the reserve. The aims are as follows: 1) to summarise lion grouping patterns per management section in HUP and test whether significant differences in grouping patterns occur between the management sections; 2) summarise environmental variables per management section;

3) provide a basic spatially structured description of lion biology in the reserve using the summaries of grouping patterns and environmental variables.

The raw lion data used here are identical to those described in Chapter Two, however no reductions to binary scale have been performed since the focus here is on descriptions of grouping patterns.

3.2 Materials and Methods

Lion data were extracted per section for each of the following four variables: adult females in mixed group sizes; adult males in mixed group sizes; cub group sizes; and number of cubs per adult female. This was done for both the 1973 - 1984 and 1985 - 1999 time periods using the ArcView INTERSECT THEME command found in the Xtools extension. In this manner, sightings occurring in each section (and for each time period) were isolated and saved as separate ArcView shape files with their attendant database files. The database files were then opened in Quattro Pro 8 where the relevant calculations and manipulations were made. Statistical analyses took place in Minitab 12.1 where Kruskal Wallis one way ANOVA was used to test for differences among the five management sections for each of the four variables chosen. Only four variables were utilized so as to avoid over analysing the data and the attendant alterations in significance levels which need to be made (Schork and Remington, 2000). Non-parametric ANOVA was chosen since the data were not normally distributed.

Habitat data were obtained using the EXTRACT command in Idrisi. In this manner, averages for each section for altitude, rainfall, distance from rivers, vegetation and, in the case of the 1985 - 1999 period, prey, were extracted. In order to illustrate the influence of these environmental factors on grouping patterns within the reserve, scatter plots (Appendix 4) have been provided which show the relationship between Kruskal Wallis rank (for each of the five

sections) and the corresponding average environmental value for each section. Kruskal Wallis rank was chosen since the measure of location used in this case (namely the median) was in many instances of equal value and would thus not serve to illustrate differences in location adequately.

Section abbreviations which occur throughout this chapter are as follows: Manzibomvu = 1; Nqumeni = 2; Masinda = 3; Mbhuzane = 4; Makhamisa = 5. A map showing the boundaries of these sections can be found in Chapter 2 (Fig. 2.1).

3.3 Results

3.3.1 Environmental data

To illustrate the differences in environmental conditions among the five sections in HUP, the average values derived for each environmental variable per section have been graphically represented. These illustrations serve merely to complement the spatial representations shown in Chapter 2. Variables which have been included are rainfall (Fig. 3.1), distance from rivers (Fig. 3.2), vegetation (Fig. 3.3) and prey (Fig. 3.4).

Rainfall is highest in the northern areas of the reserve, with Manzibomvu section receiving, on average, the highest amount. The primary reason for this is that the northern areas of the reserve are higher in altitude (see Chapter 2). Manzibomvu is also closest, on average, to main rivers while Nqumeni is furthest. It is questionable whether, at this scale, distance from main rivers is of importance in influencing lion grouping patterns. Another factor compounding this issue is that section boundaries in many instances are designated by main rivers.

With regards vegetation, general trends within the reserve have been discussed in Chapter 2. On a per section basis, several important aspects are noteworthy. Firstly, regarding the 1973 - 1984 time period: there is no open woodland present in either Manzibomvu or Nqumeni, with
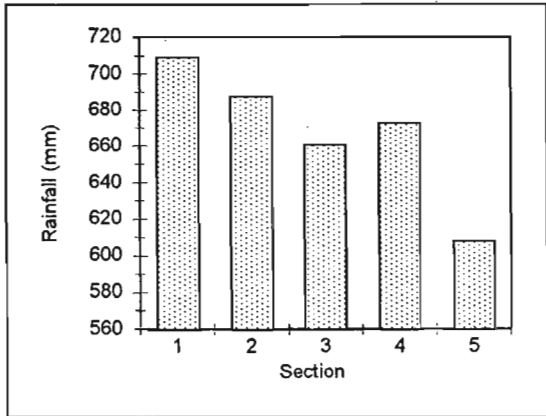
Figure 3.1: Average rainfall per section in HUP (See Chapter 2 for calculations).
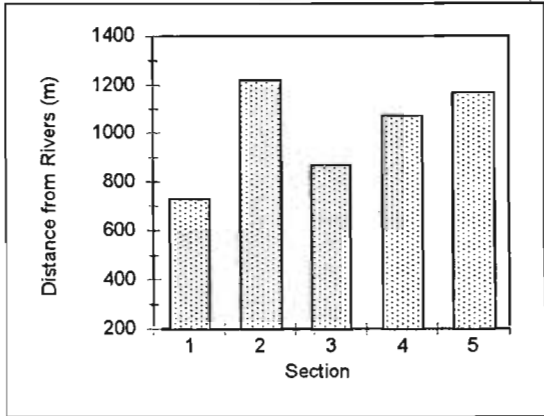
Figure 3.2: Average distance from main rivers per section in HUP

a
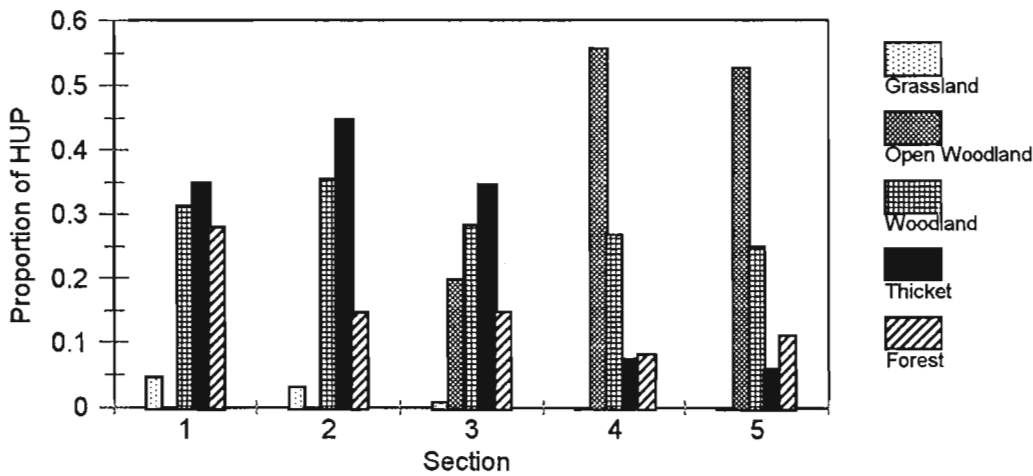
b
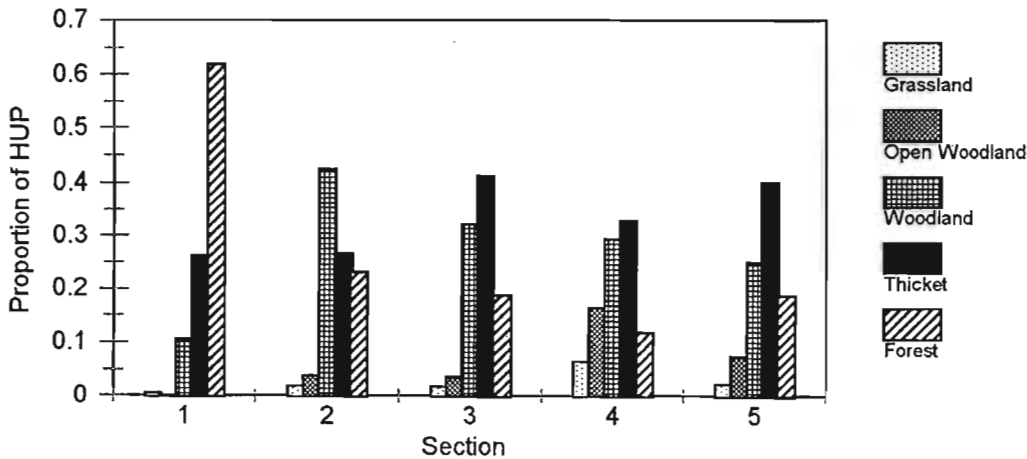
Figure 3.3: Vegetation composition per management section in HUP for the (a)1973 - 1984 time period and (b) 1985 - 1999 time period.
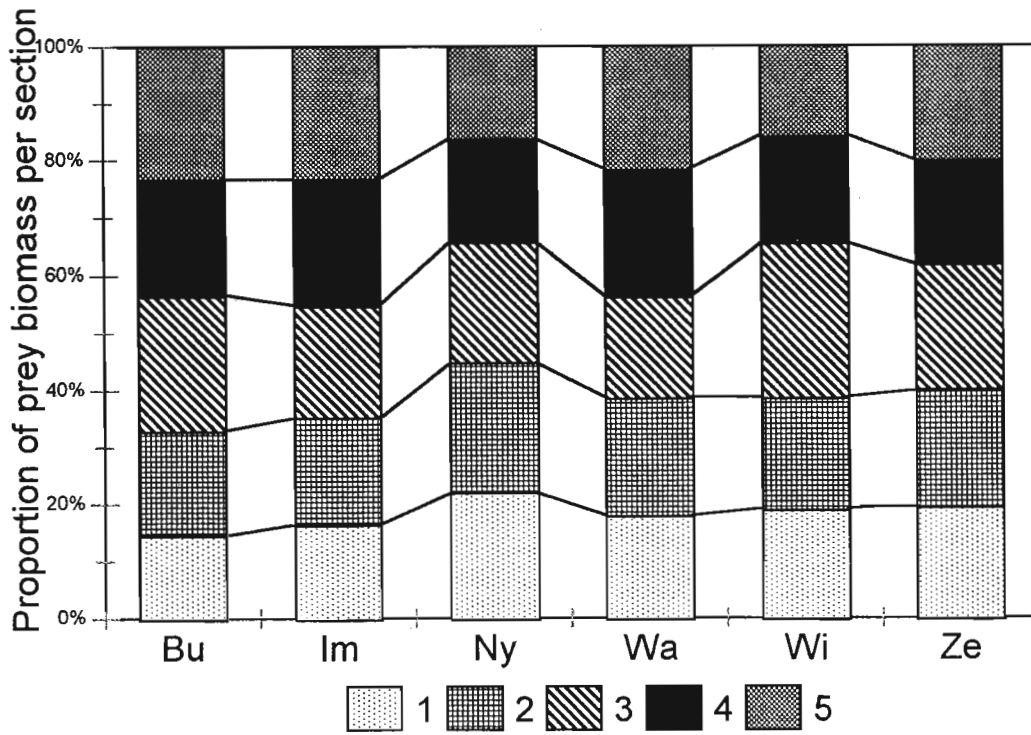
Figure 3.4: Prey biomass apportionment among the five management sections of HUP. Bu = buffalo; Im = impala; Ny = nyala; Wa = warthog; Wi = wildebeest; Ze = zebra.

most of the vegetation being woodland, thicket or forest. In contrast, open woodland comprises most of the vegetation in Mbhuzane and Makhamisa with relatively small proportions of thicket and forest being present. Masinda contains similar proportions of all vegetation types, although thicket and woodland do predominate. There is very little grassland in any of the sections.

The 1985 - 1999 period is somewhat different: In all sections barring Nqumeni, there has been an increase in thicket, such that Mbhuzane and Makhamisa have become dominated by thicket and woodland at the expense of open woodland. Masinda, Mbhuzane and Makhamisa all exhibit fairly similar vegetation compositions although Mbhuzane still contains the largest proportion of open woodland in the reserve. Manzibomvu is dominated by forest while Nqumeni is dominated by woodland.

In general, prey within the reserve appear to be fairly evenly distributed among the different sections as has been noted in the past (Anderson, 1981). Some noteworthy differences are as follows: Manzibomvu and to a lesser extent Nqumeni both have low proportions of Buffalo

and Impala, while both of these sections contain high proportions of Nyala. Both Masinda and

Makhamisa contain high proportions of Buffalo. Masinda also has the largest proportion of

Wildebeest, whilst having relatively low proportions of Impala and Warthog. Makhamisa in

contrast contains higher numbers of Impala and relatively few Wildebeest.

3.3.2 Lion grouping patterns

Adult females in mixed groups

The results of all Kruskal Wallis tests conducted can be found in Table 3.1. There were

significant differences in group sizes for both the 1973 - 1984 period (p<0.001) and the 1985 -

1999 period (p=0.001). Median group sizes were highest in Mbhuzane and Makhamisa for both

the 1973 - 1984 (Fig. 3.5) and 1985 - 1999 (Fig. 3.6) period. The median groups size for Masinda

declined from 2 during the 1973 - 1984 period to 1 during the 1985 - 1999 period. Comparisons

of the female data with environmental variables yield the following (See Appendix 4 for scatter

plots): Group sizes were larger in areas where open woodland predominated although this

situation is not as clear during the 1985 - 1999 period. Group sizes were largest in sections

containing minimal thicket during the 1973 - 1984 period although during the 1985 - 1999 period

this was not in evidence. Female group size declines with increasing rainfall. In terms of prey,

there does not appear to be an increase in group size with increasing buffalo biomass, although

regarding impala, the sections with the highest groups sizes also had the largest impala biomass.

A strong trend toward smaller group sizes with increasing nyala biomass is in evidence while

there does not appear to be a relationship between group size and warthog biomass, although as

with impala, sections with the two highest group sizes (Mbhuzane and Makhamisa) are associated

with highest warthog biomass. Female group size declines with increasing wildebeest biomass

although no such relationship is exhibited between group size and zebra biomass.

Table 3.1: Summary of the Kruskal Wallis one way ANOVA tests which were conducted for the purpose of identifying whether significant differences between group sizes existed among the five management sections occurring within HUP. Tests were conducted for each of the two time periods in question.

Time Period	Age/Sex category[1]	N1[2]	N2	N3	N4	N5	P_{adj} value[3]
1973 - 1984	AFM	167	171	106	227	118	0.000
1973 - 1984	AMM	113	121	76	166	99	0.001
1973 - 1984	Cubs	85	41	36	86	49	0.064
1973 - 1984	Cubs/Female	64	34	33	78	45	0.221
1985 - 1999	AFM	47	99	46	126	91	0.001
1985 - 1999	AMM	37	87	39	95	76	0.000
1985 - 1999	Cubs	23	17	12	33	33	0.009
1985 - 1999	Cubs/Female	22	15	11	31	30	0.239

1: AFM = Adult Females in Mixed Groups; AMM = Adult Males in Mixed Groups.
2: N1...N5 are the sample sizes for each management section where 1 = Manzibomvu; 2 = Nqumeni; 3 = Masinda; 4 = Mbuzane; 5 = Makhamisa.
3: P_{adj} represents the P value adjusted for ties.

Adult males in mixed groups

Significant differences in group sizes existed among the different management sections for both the 1973 - 1984 (p = 0.001) and 1985 - 1999 (p<0.001) time period (Table 3.1). This was despite the fact that median group sizes were all equal to one during 1973 - 1984 (Fig. 3.5) while median values during 1985 - 1999 were also all equal to one except for Makhamisa section which had a value of two (Fig. 3.6).
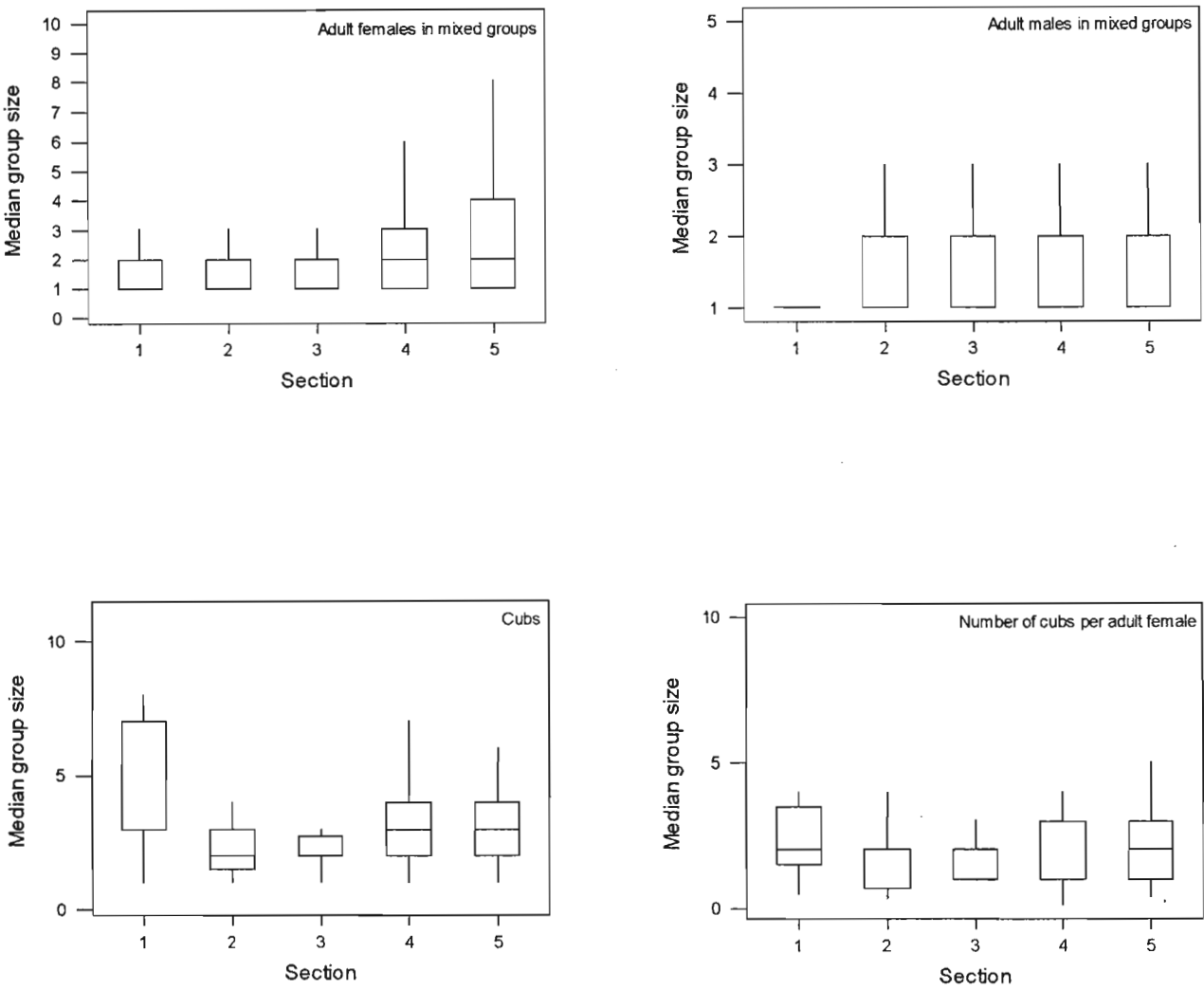
Figure 3.6: Lion group sizes for the 1985-1999 time period as shown per management section for: adult females in mixed groups, adult males in mixed groups, cubs and number of cubs per female. Figures illustrate the median, first and third quartiles and the range of the data.

Descriptions of grouping patterns in conjunction with environmental data yield the following (See Appendix 4): Open woodland did not appear to influence group sizes during the entire study period as was true for both Woodland and Thicket, although a slight trend toward increased group sizes with increasing proportion of Thicket is apparent for the 1985 - 1999 data. There is no relationship between distance from rivers and group size. A decrease in group size with increasing rainfall for both time periods in question is in evidence. There is an increase in group size with increasing buffalo and impala biomass, while group sizes are not influenced by nyala, warthog, wildebeest or zebra biomass.

Cubs

Cub group sizes were not significantly different (p=0.064) among different sections for the 1973 - 1984 data set, while significant differences (p=0.009) were found to exist during the 1985 - 1999 period. Median group sizes are illustrated for the 1973 - 1984 period (Fig.3.5) and the 1985 - 1999 period (Fig. 3.6) during which median group sizes of three were found to occur in Manzibomvu, Mbhuzane and Makhamisa, while values of two for both Nqumeni and Masinda were found (Fig. 3.6). Since no significant differences were found to exist among the different management sections for the 1973 - 1984 data, no environmental relationships will be addressed.

The only observable pattern describing cub group size and vegetation involves Woodland, where increasing proportions of Woodland correspond to a decrease in group size. Neither Open Woodland nor Thicket showed any clear influence on cub group size. Distance from rivers does not appear to affect group size either although it should be borne in mind, for both this and all previous observations, that data for sections one and two (Manzibomvu and Nqumeni) for the 1985 - 1999 period may be erroneous as mentioned earlier. Neither rainfall nor prey were observed to influence cub grouping patterns although an increase in Impala biomass does result

in an increase in group size, with the exception of Manzibomvu section. It may be that nyala are more important in this section in influencing group size.

Cubs per adult female

No significant differences among sections for either time period existed (Table 3.1). There were therefore no differences in reproductive output/productivity among the management sections in HUP throughout the study period. Median values are illustrated in Figures 3.5 (1973 - 984) and 3.6 (1985 - 1999).

3.4 Discussion

Lion grouping patterns are influenced by a number of both environmental and social factors such as prey size, availability, habitat, capture efficiency, territorial defence, co-operative cub defence and creche formation and kinship (Caraco and Wolf, 1975; van Orsdol *et al.*, 1985; Packer *et al.*, 1987; Packer *et al.*, 1990).

The finding that significant differences exist between grouping patterns in the five management sections of HUP would indicate that the aforementioned environmental and social factors shaping grouping patterns exert differing influences within the reserve.

Social factors influencing grouping patterns in HUP cannot be accurately ascertained owing to the nature of the data which have been used. As mentioned previously, however, most prides in HUP have established themselves in the southern regions of the reserve, namely Masinda, Mbhuzane and Makhamisa sections, a trend which has been persistent throughout the study period and which has been described by the delimitations of pride boundaries calculated throughout the time period in question (Anderson, 1975, 1976; Maddock *et al.*, 1996). It therefore appears that lion activity is generally greater in the southern sections of the reserve than

in the northern sections. This coupled with the fact that the southern sections of the reserve are comprised of more open vegetation (even though this situation has changed over the study period) and less hilly topography may result in a "higher visibility" situation where interaction (and possibly confrontation and conflict) with other lions occurs more frequently. (The presence of open habitats has been proposed as one of the factors promoting the evolution of group living in lions (Packer, 1986)). With an increased risk of conflict, it may be beneficial for lions to form larger groups since groups of females are more effective in defending cubs from infanticidal males and also suffer lower rates of pride takeovers by males (Packer *et al.*, 1990). Inter-group conflicts between females are also most often won by the larger group (Packer *et al.*, 1990). The presence of high abundances of larger prey in the southern areas may promote females living in larger groups in these areas, in accordance with Packer *et al* (1990). Group sizes have been found to increase with increasing prey body size (Caraco and Wolf, 1975; van Orsdol, 1982). The converse of this may also be true for HUP as was illustrated by the marked downward trend in group size with increasing nyala biomass. Thus in the northern areas of the reserve, where vegetation and cover are both in extreme abundance, along with a corresponding increasing abundance of small to medium prey species, smaller adult female group sizes are favoured, since there is no nutritional disadvantage to foraging alone as has been shown by Packer *et al.* (1987, 1990) and intraspecific competition is unlikely to be as high as it is in the southern sections (Mbhuzane, Masinda and Makhamisa).

The presence of high abundances of buffalo and impala in the southern sections also promotes increased group sizes of adult males in mixed groups. Male coalitions exhibit greater reproductive success with increasing coalition size (Packer *et al.*, 1987), thus it is important that males belong to coalitions which are greater in size than one individual. The data for adult males in mixed groups should provide at least an approximation of coalition size since mixed groups

refer to the presence of other animals in the group which are most likely to be adult (pride) females. Median coalition sizes in males have fluctuated in the Serengeti between values of two and three, with these fluctuations being attributed to differences in survival rates of cubs in natal cohorts (Packer *et al.*, 1987). In this system (HUP), while rainfall is unlikely to affect cub survival as dramatically as has occurred in the Serengeti, culling of sub-adult males may have influenced adult male group size dynamics. An increase in male group size with increasing buffalo and impala biomass has also been reported in the Kruger National Park (Donkin, 2000), with the importance of buffalo and impala as prey species to males also being highlighted in this system (Funston *et al.*, 1998).

The reason for a decline in group size for both adult males and adult females in mixed groups with increasing rainfall is most likely due to an influence on vegetation density, as discussed above, and on vegetation structure which in turn influences resident herbivore composition and demography (Mills *et al.*, 1995). This trend has also not remained constant during the 1985 - 1999 time period since, while male group sizes exhibit a relationship with rainfall, female group sizes do not.

The smaller cub group sizes observed in sections containing higher proportions of Woodland is in direct contrast to the situation in the Kruger National Park (Donkin, 2000), although it should be remembered that these data (HUP 1985 - 1999 period) may be misleading. Most environmental variables appear not to influence cub group sizes in HUP thus group size variability may be governed predominantly by social mechanisms such as creche formation. No relationship between litter size and food availability was found by van Orsdol (1985) in an analysis conducted across ten different habitats throughout Africa.

Interestingly, although cub group size differed significantly among sections, the number of cubs per female did not. This indicates that while grouping patterns were variable throughout

the reserve, this never affected female productivity, which also may indicate that northern areas provided habitat which was of similar quality to that in the southern areas. From a prey perspective, this may well be true. Prey have been evenly distributed and in abundance throughout the reserve since the beginning of the study period (1973) as described by Anderson (1981) who provides a ratio of prey animals to lion (including cubs) of 270:1. This coupled with a well distributed permanent water source provided by the main rivers (Anderson, 1981) and abundant cover for hunting throughout the reserve reinforces this argument. It must however be remembered that reproductive output is governed by a number of social factors as well (Packer *et al.,* 1987; 1990).

Habitat conditions and lion grouping patterns in HUP are variable and this chapter has served to identify and describe this variability for the five management sections which comprise the reserve and in doing so, provides a brief description of lion biology within HUP. A better understanding and knowledge of the data to be used in modelling the spatial ecology of lions in HUP has thus been achieved.

Chapter 4

Regression Modeling and Validation

4.1 Introduction

The usefulness of linear models in an ecological context for the testing of broad scale

hypotheses (Cumming, 2000) has been discussed in Chapter 1. Such models are able to provide

quantitative descriptions of ecological patterns and processes which can then be used to predict areas

in which such processes are most likely to occur (Legendre and Legendre, 1998; Cumming, 2000).

Accuracy of these predictions is dependant on the statistical and ecological components which

comprise the modelling process, the quality of the data and the extent to which predictions are

extrapolations or interpolations (Nicholls, 1989).

The three major stages in model formulation are the specification of a model, parameter

estimation and critical assessment of the model (Nicholls, 1989).

The choice of which statistical model to use is based largely on the nature of the response

variable in question (Nicholls, 1989). The response variable in this case was binomial hence logistic

regression was chosen (Trexler & Travis, 1993; McConway et al. 1999).

This chapter will be concerned with parameter estimation and critical assessment of the model

and, hence, the primary aims will be to firstly, test the hypotheses posed in Chapter Two regarding

the influence of environmental variables on territory and home range location. Secondly, to test the

accuracy of the models themselves and thus the general hypothesis stated in Chapter one, that choices

of areas for territory and home range are based on resource/habitat quality. The objectives were to

firstly develop logistic regression models for each of the four age/sex categories described in Chapter

Two and in doing this, to evaluate those environmental variables contributing significantly to

describing space use by lions in HUP. Secondly, using these models, predictions of areas most likely to be used by lions for territory and home range establishment were made. Thirdly, a validation data set was collected using spatially explicit observations made of an introduced pride to test the accuracy of the model.

4.2 Materials and Methods

Stepwise logistic regression was used to develop models for each of the four lion variables (which were each split into the two Sighting Categories mentioned in Chapter Two) for the two time periods in question. This would have generated a total of sixteen basic models, however, owing to a lack of data, the cub model for Sighting Category two (1984-1999) was omitted. Two extra models, for females in groups of two or more, were included in order to cater for significant interactions which were found to occur. In total seventeen models were formulated. The models were then applied to their relevant environmental variables using the Idrisi Image Calculator.

In addition to the stepwise method (which incorporates both forward and backward selection), backward elimination of variables from a saturated model was also used to check models derived from the stepwise procedure as advocated by McConway, Jones and Taylor (1999). Regression diagnostics were performed on all models for the 1973 -1984 data. In some cases, new models which were derived, performed better than, and therefore replaced, their predecessors. This has been noted where it has occurred and is indicated if the first letter in a model name is a lower case "n". Model names are given in parentheses and are written directly above the relevant model equation in the following format e.g.: (73CubC1), where *73* refers to the time period for which the model applies, *Cub* is the relevant lion variable and *C1* refers to Sighting Category one. No diagnostics were performed on the 1985 - 1999 models for reasons which will be discussed at a later stage in this

chapter.

Models for 1973 - 1984 data were generated from all 819 grid cells comprising the study area, although a number of grid cells were omitted from the data set following diagnostic checking and subsequent additional model generation. These models did not incorporate any prey or hyaena den data. Models for 1985 - 1999 data were only generated from 680 grid cells, since all cells comprising the Northern section of the reserve were omitted from analyses, as explained in Chapter Three.

The basic equation for the logistic model is:

$$f(x) = c + b_1 x_1 + b_2 x_2 + ... + b_n x_z$$

where c = a constant, $x_1...x_z$ are explanatory variables and $b_1...b_n$ are their coefficients; $f(x) = log$ [p/(1-p)], the log odds of success, where p is the probability of success or presence and (1-p) is the probability of failure or absence (Trexler and Travis, 1993; McConway, Jones and Taylor, 1999).

In order to obtain sighting probabilities (on a scale from zero to one) this equation must then be substituted into the following (logistic function):

$$\pi = e^{f(x)} / 1 + e^{f(x)}$$

where e is the natural base and $f(x)$ is the linear model described above (Trexler and Travis, 1993; McConway *et al.*, 1999).

In this manner a single map for each model showing the sighting probabilities generated, was obtained. These maps were then validated using radio telemetry locational data obtained from a pride of six lions introduced in August, 1999.

Abbreviations that appear in the models listed below are as follows: river dist - distance from main rivers; rivdisq - distance from main rivers squared; road dist - distance from roads; rddisq - distance from roads squared; thicket - percentage of thicket per grid cell; grassland - percentage of

grassland per grid cell; open woodland - percentage of open woodland per grid cell; woodland - percentage of woodland per grid cell; intersection - presence/absence of an intersection; warthog - available warthog meat biomass; kudu - available kudu meat biomass; vegNDC - number of different vegetation classes per grid cell; den dist - distance (in meters) from hyaena dens. An asterisk between two variables enclosed in brackets implies an interaction eg: [thicket*public roads].

The squared distances referred to above have been included to cater for possible non-linear responses (Trexler & Travis, 1993). All models listed below are significant ($p<0.001$) with the exception of the cub model (Sighting Category 1) for the 1985 - 1999 data, which is significant at $p = 0.003$. All variables which are included in the models are significant at $p<0.05$, unless otherwise stated.

Validation data were prepared using point locations (determined by radio telemetry) of an introduced pride comprising three adult females (one of whom died soon after introduction and was consequently omitted from the study) and three adult males. The lions split into two distinct groups, one of which comprised two brothers (called the Malopo males) and the other, two females and a male, although one of the females (Oneye) was frequently seen separate from the remaining pair (named the Madikwe male and female). Four lions had radio collars, one of the Malopo brothers, Oneye and the Madikwe male and female. This enabled tracking of effectively all the introduced lions to occur. Locations of the Malopo males were used in testing all adult male models, locations of the Madikwe male and female were used in testing models of males seen with females. Locations of the Madikwe female and Oneye (when seen together) were used to test models of females in groups of two or more, and were also used to test the cub models.

In all, these lions were tracked for a total of 373 days following introduction to the park. Care was taken in omitting same day observations in an attempt to minimise the effect of temporal

autocorrelation.

Telemetry location data were first imported to Cartalinx, where a map of all observations was compiled. This map was then exported to ArcView, where maps of each of the groupings mentioned above (adult males only, males with females and adult females in groups of two or more) were derived.

In order to obtain probability surfaces, the KERNEL HOME RANGE module located in the Animal Movement extension to ArcView ver. 1.1 (Hooge and Eichenlaub, 1997) was run on each of the point location maps. Kernel methods provide a non-parametric estimation of an animal's utilization distribution, as a probabilistic model, within a particular area (Worton, 1989; Seaman & Powell, 1996; Seaman, Griffith and Powell, 1998).

Arcview 3.1 makes use of a fixed kernel bandwidth with bandwidth (h) either being designated by a user, calculated on an ad hoc basis, or calculated using Least Squares Cross Validation (LSCV) (Hooge & Eichenlaub, 1997). In determining kernel home ranges in this study, bandwidth was calculated using LSCV, as advocated by Seaman and Powell (1996), who found, in a study evaluating the accuracy of kernel density estimators, that fixed kernels using LSCV to calculate bandwidth produced the most accurate home range estimates. The number of point locations used to generate Kernel estimates are as follows: Malopo Males: 120; Madikwe Male and Female: 125; Madikwe Female + Oneye: 62.

After kernel generation in Arcview the grids produced (at a scale of <25m grid cell size) were first converted to Ascii format and were then exported to Idrisi. These grid maps were then resampled to the required dimensions in order to obtain probability values on a 1km grid scale. A number of grid cells occurring only partially within the borders of the reserve were included during this procedure, contrary to prior analyses involving model formulation. The reason for this was that exclusion of

these cells would have resulted in a substantial reduction in the number of data values being used to test the models. Predicted probabilities have been produced for these border grid cells as can be seen from the figures shown later in the chapter.

All predicted data values and validation data values were then extracted to a common database and exported to Genstat.

Spearman's Rank correlation was used to test for correlations between predicted (model) and observed (kernel) data values. Correlations which arise should be negative since the probabilities shown on the predictive maps increase as the chance of seeing lions gets better, while kernel probabilities, which reflect probable home range area, become lower in value the closer one gets to core areas, where high densities of sightings have occurred. This is because, for example, the 95% kernel probability contour represents 95% of a particular home range area, and accounts for most, if not all observations. In contrast the 5% contour, which has a high kernel density, bounds a far smaller area since it represents 5% of the total home range area and is centered on areas of high sighting concentration (Worton, 1989). Owing to the large areal size of the 95% kernel and the fact that all observations, including outliers, are accounted for, the probability of seeing the animal/s in question at a particular point is very low. Conversely, although the 5% kernel only represents 5% of the home range area it is far smaller and illustrates a high sighting density, thus the probability of seeing animals here is very high.

Correlations have also been restricted to those grid cells for which there is home range validation data available.

4.3 Results

Models in all instances, except the cub count one model for the period 1985 - 1999, were

significant at p<0.001. Variables contributing significantly to the models are shown below (Table 4.1).

Probabilistic maps illustrating each model have also been compiled (see Table 4.1 in referring to

figures). See Appendix 5 for model details.

Table 4.1: Summary of significant environmental variables contributing to each of the 17
formulated logistic models describing lion territory distribution.

Model Name (figure referring)	Variables included
73CubC1 (Fig. 4.1a)	public roads, river dist, rivdisq.
n73CubC2 (Fig. 4.1b)	public roads, river dist, slope, woodland
n73FemC1 (Fig. 4.1c)	public roads, river dist, grassland
n73owfmC1 (Fig. 4.1d)	public roads, river dist, open woodland, [open woodland*public roads]
n73thfmC1 (Fig. 4.1e)	public roads, river dist, thicket, [thicket*public roads]
73FemC2 (Fig. 4.1f)	public roads, rddisq, river dist, rivdisq, road dist
n73M&F C1 (Fig. 4.1g)	public roads, river dist
73M&F C2 (Fig. 4.1h)	public roads, river dist
n73Mal C1 (Fig. 4.1i)	public roads, river dist
73Mal C2 (Fig. 4.1j)	public roads, river dist, rivdisq, rddisq
85Cub C1 (Fig. 4.2a)	slope
85Fem C1 (Fig. 4.2b)	public roads, kudu, vegNDC
85Fem C2 (Fig. 4.2c)	thicket, vegNDC, warthog, intersection
85M&F C1 (Fig. 4.2d)	thicket, vegNDC, warthog
85M&F C2 (Fig. 4.2e)	intersection, thicket, warthog, den dist
85Mal C1 (Fig. 4.2f)	warthog, thicket, rddisq, road dist
85Mal C2 (Fig. 4.2g)	thicket, vegNDC, den dist, altitude, river dist

Figure 4.1 a-d: Model predictions expressed as probabilities for the (a) 1973 - 1984 Cub C1 model; (b) 1973 - 1984 Cub C2 model; (c) 1973 - 1984 Fem C1 model; (d) 1973 - 1984 Fem C1 (+open woodland interaction) model.
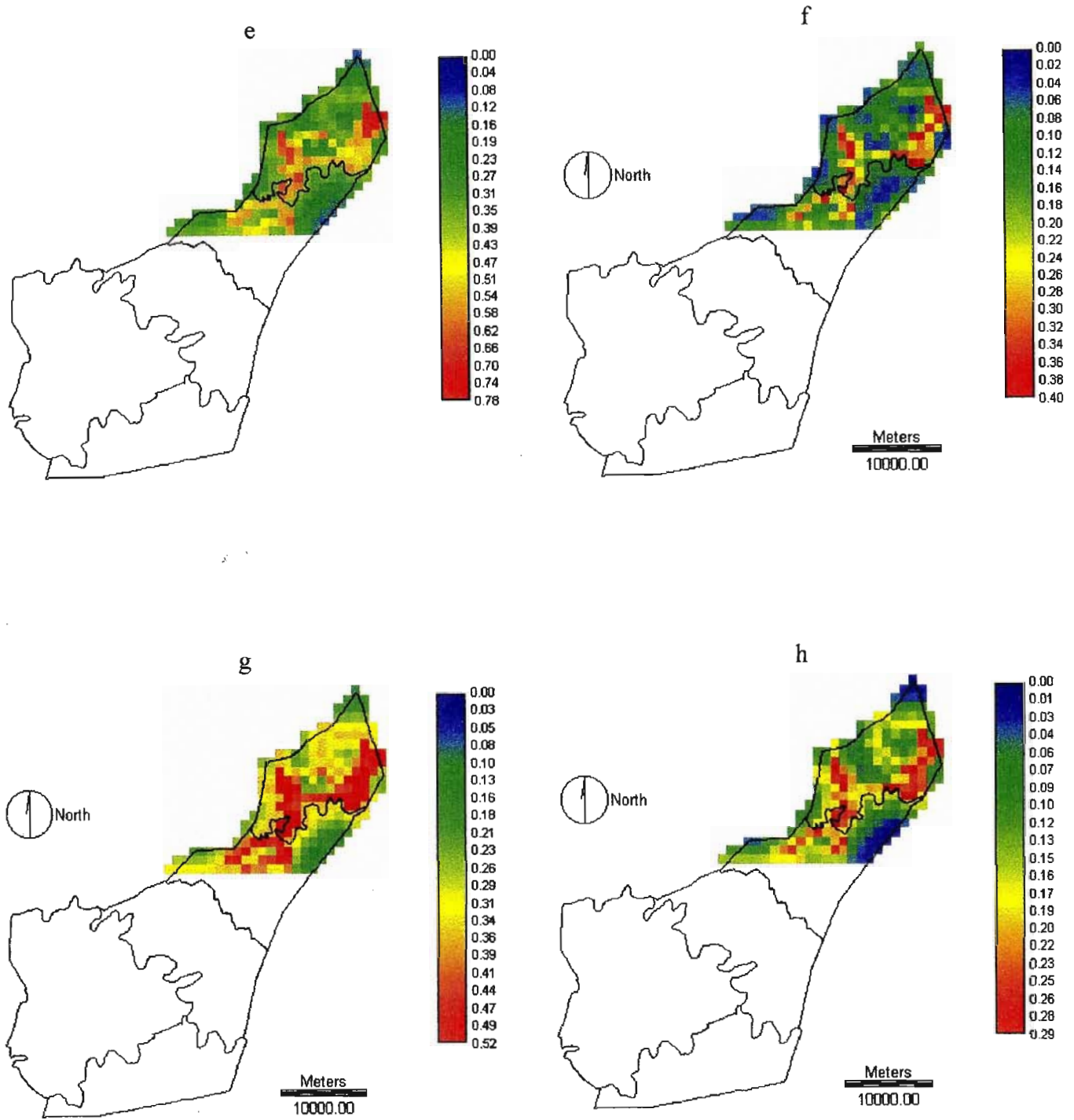
Figure 4.1 e-h: Model predictions expressed as probabilities for the (e) 1973 - 1984 Fem C1 (+ thicket interaction) model; (f) 1973 - 1984 Fem C2 model; (g) 1973 - 1984 M&F C1 model; (h) 1973 - 1984 M&F C2 model.
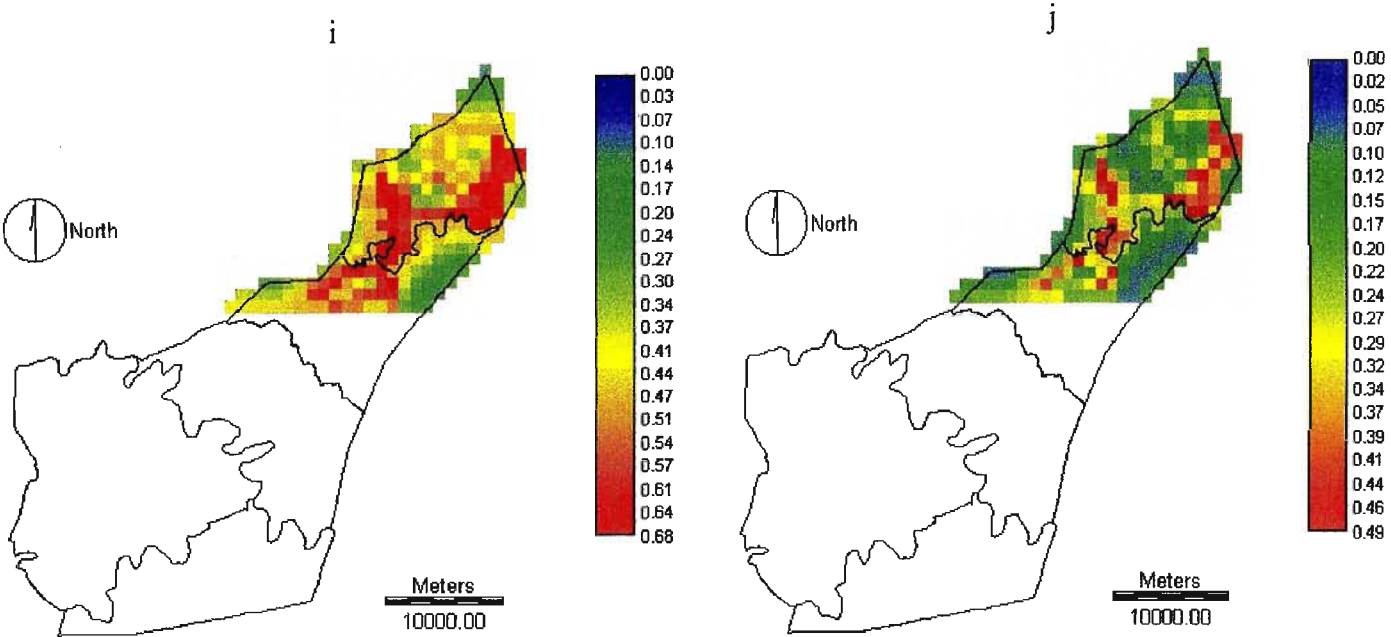
Figure 4.1 i-j: Model predictions expressed as probabilities for the (i) 1973 - 1984 Mal C1 model; (j) 1973 - 1984 Mal C2 model.
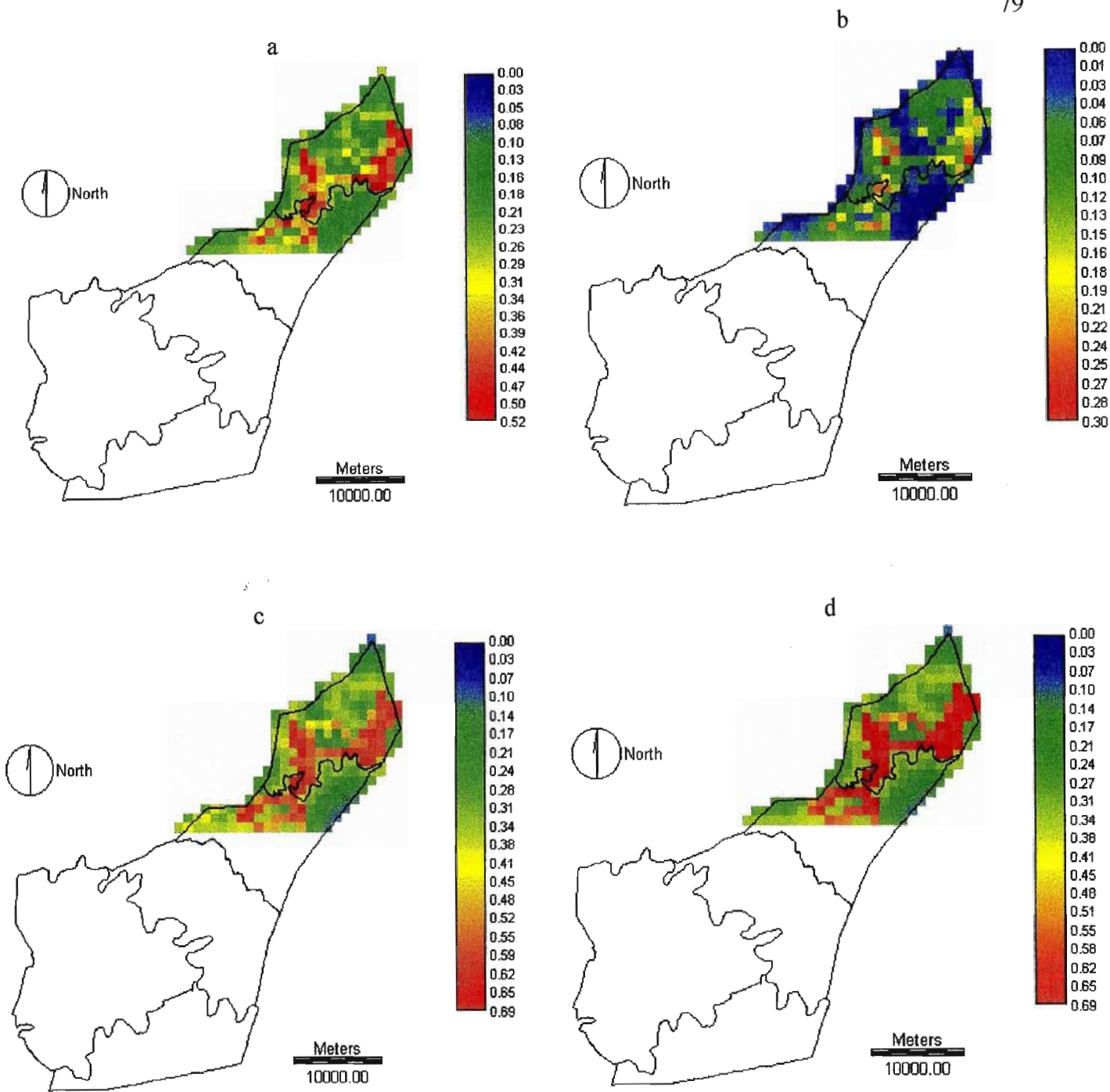
Figure 4.2 a-d: Model predictions expressed as probabilities for the (a) 1985 - 1999 Cub C1 model; (b) 1985 - 1999 Fem C1 model; (c) 1985 - 1999 Fem C2 model; (d) 1985 - 1999 M&F C1 model.

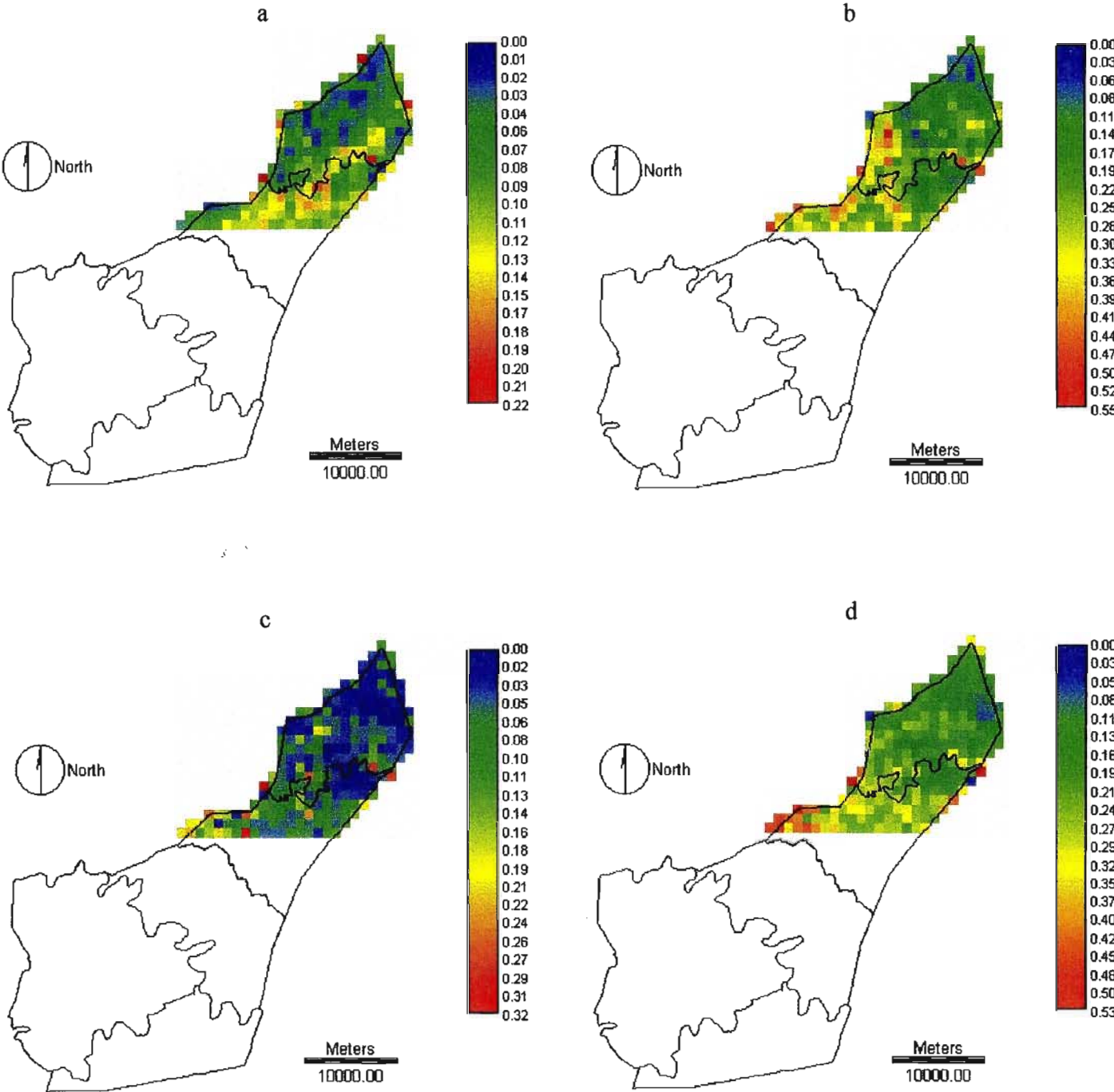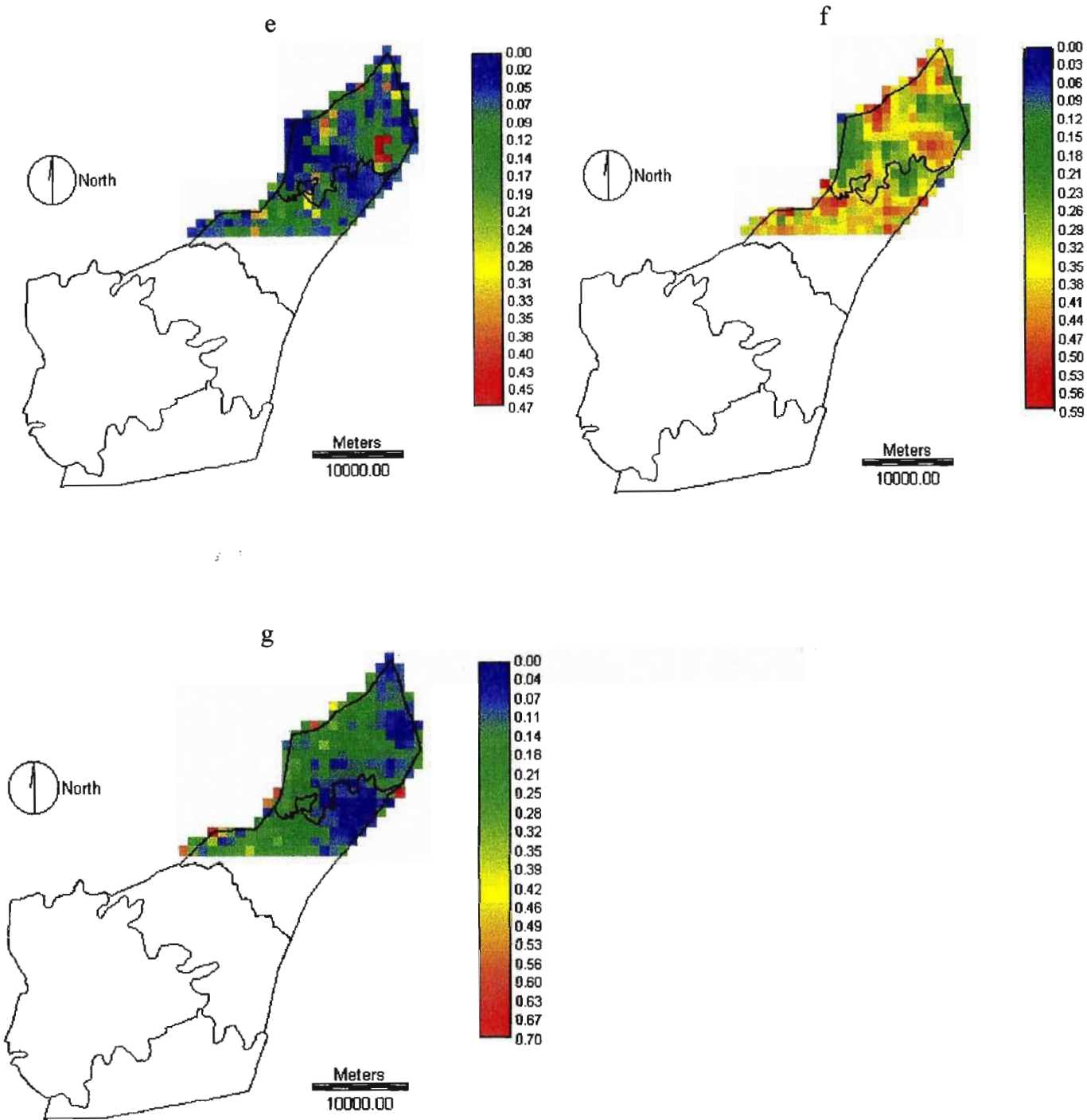Figure 4.2 e-g: Model predictions expressed as probabilities for the (e) 1985 - 1999 M&F C2 model; (f) 1985 - 1999 Mal C1 model; (g) 1985 - 1999 Mal C2 model.

An example of kernel generation (for the purposes of validation) in ArcView has been

provided (Fig 4.3) as have maps of kernel home ranges (at 1km grid scale) for each of the lion groups

(Malopo Males; Madikwe Male and Female; Madikwe Female + Oneye) used for validation

purposes (Fig. 4.4). Spearman's Rank correlations between model predictions and validation data

reveal that many of the models performed poorly (Table 4.2).

Table 4.2: Correlations between model data and validation data. Expansions of model
abbreviations can be found in the model descriptions above. (Note: Degrees of Freedom represent
the number of grid cells evaluated not the number of points used in generating Kernel Estimates)

Model	Correlation	d.f.	P - value
73cub C1	-0.32870	47	0.02*
n73cub C2	-0.28640	47	0.05*
85cub C1	-0.15120	47	0.30
n73fem C1	-0.33370	47	0.02*
73fem C2	-0.35150	47	0.01*
n73owfm C1	-0.32760	47	0.02*
n73thfm C1	-0.35000	47	0.01*
85fem C1	+0.07728	47	0.60
85fem C2	+0.16230	47	0.27
n73m&f C1	-0.16010	105	0.10
73m&f C2	-0.15450	105	0.11
85m&f C1	+0.36830	105	0.00**
85m&f C2	-0.03541	105	0.72
n73mal C1	-0.13620	101	0.17
73mal C2	-0.11480	101	0.25
85mal C1	+0.04992	101	0.62
85mal C2	+0.07144	101	0.47

Regarding cub models, correlations with validation data were significant for both the 73cubC1 model

(p<0.05) and the n73cubC2 model (p=0.05), although a non-significant (p=0.3) negative correlation

was found for the 85cubC1 model

Kernel Home Range of the Malopo Males
for 377 days following introduction.

85
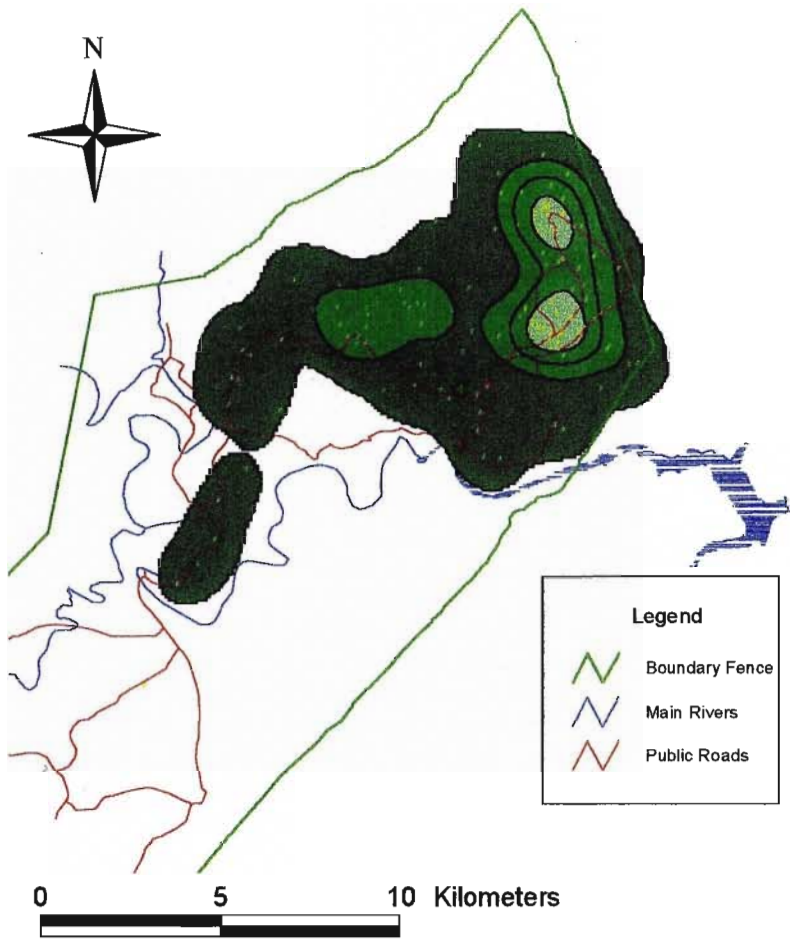
Figure 4.3: Kernel Home Range of the Malopo males for 377 days following introduction. Contours shown represent 25% (light green), 50%, 75% and 95% (dark green) of the calculated home range area. Yellow dots show actual telemetry point locations.
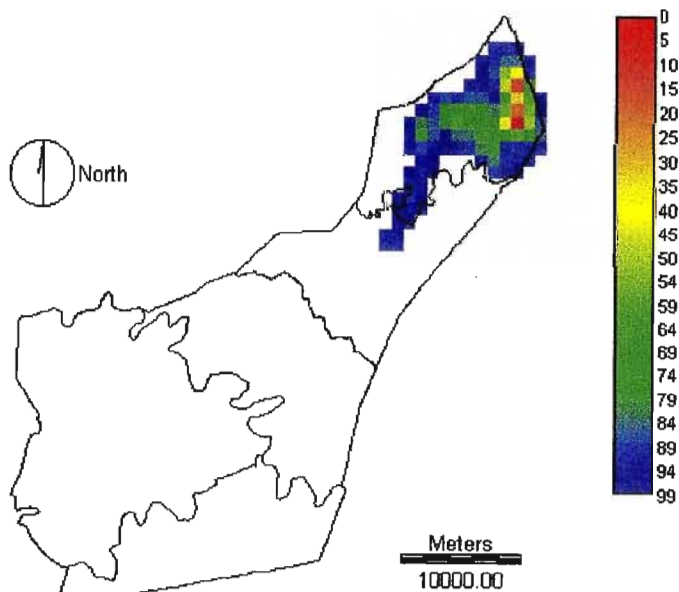
Figure 4.4a: Adult male lion model validation data
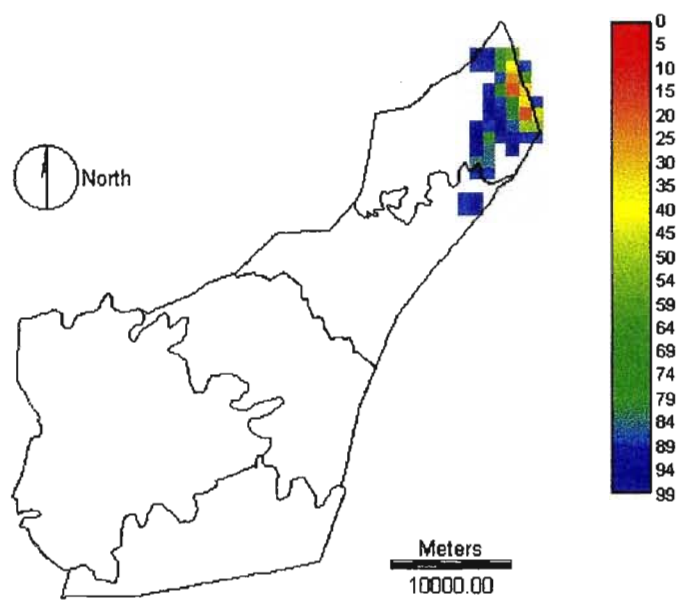
Figure 4.4b: Adult female lion model validation data
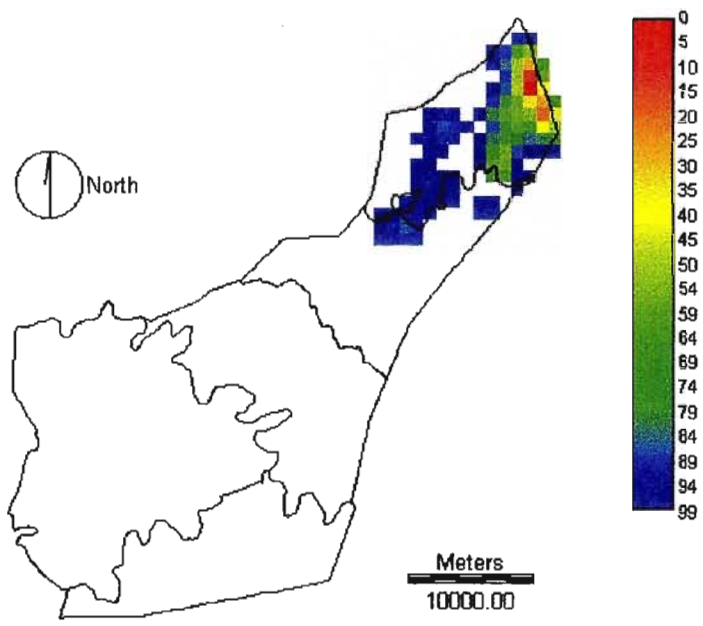
Figure 4.4c: Adult male & female lion model validation data (male & female refers to adult male and female animals which were seen together)

Since cub sightings were utilized, based on the premise that grid cells in which they occurred were indicative of territories, tests of these models were conducted using the validation data set of females in groups of two or more.

The variables of importance in the 73cubC1 model were presence/absence of public roads and distance from rivers. The probability of seeing cubs increases for those grid cells where public roads are present, while in those cells where there are no public roads, the probability is significantly reduced.

The relationship between cub sightings and distance from rivers is complex and not readily interpretable, owing to the existence of a significant quadratic term. Initially, as distance from rivers increases, the probability of seeing cubs declines. This is expected since rivers in HUP provide both water and cover. Once past approximately 2000m, however, the probability of seeing cubs begins to increase with distance from rivers, i.e the relationship switched from a negative to a positive one. This anomaly can be explained as having arisen due to the model fitting process (see Discussion). Manipulations of the models and the data set did not arise in any improvement of fit to the validation data. It should be noted however, that the range of predicted probability values considered for validation did not include areas greater than 2500m from main rivers and 3000m from roads. The validity of the increasing portion of the quadratic function was therefore not evaluated.

The n73cubC2 model, while it does represent an improvement on the previous model generated for these data, does not improve fit with the validation data. In addition to this, the model is not as efficient as the 73cubC1 model since four variables were included as opposed to three for the 73cubC1 model. The inclusion of a positive slope term is also questionable since a preference for flatter areas (toe slopes of hills and river plains) would be expected, as was found in the 85cubC1 model.

The n73thfmC1 model is the "best" or most parsimonious model describing female data since it utilizes four variables, as opposed to the five required by the 73femC2 model, while still producing an equivalent significance of fit with the validation data. The positive interaction between public roads and percentage of thicket per grid cell implies that female lions in groups of two or more are more likely to be seen on or close to roads in areas where there is a large amount of thicket. In contrast, the opposite is true of areas in which there is a high occurrence of open woodland, since in these areas, lions are less likely to be seen on (or close to) public roads, as is shown by the significant negative interaction term included in the n73owfmC1 model.

The 73FemC2 model incorporates two quadratic terms which describe distance from rivers and distance from roads. Re-formulations of the model following diagnostic checking were unsuccessful in improving fit.

As explained in the cub models, the inclusion of quadratic terms in the 73FemC2 model is attributable to the model fitting process, rather than being indicative of a biological relationship. While tests of correlations between validation and prediction data produced the highest r_s value for any of the models, only the first portion of the quadratic relationship was in fact tested (see cub model explanations). The relationship is non-linear, and was expected to be so, however, the over-riding effect of the positive quadratic term at distances more than 2500m from rivers (and 3000m from roads) was not expected. Interpolations beyond 2500m may thus result in erroneous predictions, while extrapolations beyond 4000m would most certainly result in extremely misleading predictions, highlighting one of the limitations of several models which have been developed.

Neither of the models formulated from the 1985 - 1999 data produced significant correlations with the validation data set, although both models accounted for a significant ($p<0.001$) amount of deviance. The possible reasons for this lack of fit (with validation data) are twofold: either the models

themselves are poor or, because they were formulated using data from the central and southern areas of the reserve, extrapolations of probabilities in the North of the reserve are invalid.

Once again, the importance of local infrastructure has been established with the inclusion of public roads in the 85femC1 model and intersection presence/absence in the 85femC2 model.

Fits of the 1973 - 1984 Male seen with Female models with the validation data were not highly significant, however, in comparison with the 1985-1999 models, the fits are good. The 85m&fC1 model produced a highly significant (p<0.001) positive correlation with the validation data which is in direct contrast with the expected relationship (negative correlations were expected as was explained previously in the chapter) and shows that the model does not indicate core areas of habitation in this particular instance.

Presence of public roads and proximity to rivers increase the probability of sighting male and female lions together, with these two variables being the only significant contributors to both of the 1973-1984 models. Once again it is of interest to note that neither of these variables was significant in the 1985-1999 models. In stead, the 85m&fC1 model indicates that grid cells containing a high percentage of thicket are avoided, while increasing warthog biomass and increasing vegetation structural complexity resulted in increased probabilities of sighting male and female lions together and hence increased preference for such habitat characteristics. The preference for areas close to hyaena dens shown in the 85m&fC2 model was not expected and is probably erroneous. It was realised, *a priori*, that models including terms related to hyaena dens were likely to be questionable, owing to the non-static nature of den sites over long periods of time (see Chapter Two).

The correlations of all model predictions pertaining to Male data with the relevant validation data set were non-significant.

Adult male lions were seen more often close to rivers and in grid cells where public roads are

present. The effects of the quadratic terms included in the 73MalC2 and the 85MalC1 model are the same as those described for Cubs and Females and will not be addressed further.

During the 1985 - 1999 period the probability of seeing males increases with increasing Warthog biomass and declined with increasing thicket predominance and distance from rivers. Preferences (as shown by repeat sightings data) for grid cells close to hyaena dens and rivers, high in altitude and having high vegetation structural diversity but low densities of thicket are shown by the 85MalC2 model. Two of these variables are contradictory to one another (high altitudes and proximity to main rivers) and one is contradictory to what is expected, namely distance from hyaena dens. These somewhat conflicting findings may have arisen due to a lack of "presence" data points. Problems associated with Hyaena den data were raised in the Male and Female section above.

4.4 Discussion

One of the major causes of outliers in logistic regression is due to recording a "presence" in a grid cell when there was in fact an "absence" and vice versa (McConway *et al.*, 1999). Although it cannot be assumed, in this study, that lions never occurred in grid cells which were designated as having zero occurrences i.e. absences, it can be reasonably assumed that prides never (or at least hardly ever) occurred in these grid cells. However, while this is certainly true of the 1973 - 1984 data set, during which intensive monitoring of prides took place, it may not be true of the 1985 - 1999 data set as was stated in Chapter Three.

Detection of observations which exert undue influence on fitted models falls into the realm of regression diagnostics (Nicholls, 1989). These include examinations of residual plots, leverages and modified cook statistics which are neither as helpful nor as informative when used in binary regression as opposed to their use in other types of generalized linear models (McConway *et al.*,

1999). In this case, critical evaluation was only performed on the 1973 - 1984 models. A number of quadratic terms were found to be significant in the initial modeling stages, for which there was no adequate biological explanation. On examination of the models it was found that proportionally very few sightings occurring more than 2500m from rivers and 3000m from roads were having undue influence on the regression models. A number of these cells were also found to have both high residuals and leverages. As a consequence, all 1973 - 1984 models were re-formulated using a data set from which all grid cells occurring more than 2500m from rivers and 3000m from roads were omitted. These new models were then compared to the validation data set, and where correlations were found to be improved, the new model was utilized.

Diagnostics were not performed for any of the 1985 - 1999 models. The reasons for this were as follows: Firstly, since the models were formulated only from grid cells located in the central and southern areas of the reserve, which are both topographically and vegetationally different from the northern areas, any predictions pertaining to the northern areas based on these models are likely to be extrapolations and therefore of questionable accuracy. Secondly, owing to the uniformly poor fit of the 1985 - 1999 model predictions to the validation data set (even though the models themselves were significant at $p < 0.001$) and given the poor quality of sightings data for the 1985 - 1999 period, the likelihood of improving these models following critical evaluation was not thought to be significant.

With regards validation data, since the new pride was introduced into an area in which there were no resident prides, there were no constraints on their movements throughout the area, other than those imposed by their surrounding environment. The introduced lions were thus able to make un-restricted choices of areas in which to establish a territory. In addition to this, all locational data were collected by means of radio telemetry conducted predominantly from vehicles, the movements

of which were not restricted to public roads, but included management tracks as well. Much of the bias regarding over-sampling due to sightings on or close to public roads (as may have been experienced with the model formulation data sets) has thus be alleviated. Significant correlations which may arise between model prediction data and validation data would therefore negate the argument that significance of the public road term in many of the models is merely due to the fact that oversampling in close proximity to roads has occurred. This should be considered in the model interpretations.

A final point of consideration relates to the influence of sample size on model fit (Cumming, 2000). It has been shown that the accuracy of logistic models declines as the number of cells scored "1" (presence) declines and in addition to this, logistic models are biased toward the larger set of values, either presences or absences, as the case may be (Cumming, 2000). The designation of two categories of presence, one incorporating all sightings (count one data) and the other incorporating only two or more sightings per grid cell (count two data) as explained in Chapter Three, may thus give rise to inaccuracies in model predictions. Large proportions of data have been excluded from models involving count two data leaving these models prone to the bias described above. Ultimately, however, model accuracy should be assessed on the basis of comparisons with validation data.

Regarding the 1973 - 1984 cub models, the fact that cubs are seen more often on public roads may be an indirect reflection of a preference for traveling on roads shown by adult female lions. Cubs are, of all lion categories utilized in this study, the most difficult to visually locate. The problem of oversampling on roads, which was addressed in Chapter Two, may thus be exaggerated in this case, thereby resulting in the apparent importance of public roads, since cubs would very rarely be seen off public roads.

The preference for steeper areas and areas in which woodland (n73CubC2) occurs may be due

to the fact that females with cubs up to a month old tend to remain in areas of abundant cover (Packer *et al.* 1990). Steep areas are associated with small tributaries and river gullies which provide good cover. Cub group sizes have been found to be largest in woodland areas in Kruger National Park, a fact which was attributed to the abundance of cover available in woodland areas (Donkin, 2000). In this study, during the 1985 - 1999 period, cub group sizes were smaller in sections having a high proportion of woodland, however during the 1973 - 1984 period, to which this model refers, no significant differences among management sections were found. Smaller cub group sizes in woodlands may not reflect an avoidance of these habitats. In fact, repeat sightings of cubs were made under the conditions outlined by the n73CubC2 model owing to the fact that this model refers to sighting category two, from which single sightings of cubs per grid cell have been omitted (Chapter Three). This would seem to indicate a preference for these (steep woodland and riverine) areas.

All female models for the 1973-1984 period produced significant correlations with the validation data (p<0.05), whilst neither of the models for the 1985-1999 data were significant. This in itself is notable since even though prey (which is considered one of the most important variables in explaining territory location) data were not included in the 1973 - 1984 analyses, significant fits to an independently collected data set were still found to occur. Prey may be indirectly represented by distance from rivers and it would be expected that higher prey concentrations be observed close to rivers. Simple tests for correlations between these variables however revealed no significant relationships between prey concentrations and distance from rivers. The effect of seasonality was not evaluated, nevertheless since main rivers are the only water sources in winter, herbivores, while not necessarily remaining close to rivers, would still need to visit rivers to obtain water (Steele, 1970). Lions were found to center their ranges around water holes during the winter months in the Phinda Resources Reserve (Hunter, 1998). A similar scenario has been reported for the Ngorongoro Crater

(Packer *et al.*, 1987). Prey distribution in HUP is both plentiful and fairly uniform (Anderson, 1981) which may, to a certain extent, have offset the effect of prey on lion distribution within this particular reserve. With regards all 1973-1984 models, proximity to rivers and presence of public roads increase the probability of seeing adult female lions in groups of two or more.

The interactions between roads and vegetation described by the 73thFemC1 and 73owFemC1 models are of interest and illustrate a differential utilization of roads governed by vegetation structure. Roads provide both quick and easy avenues of travel through areas dominated by thicket, however, the more open the vegetation, the less likely female lions are to travel on roads. With regards territory location, efficient lines of travel, such as roads, are selected for in areas where high densities of thick vegetation are prevalent, as shown by the significant correlations with the validation data set, with the importance of economical lines of travel declining as vegetation structure becomes more open. The requirement large carnivores have for connections for travel on a daily to seasonal basis within their home ranges is known, as is the fact that such corridors are not fixed but may vary with prevailing environmental conditions (Noss, Quigley, Hornocker, Merrill and Paquet, 1996).

The poor predictive ability shown by the 1985 - 1999 female models could be attributable to the following: It is known that following the large scale culling of lions in the northern sections of the reserve, the area comprising Hluhluwe Section was never naturally re-colonised, the possible reason being that there was no need to, given the low lion population in the reserve (Maddock *et al.* 1996). In addition to this, a large proportion of the Hluhluwe Section, in comparison with the southern sections of HUP, does not represent ideal lion habitat (C. Packer, pers. comm.). Models referring to the 1985 - 1999 period may thus reflect a set of environmental choices relevant to lions in more open habitat, which almost certainly do not fully comply with the choices made at a territorial scale, in a closed habitat. A number of different variables were found to be significant. Pride females avoid

areas of high kudu biomass and select for areas of high warthog biomass. The preference lions have for eating warthog is well known, thus selection for areas high in warthog biomass is to be expected. Warthog is the third most important prey species for lions in some areas of the Queen Elizabeth National Park, Uganda, with buffalo and bushbuck (*Tragelaphus scriptus*) being most important (van Orsdol, 1984). Similarly, warthog and buffalo were the most selected prey species for lions in the Manovo-Gounda-St.Floris National Park (Ruggiero, 1991). Interestingly, neither buffalo, wildebeest nor zebra were important in influencing lion spatial ecology. The avoidance of areas high in kudu biomass is not easy to explain, although this may be indirect evidence for avoidance of the habitat types (thick bush) preferred by kudu (Skinner & Smithers, 1990). Interpretations of the prey data should be viewed with caution owing to the nature in which these data were collected (see Chapter 2). Female lions also select for territorial areas having high vegetation structural heterogeneity as shown by the significant vegNDC term appearing in both models. This was expected since high vegetation heterogeneity was thought to provide an abundance of cover for stalking prey and is substantiated by Prins and Iason (1989) who found that hunting success greatly increased in the vicinity of ecotones (see Chapter 2). An increasing vegNDC term is also indirectly indicative of low altitudes, shallow slopes and close proximity to rivers.

With regards to the Male and Female (seen together) models the preferences shown by males and females together and by females in groups of two or more are largely similar in nature. Since these issues have been discussed above, they will not be addressed further.

The poor predictive power of all male models can largely be attributed to the differences in socio-ecology which exist between adult male lions and their female counterparts. Firstly, the presence of male lions in a particular area is not indicative of the presence of a pride in that area. Male lion distribution, as was discussed in Chapter One, is largely governed by the presence of females and

not by the presence or abundance of resources (Kruuk, 1986; Packer, 1986). They also do not remain in a particular territory for the duration of their lives, but, once ousted from a pride, will roam an area in search of another pride to take over. In addition, male lions who have gained tenure over a pride do not distribute themselves according to resource distribution within a territory. They are either found with pride females, in order to defend them from other males, or they patrol territory/home range boundaries, once again, in order to defend the pride (Funston *et al.* 1998). Thus male lion spatial ecology is subject to large amounts of variability which is not conducive to accurate habitat modeling.

While males do not distribute themselves according to available resources, they may nevertheless have preferences for certain environments above others. In this respect, high densities of buffalo and/or thick vegetation in combination with adequate impala densities were found to be pre-requisites for successful hunting by male lions in Kruger National Park (Funston *et al.,* 1998). In addition to this, the possibility that non-territorial males were purposefully occupying areas of higher buffalo density was also raised (Funston *et al.* 1998). Both of the 1973 - 1984 models indicate a selection for grid cells which are close to rivers and/or contain public roads. It is surprising that adult male lions exhibit the same (or very similar) habitat preferences as compared with pride females. The situation may, to some degree, have been influenced by the manner in which these data were collected since, during the lion monitoring programme, the focus appears to have been on sampling prides and pride areas which were largely situated close to major river systems (Anderson, 1974; 1975). This is one of the reasons for adapting the data set to a presence absence (rather than count) scale, thereby alleviating the probable effects of oversampling in certain areas. On the other hand, given that male lions hunt more successfully in areas of thick bush or woodland and high prey density (Funston *et al.,* 1998) it is not surprising that they show a preference for main rivers, where these conditions are

in many instances likely to be met.

The significant positive altitude term in the 85malC2 model is contradictory to the relationship with distance from rivers since the majority of main rivers are found at low altitudes. The only possible reason for this is the use of higher altitude areas as vantage points from which larger regions are able to be observed. This would be particularly useful to pride males patrolling territory boundaries.

4.5 Conclusions

Examining all of the models, several points of importance arise. In many instances public roads and distance from main rivers were found to be of importance. These two variables also contributed significantly to models which produced the best correlations with the validation data set. It is therefore concluded that main river systems are of great importance in determining potential areas of territory location in HUP, although the reasons for this may not only be directly linked to the rivers themselves, but rather the resources which they provide i.e. travel lines, abundant water and good hunting areas (Steele, 1970). Given the theoretical basis for this study, namely Ideal Free Distributions, preferences for areas exhibiting multiple resource benefits were expected. In the context of this reserve, main river systems are of great importance in providing a combination of food, shelter (cover) and water, three of the most vital factors influencing lion spatial ecology (C. Packer, pers. comm.). In addition to this, efficient lines of travel, in this case public roads, are selected for in areas (such as those characterised by a high proportion of thicket) where travel is restricted. Ease of travel on roads may also be of importance since management roads, which are often overgrown with vegetation, were not found to be of significance in any of the models. The differentiation between management and public roads was made because it was expected that such differences in utilization

could exist. Vegetation types were largely found to be of little importance, except in interactions with public roads i.e unless vegetation impaired travel through an area. While avoidance of grid cells having a high proportion of thicket and a preference for cells high in structural heterogeneity was found to occur, these results were only established for 1985 - 1999 models, the predictions of which did not correlate well with the validation data set. Given the scale at which analyses were conducted, this is perhaps to be expected, although it was hypothesised that lions would favor territories having a higher proportion of open woodland and would avoid areas having large amounts of thicket and forest. Neither slope nor altitude were of importance in territory location, although a preference for main rivers may indirectly imply a preference for lower altitudes and shallower slopes.

Chapter 5

General Discussion

That consumers (animals in general) aggregate in patches which they perceive as being most profitable and where expected rate of intake is highest is a well known ecological phenomenon (Begon, Harper and Townsend, 1990) and is one of the basic tenets of Ideal Free Distribution (IFD) theory (Milinski and Parker, 1991). While IFD theory is not applicable to lion grouping patterns, owing to the large number of complexities (communal cub defense etc.) prevalent in lion social ecology (Pusey and Packer, 1987; Packer *et al.*, 1990) it nonetheless provides some useful basic principles regarding patch selection and, in terms of this study, territory selection. It was expected, on this basis, that lions would choose a territory in which the best possible resource set could be found, since territories are of extreme importance in ensuring reproductive output and, ultimately, the persistence of a pride through successive generations (Packer *et al.* 1990; Heinsohn and Packer, 1995).

Lions in HUP have shown a marked preference for high quality resource patches by their selection, in almost all model cases and throughout the 1973 - 1999 study period, of areas in close proximity to main rivers. In addition to this, the differential preference for public roads shown by adult pride females is congruent with accepted theories of optimal foraging which suggest that optimality is affected by the time and effort, both of which should be minimised for maximum benefits, spent traveling between patches (Begon *et al.*, 1990). The importance of efficient lines of travel to large carnivores in a territorial context has been highlighted (Noss *et al.*, 1996). Lions are both large and highly mobile animals and it would not be unreasonable to hypothesise that they would select for areas characterised by efficient lines of travel. Such choices are most likely to be affected

by habitat characteristics which hinder passage through particular areas, such as dense vegetation and steep hilly terrain. While this has been corroborated by the models (specifically for adult females in groups of two or more) there is potential bias toward increased numbers of sightings closer to roads which is attributable to observers traveling more often on roads. Definitive statements regarding the statement that optimal choices incorporate issues such as accessibility are, in this case, hindered. In view of this fact, future modeling of lion spatial ecology which takes place should be concerned, in part, with a formal attempt at quantifying potential biases, a task which is not always possible when dealing with historical data as in this study.

Although faults with the data used in this study exist, which is inevitable given the purpose for and manner in which these data were collected, the fact that significant correlations with validation data have been found nevertheless indicates that several of these models provide meaningful descriptions, and hence contribute a valuable first step in understanding and modeling preferred territorial habitat characteristics of lions in HUP. The use of these models as predictors of territory location implies causality among the relevant variables (Legendre and Legendre, 1998). It is recognised that definitive statements of causality are confused by the inter-relationships among variables (Cumming, 2000). For example, lions may not choose to locate a territory or home range in an area because of the presence of a main river, but rather because of the resources provided by the river, namely water and possibly good hunting areas and efficient lines of travel. Such resources may, in a different context or reserve, be exhibited in a different manner, thus extrapolations to different reserves should be undertaken with extreme caution. It is further recognised that there is no single "best" model and it is quite likely that variables which were in some instances not included in the models (for example prey in the 1973 - 1984 models) may contribute significantly in explaining territory location. Furthermore, significant variables contributing to models which did not produce

accurate predictions should not be ignored.

This study has been exploratory and must not be seen as a final step in the modeling process. Rather, a number of broad scale hypotheses and descriptions have been evaluated and several factors of importance have been identified, from which additional hypotheses can be tested in a more rigorous fashion. In this instance, data which were collected for validation purposes in this study could be used to generate additional multi-scale models using current habitat data. A new set of validation data should also be obtained since the effectiveness of the modeling process is greatly reduced if no validation of the formulated models is performed. This is clearly demonstrated by the fact that although16 of the 17 regression models were statistically significant ($p<0.001$) as were the parameters contributing to these models, comparisons with validation data revealed that of these models, only 6 were moderately ($0.05> p >0.01$) accurate in predicting potential territory and home range areas. Future modeling exercises, not only those regarding lions, should therefore make provision for the collection of an independent set of data to be used in accuracy assessment as this is an essential step in developing meaningful and useful models (Morrison *et al.*, 1992). It is also of interest that models which produced significant correlations with corresponding validation data were those describing distribution of females in groups of two or more which suggests that future modeling of territory and home range selection should focus on females. Female decision making regarding optimality of areas is therefore consistent whereas choices made by males are subject to far more variation.

Finally, it must be remembered that the relevant scales (time and space) at which hypotheses have been formulated and assessed is large since issues relating to choices of territory have been addressed. The fact that certain habitat characteristics are of importance at this scale does not necessarily indicate that these characteristics will have the same influences at far smaller scales (Levin,

1992). Lions in HUP do make large scale choices of areas for territory establishment based on habitat quality, with this quality being determined by accessibility and profitability in terms of good hunting areas, abundant cover and water supply all of which are provided by main river systems. The fact that no definite influence of prey type and density on lion distribution was found is most likely due to the fact that there is no shortage of prey (well distributed) in HUP nor has there been a shortage in the past (Anderson, 1981). The influence of prey could also only be evaluated for the 1985 - 1999 time period. Prey should not therefore be ignored in future for the additional reason that food sources are believed to be the primary factor contributing to patch optimality or quality (Begon *et al.*, 1990).

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Appendix 1

General Principles

A number of modules were used repeatedly in IDRISI for data manipulation. Each of these will be briefly described and discussed.

RECLASS

This module reclassifies the values in an input image to those individual values or ranges of values specified by the user (Eastman, 1999). The RECLASS module was used extensively in manipulations of the vegetation data, where it was necessary to reduce several vegetation types to a single broad category.

ASSIGN

ASSIGN is used in assigning new values to an image. This is done by creating a values file in which the values from the original image occur, in a column, on the left, while new values to be assigned occur on the right, thus original values act as identifiers for their new replacement values (Eastman, 1999).

EXTRACT

EXTRACT is used to derive summary statistics (minimum, maximum, sum, average etc.) for an image based on a feature definition image (Eastman, 1999). An example would be the extraction of grid cell specific altitude data from an altitude map (DEM) so as to place them in a values file (which can then be imported to a database). In the values file there would thus be lines numbered 1 through 819 (grid cell identifiers), with each line being associated with an altitude value. A similar procedure was adopted for extractions of all other habitat data to a number of databases which were then combined at a later stage to produce a single environmental database for each of the two study periods (1973 - 1984 & 1985 - 1999).

CONTRACT

CONTRACT reduces (contracts) the number of rows and columns in an image, thereby decreasing the resolution (Eastman, 1999). Many of the original data maps used in this study had finer resolutions than were required for the final analyses. CONTRACT was used in order to coarsen these data. Contraction may occur in one of two manners, either by pixel thinning or pixel aggregation. Pixel thinning involves dropping every nth pixel from an image, while pixel aggregation gives a resultant pixel value which is the mean of the original (higher resolution) composite pixels (Eastman, 1999).

IMAGE CALCULATOR

The image calculator is used when applying mathematical models or expressions which incorporate images. For example, in this study it was used to relate an algebraic rainfall model to an altitude map, in order to produce a map of rainfall throughout the reserve (described in greater detail below). Image calculator was also used in calculating maps giving a spatial representation of probabilities of seeing lions as predicted by the various logistic models which were derived (Chapter Three).

RASTER AND VECTOR IMAGES

Vector images are composed of a series of points (and their associated co-ordinate locations) which, when joined together, either comprise lines or bounded areas (polygons), depending on the type of feature being displayed (Eastman, 1999). Raster images, in contrast, are made up of cells. Here the study area in question is divided up into a grid, with every cell in the grid having associated information on the attribute being displayed, e.g altitude (Eastman, 1999). Raster images can be converted to vectors and vice-versa.

Appendix 2

Index image production

A 0, 1 binary image of the park at 1km resolution was first calculated using the RECLASS module in IDRISI. This image was then exported to Cartalinx (after being converted to vector format in IDRISI) and was overlain on (placed on top of) a background vector image of the park. All grid cells that fell only partially within the park boundaries were deleted. The resultant vector image was then exported back to IDRISI and was converted into raster format.

Using a spreadsheet package, the numbers 1 to 3249 (57 rows x 57 columns at 1km resolution) were placed in a column. The file was then saved as text, and the extension changed to .IMG. It was then opened in IDRISI, after first editing it's Documentation File (which consists of a number of lines containing important information about an image file), and multiplied by the binary image to obtain an image of the park with sequentially rising cell identifiers. These identifiers were altered, using the IDRISI database workshop and the ASSIGN command, and re-numbered 1 to 819, thus giving the final index image with grid cells numbered (top to bottom and left to right) from 1 to 819 within the reserve. All data used in the project refer to this index image.

Image definition.

All images used in this study have the following basic associated documentation:

Reference system: lo31

Reference units: meters

Min. X : 61000

Max. X: 118000

Min. Y : -3154000

Max. Y: -3097000

The reference system listed above is based on a Transverse Mercator projection using the Cape (South Africa) Datum and a modified Clarke 1880 ellipsoid with an origin longitude of 31°. I obtained the lo31 reference system parameter file from the HUP Research Center as IDRISI never had this reference system in it's archive. A reference system parameter file is simply a file which supplies the details required for use of a particular reference system (Eastman, 1999). These data are required in order to relate earth surface locations to their corresponding locations (on digital maps) within a GIS (Eastman, 1999). For further detail on georeferencing, refer to volume 1 of the Idrisi32 Guide to GIS and Image Processing (Eastman, 1999).

Appendix 3

General Problems

Certain problems with the data used in the project were encountered and these will be highlighted and possible solutions suggested.

The first issue relates to the use of different computer programs and file formats. Using a large number of different formats and programs is not only time consuming but can also become extremely troublesome, when converting from one format to another. It is suggested that programs and file formats compatible with one another be used in the future production of digital maps. For example, if Idrisi is used frequently, then Cartalinx should be used as an attendant vector based program. Cartalinx is also easily used in conjunction with ArcView and it makes use of the Microsoft Access database engine (as does Idrisi), which allows for powerful and efficient data manipulation to occur. Using the above G.I.S. programs would negate the use of .DXF and .DGN files which can often become problematic.

With regards actual data used, problems were encountered in compilations of prey and vegetation maps. Prey data were based on line transect records from the years 1996 and 1998. For these records it is recommended that every tag on each transect be assigned a positional location (in lo co-ordinates) using a G.P.S. With the 1996 and 1998 data, only about half of the transects had associated G.P.S. locations. Some were simply start and end points, and others had every fifth tag located. Since all the transect records refer to a particular tag location (see the Prey section above) this introduces substantial positional error to the data set, and ultimately limits the minimum (ecological) scale at which these data can be analysed. Once again, these data should be recorded in a G.I.S. friendly manner to facilitate efficient data input. It is recommended that a G.I.S package such as Cartalinx be used since it is fully compatible with both Idrisi and ArcView. This would, as

explained above, negate the use of a number of different programs and file formats thus circumventing associated complications.

The lack of transect data in the wilderness area was also problematic. While no data existed for this project, point transects have subsequently been positioned in the area and observational data are obtained in this manner. (Point transects have been chosen as there is minimum management impact in utilizing such a method. This is in contrast to line transects which have to be mown, a practice which would run contrary to the minimum impact management policy implemented in the wilderness area)

The biggest drawbacks with the vegetation data were the difficulty in reducing the two maps to the same basic comparable vegetation classes and the length of time spanned by the two maps. In view of the fact that vegetation in the reserve can change at a rapid rate, it may be necessary to obtain either satellite images or digital photographs of the reserve taken every two to five years, which can then be classified into vegetation maps, using the system developed in 1996 by Meier. In this respect, it is important to decide on a classification and to continue it's use thereby maintaining consistency in the interests of future comparisons and long term monitoring. Once again, cost may become an issue, however the possibility of using maps in conjunction with, for example, the Working for Water Project could perhaps take place.
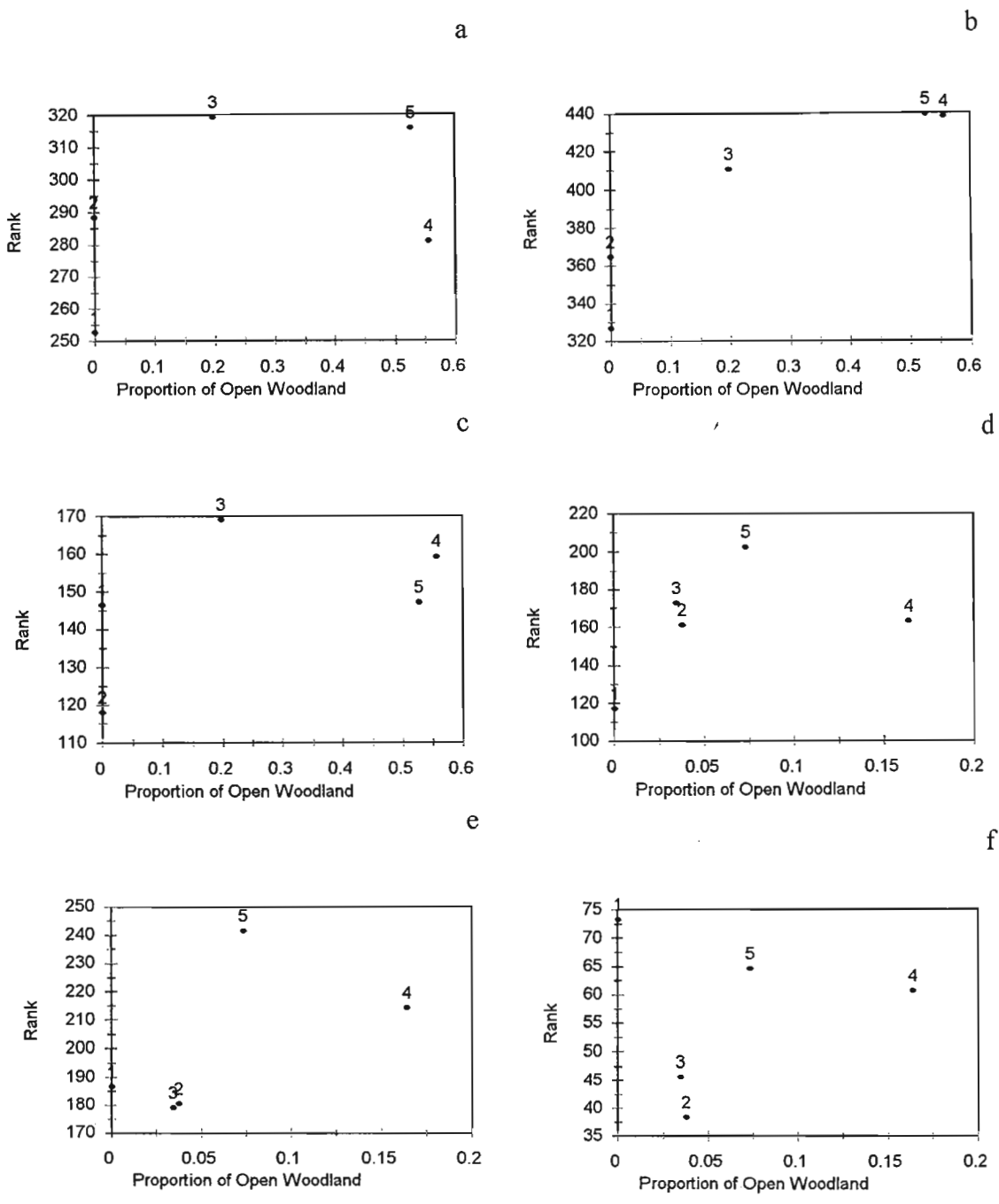
Appendix 4

Figure 4.1: The relationship between proportion of open woodland and group sizes for (a) adult males in mixed groups [1973 - 1984]; (b) adult females in mixed groups [1973 - 1984]; (c) cubs [1973 - 1984]; (d) adult males in mixed groups [1985 - 1999]; (e) adult females in mixed groups [1985 - 1999]; (f) cubs [1985 - 1999]. Management sections are denoted by the numerals labelling each point. Higher ranks equate to larger group sizes.
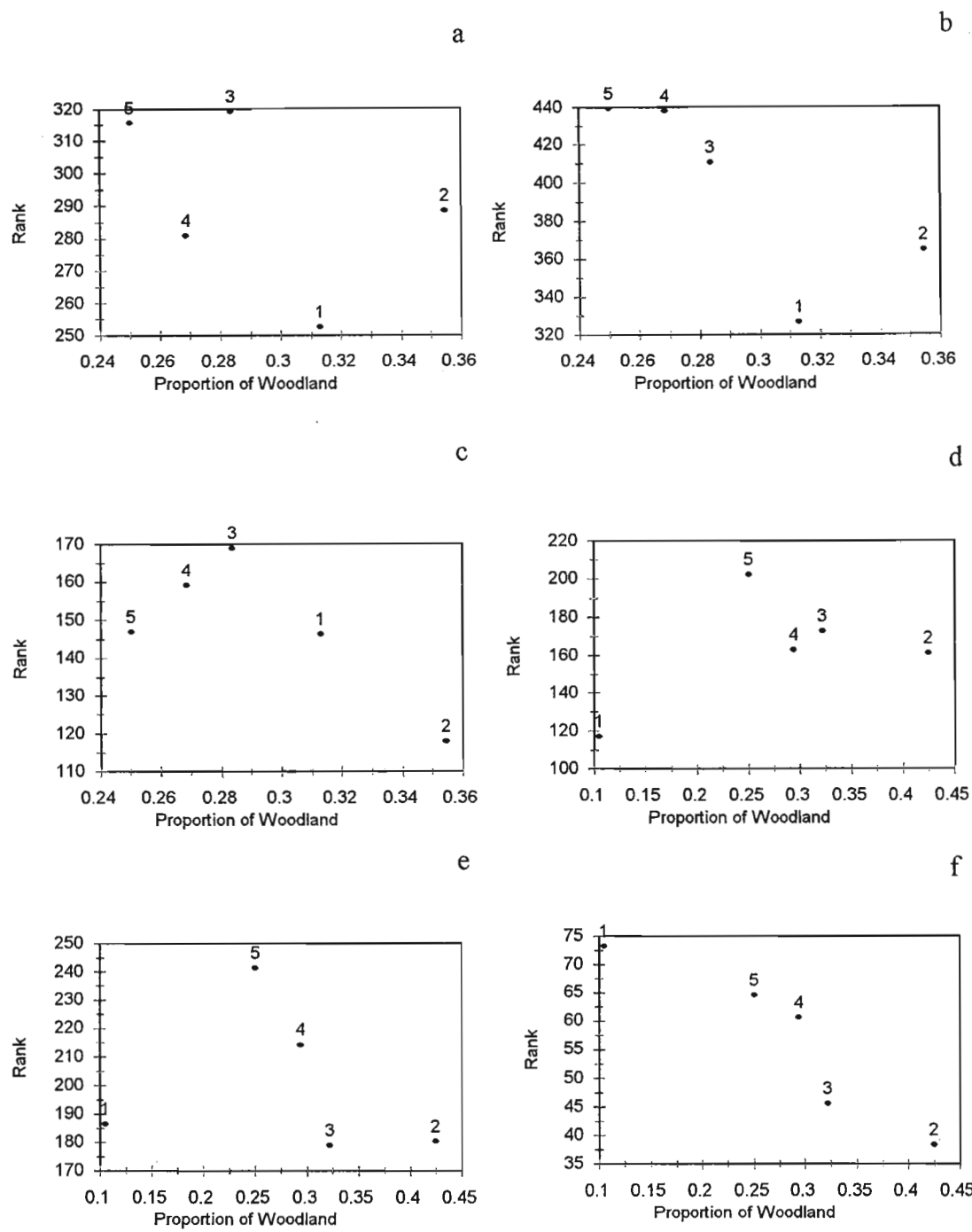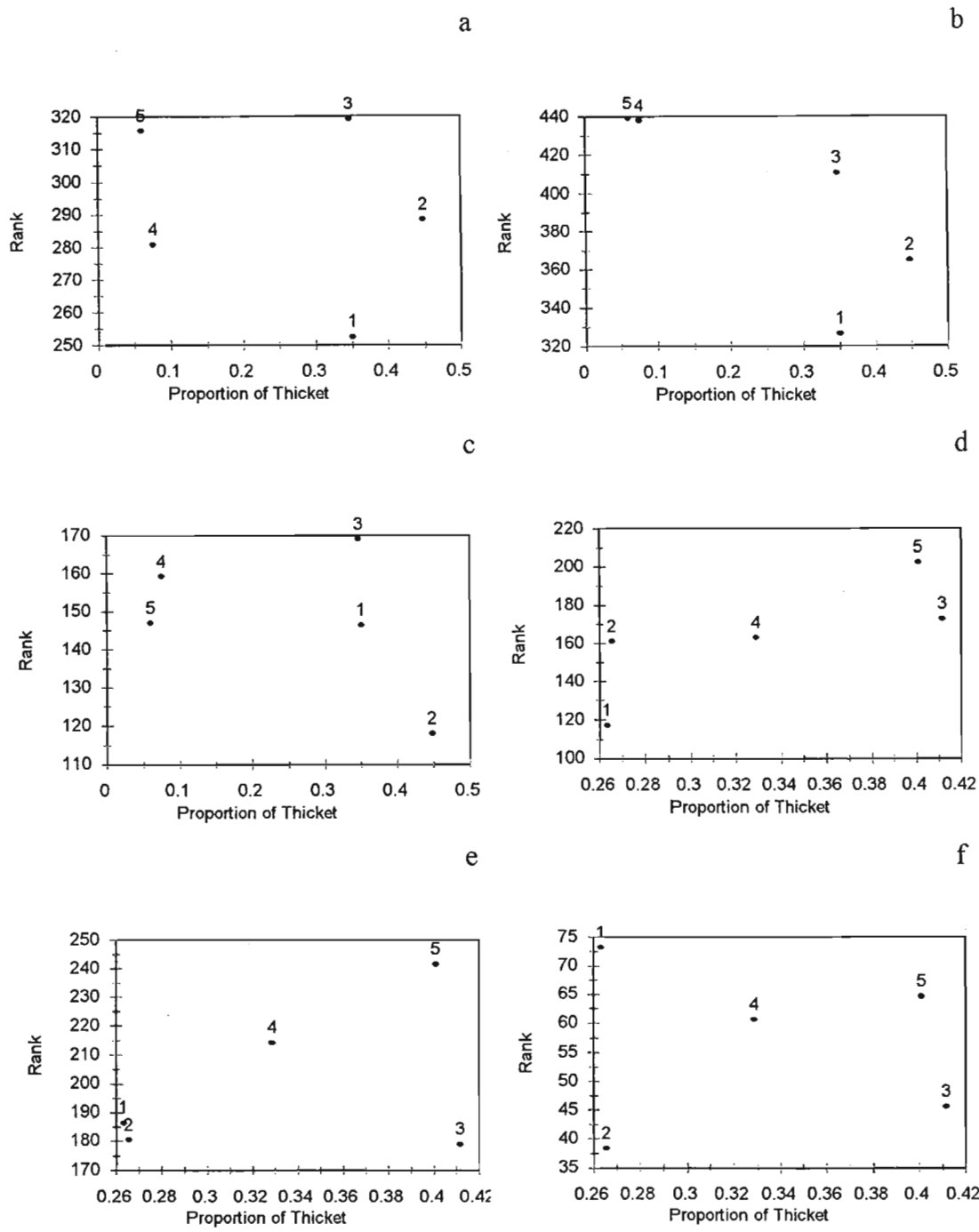
Figure 4.2: The relationship between proportion of woodland and group sizes for (a) adult males in mixed groups [1973 - 1984]; (b) adult females in mixed groups [1973 - 1984]; (c) cubs [1973 - 1984]; (d) adult males in mixed groups [1985 - 1999]; (e) adult females in mixed groups [1985 - 1999]; (f) cubs [1985 - 1999]. Management sections are denoted by the numerals labelling each point. Higher ranks equate to larger group sizes.
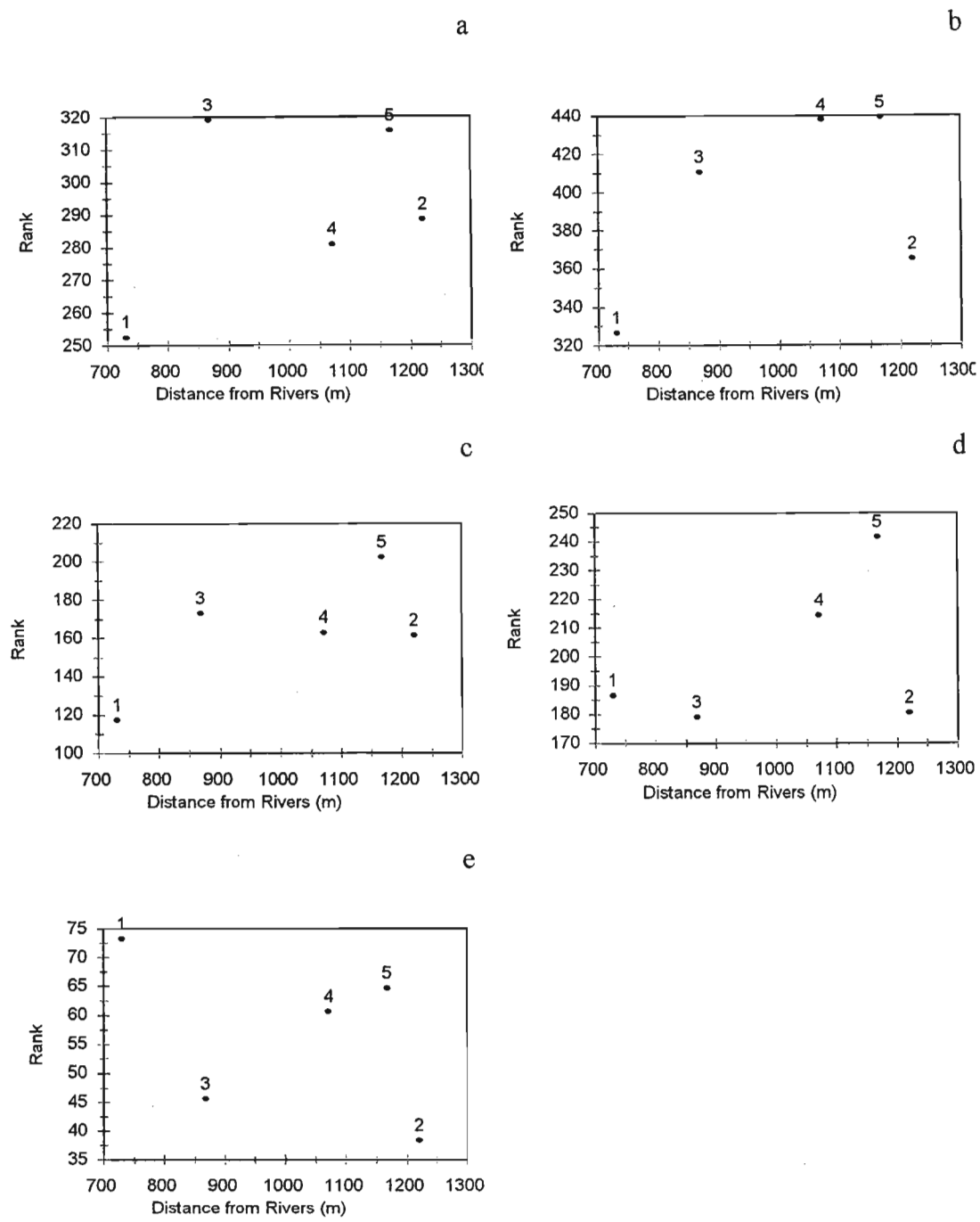
Figure 4.3: The relationship between proportion of thicket and group sizes for (a) adult males in mixed groups [1973 - 1984]; (b) adult females in mixed groups [1973 - 1984]; (c) cubs [1973 - 1984]; (d) adult males in mixed groups [1985 - 1999]; (e) adult females in mixed groups [1985 - 1999]; (f) cubs [1985 - 1999]. Management sections are denoted by the numerals labelling each point. Higher ranks equate to larger group sizes.

Figure 4.4: It is likely that the effect of distance from rivers on grouping patterns can not be determined at this scale for (a) adult males in mixed groups [1973 - 1984]; (b) adult females in mixed groups [1973 - 1984]; (c) adult males in mixed groups [1985 - 1999]; (d) adult females in mixed groups [1985 - 1999]; (e) cubs [1985 - 1999]. Management sections are denoted by the numerals labelling each point. Higher ranks equate to larger group sizes.
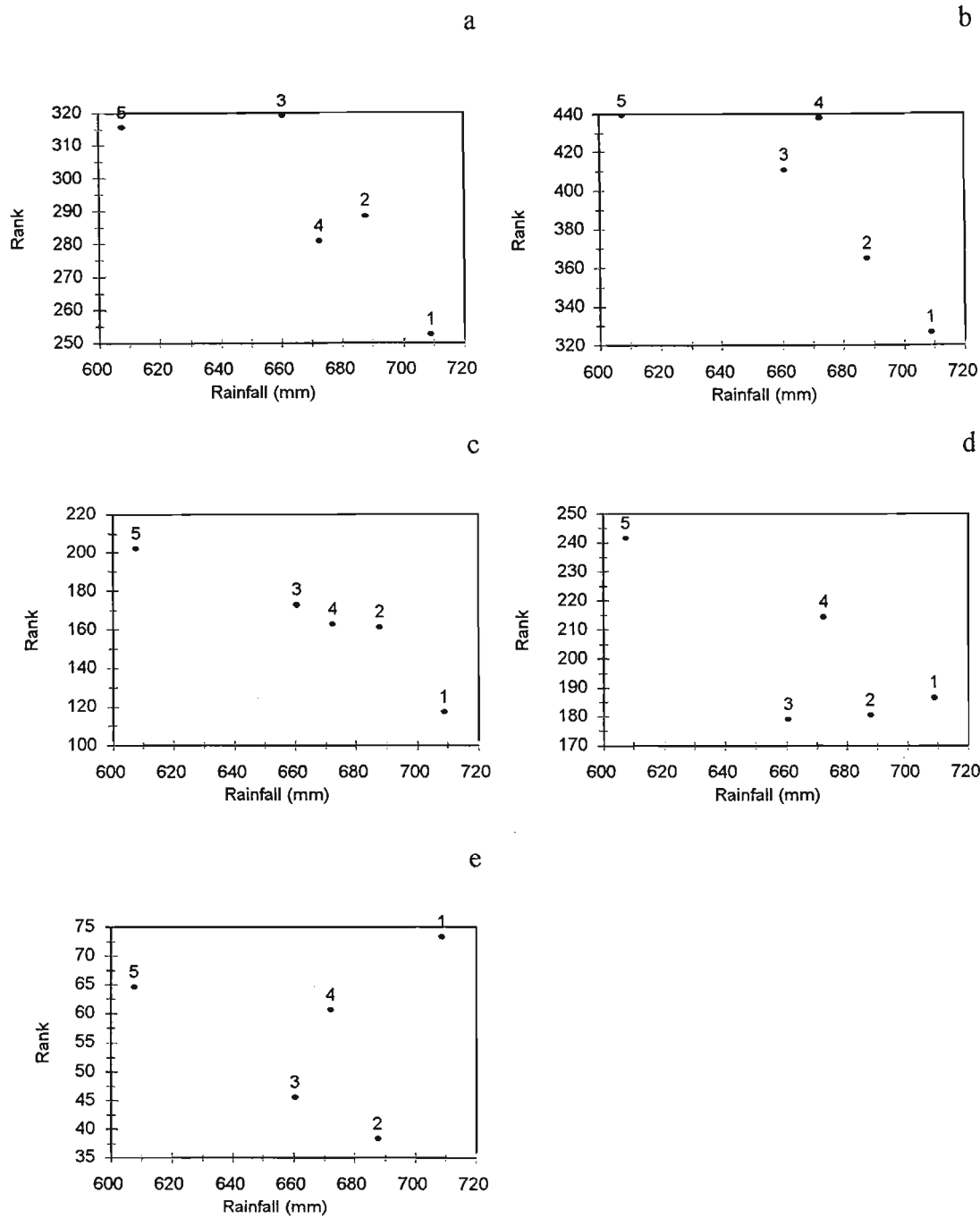
Figure 4.5: Group sizes may be affected by mean annual rainfall differences within the reserve. The following groups are illustrated: (a) adult males in mixed groups [1973 - 1984]; (b) adult females in mixed groups [1973 - 1984]; (c) adult males in mixed groups [1985 - 1999]; (d) adult females in mixed groups [1985 - 1999]; (e) cubs [1985 - 1999]. Management sections are denoted by the numerals labelling each point. Higher ranks equate to larger group sizes.
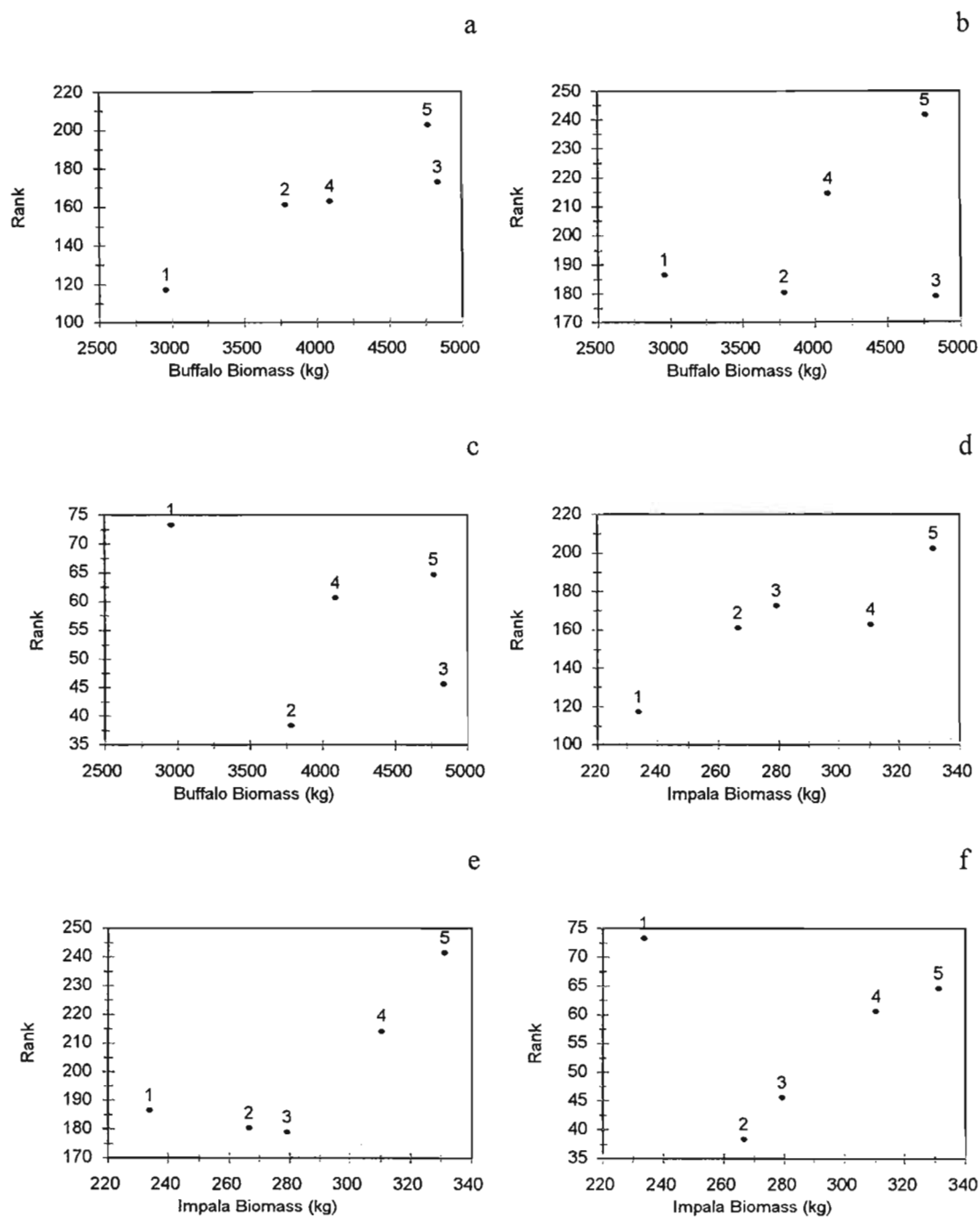
Figure 4.6 a-f: The availability of different prey species may influence grouping patterns. Group sizes related to Buffalo biomass are shown for (a) Adult males in mixed groups; (b) Adult females in mixed groups; (c) Cubs; and for Impala biomass (d) Adult males in mixed groups; (e) Adult females in mixed groups; (f) Cubs. Low ranks are indicative of smaller group sizes.
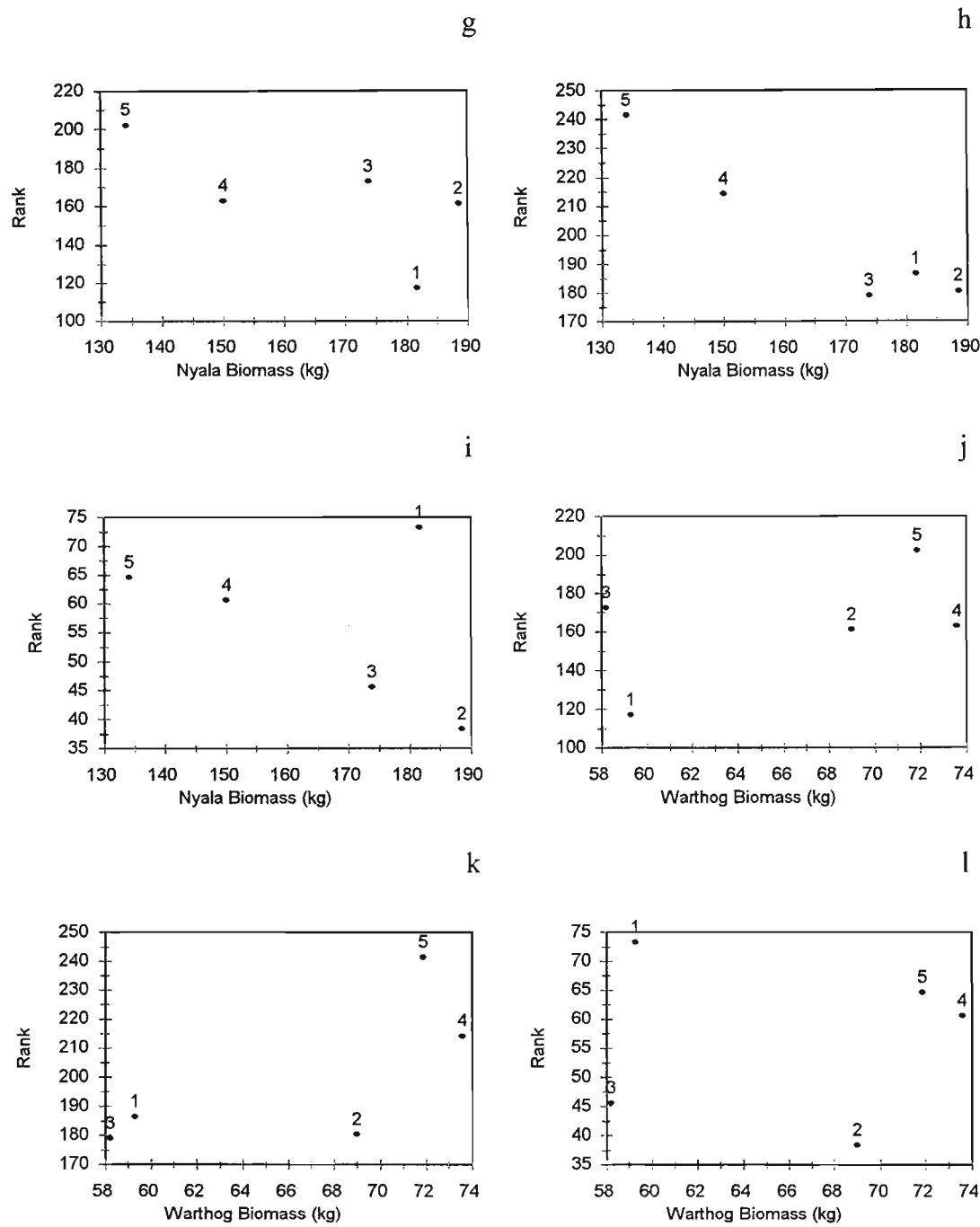
g

h

i

j

k

l

Figure 4.6 g-l: The availability of different prey species may influence grouping patterns. Group sizes related to Nyala biomass are shown for (g) Adult males in mixed groups; (h) Adult females in mixed groups; (i) Cubs; and for Warthog biomass (j) Adult males in mixed groups; (k) Adult females in mixed groups; (l) Cubs. Low ranks are indicative of smaller group sizes.
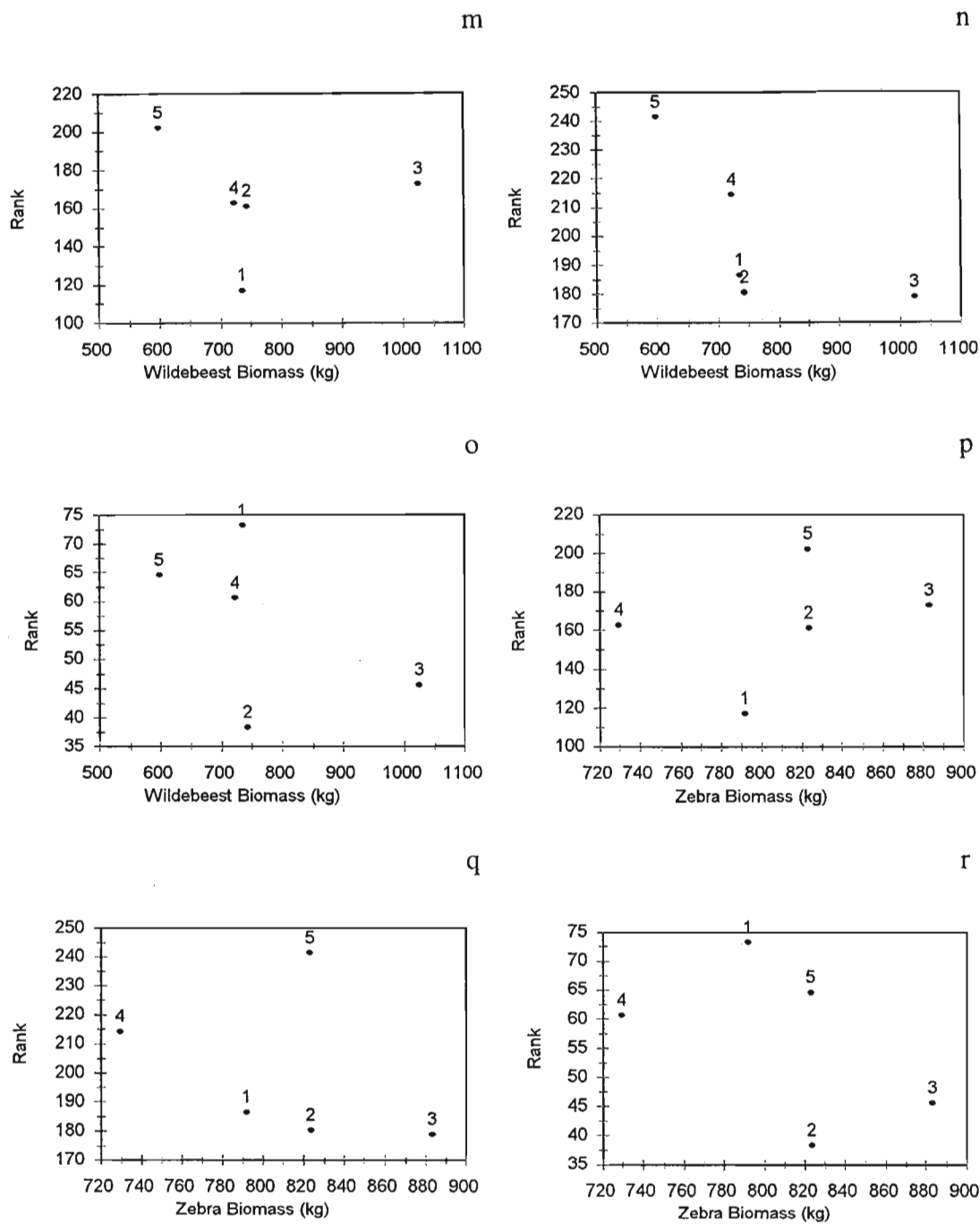
Figure 4.6 m-r: The availability of different prey species may influence grouping patterns. Group sizes related to Wildebeest biomass are shown for (m) Adult males in mixed groups; (n) Adult females in mixed groups; (o) Cubs; and for Zebra biomass (p) Adult males in mixed groups; (q) Adult females in mixed groups; (r) Cubs. Low ranks are indicative of smaller group sizes.

Appendix 5

Model Details

Cubs: 1973 - 1984 data

Sighting Category 1 (73CubC1):

$$f(x) = -0.701(\pm0.206) + 0.961(\pm0.181) \text{ x public roads} - 0.001408(\pm0.000371) \text{ x}$$

$$\text{river dist} + 0.00000034(\pm0.000000125) \text{ x rivdisq.}$$

Residual Deviance: 823.7 (815 d.f.)

Sighting Category 2 (n73CubC2):

$$f(x)= -3.792(\pm0.555) +1.376(\pm0.322) \text{ x public roads} - 0.001153(\pm0.000358) \text{ x}$$

$$\text{river dist} + 0.1175(\pm0.0422) \text{ x slope} + 0.01661(\pm0.00681) \text{ x woodland}$$

Residual Deviance: 303.3 (699 d.f.)

Sighting Category 1: There were no significant interactions between public roads and vegetation cover. It should be mentioned, however, that there was a negative interaction between open woodland and public roads, (P = 0.074) as was found with the female data. Because the term does not add a significant amount of change, it has not been added to the model.

Sighting Category 2: Following diagnostic checking, two variables were dropped from the original model, while still maintaining a significant fit to the validation data. No significant interactions.

Females: 1973 - 1984 data

Sighting category 1 (n73FemC1):

$$f(x) = -0.461 + 1.011(\pm0.174) \text{ x public roads} - 0.000485(\pm0.000136) \text{ x river dist} +$$

$$0.0341(\pm0.0169) \text{ x grassland}$$

Residual Deviance: 872.9 (700 d.f.)

incorporating open woodland interaction (n73owfmC1):

$$f(x) = -0.485(\pm0.172) + 1.323(\pm0.231) \text{ x public roads} - 0.000448(\pm0.000137) \text{ x}$$

$$\text{river dist} + 0.00114(\pm0.00318) \text{ x open woodland} - 0.01194(\pm0.00539) \text{ x}$$

[open woodland*public roads]

Residual Deviance: 870.8 (699 d.f.)

incorporating thicket interaction (n73thfmC1):

$$f(x) = -0.372(\pm0.167) + 0.540(\pm0.241) \text{ x public roads} - 0.000456(\pm0.000136) \text{ x}$$

$$\text{river dist} - 0.00321(\pm0.00374) \text{ x thicket} + 0.01774(\pm0.00668) \text{ x}$$

[thicket*public roads]

Residual Deviance: 869.2 (699 d.f.)

Sighting Category 2 (73FemC2):

$$f(x) = -1.030(\pm0.364) + 0.907(\pm0.283) \text{ x public roads} +$$

$$0.00000022(\pm0.000000073) \text{ x rddisq} - 0.001575(\pm0.000459) \text{ x riverdist} +$$

$$0.000000398(\pm0.000000155) \text{ x rivdisq} - 0.000769(\pm0.000371) \text{ x road dist}$$

Residual Deviance: 596.6 (813 d.f.)

Sighting Category 1: When incorporating all significant interactions between public roads and vegetation type, the model was "swamped" with the result that several terms found significant previously, now became non-significant. The matter was resolved by simply having two models for Fem C1 data, one incorporating the interaction of thicket and public roads (no open woodland interactions), and the other incorporating the interaction of open woodland and public roads (no thicket interactions.). Following diagnostic checking, a number of grid cells were omitted from the data set with the result that several variables found to be previously significant were able to be eliminated without compromising the fit of the models to the validation data.

Main effects of thicket and open woodland were non-significant.

Sighting Category 2: no significant interactions.

Males with Females: 1973 - 1984 data

Sighting Category 1 (n73M&F C1):

$$f(x) = -0.515(\pm0.154) + 0.643(\pm0.174) \text{ x public roads} - 0.000430(\pm0.000136) \text{ x}$$
$$\text{riverdist}$$

Residual Deviance: 870.2 (700 d.f.)

Sighting Category 2 (73M&F C2):

$$f(x) = -1.367(\pm0.192) + 0.585(\pm0.222) \text{ x public roads} - 0.000866(\pm0.000194) \text{ x}$$
$$\text{river dist}$$

Residual Deviance: 597.2 (816d.f.)

Sighting Category 1: no significant interactions were found. Following diagnostic checking and subsequent re-fitting of the model it was found that, while no terms were able to be eliminated from the model, the fit to the validation data was improved, hence this model was chosen above it's predecessor.

Sighting Category 2: no significant interactions.

Males: 1973 - 1984 data

Sighting Category 1 (n73Mal C1):

$$f(x) = 0.058(\pm 0.146) + 0.747(\pm 0.172) \text{ x public roads} - 0.000535(\pm 0.000128) \text{ x}$$

$$\text{river dist}$$

Residual Deviance: 927.9 (701 d.f.)

Sighting Category 2 (73Mal C2):

$$f(x) = -0.684(\pm 0.221) - 0.001629(\pm 0.000397) \text{ x river dist} + 0.839(\pm 0.200) \text{ x public}$$

$$\text{roads} + 0.000000351(\pm 0.000000139) \text{ x rivdisq} +$$

$$0.000000035(\pm 0.000000016) \text{ x rddisq}$$

Residual Deviance: 787.3 (814 d.f.)

Sighting Category 1: no significant interactions. Following diagnostic checking and re-modeling, one term was dropped and the subsequent fit of the predicted values to the validation data was improved.

Sighting Category 2: no significant interactions.

Cubs: 1985 - 1999 data

Sighting Category 1 (85Cub C1):

$$f(x) = -1.264(\pm 0.311) - 0.1439(\pm 0.0503) \times slope$$

Residual Deviance: 450.4 (678 d.f.)

Sighting Category 1: No significant interactions.

Sighting Category 2: no models were formulated owing to an insufficient number of

observations/data points.

Females: 1985 - 1999 data

Sighting Category 1 (85Fem C1):

$$f(x) = -2.681(\pm 0.812) + 0.525(\pm 0.205) \times public\ roads - 0.002257(\pm 0.000807) \times$$

$$kudu + 0.677(\pm 0.224) \times vegNDC$$

Residual Deviance: 725.1 (676 d.f.)

Sighting Category 2 (85Fem C2):

$$f(x) = -6.78(\pm 1.53) - 0.0336(\pm 0.0106) \times thicket + 1.063(\pm 0.390) \times vegNDC +$$

$$0.01983(\pm 0.00710) \times warthog + 1.157(\pm 0.445) \times intersection$$

Residual Deviance: 303.5 (675 d.f.)

Sighting Category 1: No significant interactions.

Sighting Category 2: No significant interactions.

Males & Females: 1985 - 1999 data

Sighting Category 1 (85M&F C1):

$$f(x) = -3.780(\pm 0.899) - 0.01868(\pm 0.00551) \text{ x thicket} + 0.707(\pm 0.228) \text{ x vegNDC}$$

$$+ 0.01233(\pm 0.00428) \text{ x warthog}$$

Residual Deviance: 715.3 (676 d.f.)

Sighting Category 2 (85M&F C2):

$$f(x) = -2.482(\pm 0.678) + 1.655(\pm 0.414) \text{ x intersection} - 0.02601(0.00951) \text{ x thicket}$$

$$+ 0.01648(\pm 0.00728) \text{ x warthog} - 0.0001265(\pm 0.0000606) \text{ x den dist}$$

Residual Deviance: 317.0 (675 d.f.)

Sighting Category 1: no significant interactions.

Sighting Category 2: no significant interactions.

Males: 1985 - 1999 data

Sighting Category 1 (85Mal C1):

$$f(x) = -0.997(\pm 0.359) + 0.01763(\pm 0.00396) \text{ x warthog} - 0.01713(\pm 0.00485) \text{ x}$$

$$\text{thicket} + 0.00000019(\pm 0.000000051) \text{ x rddisq} - 0.000794(\pm 0.000237) \text{ x road dist}$$

Residual Deviance: 802.4 (675 d.f.)

Sighting Category 2 (85Mal C2):

$$f(x) = -5.01(\pm1.52) - 0.02977(0.00834) \text{ x thicket} + 1.103(\pm0.382) \text{ x vegNDC} -$$

$$0.0001451(0.0000513) \text{ x den dist} + 0.00740(\pm0.00241) \text{ x altitude} -$$

$$0.000410(\pm0.000206) \text{ x river dist}$$

Sighting Category 1: no significant interactions.

Sighting Category 2: no significant interactions.