HABITAT SELECTION, NUMBERS AND DEMOGRAPHICS OF LARGE MAMMALIAN HERBIVORES IN ITHALA GAME RESERVE, KWAZULU NATAL.

by

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ABSTRACT

With the purpose of improving the conservation management of Ithala Game Reserve and other similar reserves, the aims of this study were to determine the reserve's large mammalian herbivores' habitat occupancy, numbers and demographics, to investigate the feasibility of road strip counts as a census method for the same herbivores and to establish what environmental factors influence their habitat occupancy, numbers and demographics.

Four years of demographic data were collected by vehicle transects on giraffe, kudu, wildebeest and impala. During the final two years additional positional data, using GPS, were collected on these and the reserve's other large herbivores. Sightings were recorded on the basis of habitat type occupied, a GIS was then used to define area sampled and hence derive habitat occupancy densities. GIS was further used to determine both absolute population sizes and, by over-laying other available GIS data, the relevance of distance to surface water, soil type and degree of slope to species' habitat preferences.

Species showed non-random, significant habitat selections broadly in line with established preferences. Deterioration in habitat quality in winter generally lead to changes in habitat selection and the extent and nature of these changes related to the severity of resource pressure for individual species. This in turn was influenced by the species digestive strategy i.e. ruminant versus non-ruminant, grazer versus browser. Generally species showed a dry season move down the slope, moving, in some cases, onto heavier soils. Hartebeest, warthog, wildebeest and impala were strongly attracted to winter grass flushes. Lack of predation may be influencing the habitat selection decisions of impala and giraffe and kudu females, as well as allowing giraffe, wildebeest and impala to attain comparatively high densities. Giraffe density (effectively 1.8 km^{-2}) was abnormally high and their habitat quality poor, leading to a decline in numbers and low fecundity-related demographics. Wildebeest density (6 km^{-2}) was also abnormally high and this may be instrumental in the poor performance of the rare tsessebe population, which is in decline and shows low fecundity-related demographics, increased dry season pressure on other grazers in general and impala unexpectedly preferring browse habitats, rather than grasslands, in the wet season. Wildebeest fecundity declined in response to lower rainfall over the early period of lactation. Herbivores with an open social structure generally showed a dry season decrease in group size, although wildebeest and hartebeest showed, atypically, an increase. Giraffe, zebra and impala adult sex ratios were comparatively less female biased, probably due to minimal predation. Territorial behaviour, virtually year round by wildebeest bulls and over the rut by impala bulls, imposed spatial sexual segregation between breeding and bachelor herds in these species. Outside of these periods, and generally in species not exhibiting territoriality, social sexual segregation was maintained and appeared to relate to differing activity budgets. Areas of concern for management are highlighted.

Numbers results were generally acceptable and the method is proposed as a cost effective alternative in reserves with diverse topography. Underlying environmental determinants of habitat occupancy, numbers and demographics, together with associated annual or seasonal changes, were habitat quality, competition and predation.

PREFACE

The field work described in this dissertation was carried out in Ithala Game Reserve, KwaZulu Natal from November 2000 to September 2004. The first two year's field work was supervised by Ian Rushworth, Regional Ecologist at KZN Wildlife and the last two by Bruce Page, Lecturer at the School of Life and Environmental Sciences, University of KwaZulu Natal, Durban. All analysis was carried out at the author's home in Pietermaritzburg and supervised by Bruce Page.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

C.A.J. O'KANE 25th March

LIST OF CONTENTS

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CHAPTER ONE

GENERAL OVERVIEW

Introduction

Conservation of maximum biodiversity for posterity is the stated goal of all contracting parties to the Global Biodiversity Convention (WRI/IUCN/UNEP 1992) and of the National Parks of South Africa (Anon 1987). For biodiversity to be maintained in game reserves, especially enclosed ones, management require knowledge of the habitat preferences, numbers and demographics of the animals within (Owen-Smith 2002a).

From the records of the earliest travellers it has been acknowledged that a relationship between animals and their environment exists. Earlier researchers described, in descriptive terms, animals' favoured habitats and, based on this habitat selection, identified associations of different animal species favouring the same set of environmental features (Pienaar 1963). Tinley (1969) proposed using more objective means of assessing habitats and, subsequently, Hirst (1975) undertook a more comprehensive study of the factors affecting habitat selection by large herbivores. With a growing understanding, in more recent years, of the population dynamics of animal populations, it has become increasingly clear that the suitability of the habitat and its role in determining the trends of the associated animal populations is of fundamental importance (Beardall et al. 1984). Especially within an ecosystem context a clear understanding of the factors influencing habitat selection, together with an understanding of the salience of the different habitat factors for the various animal populations, is considered a prerequisite for the objective interpretation of the interactions between animals and their environment. It is also a prerequisite to understanding their distribution and abundance and to determining possible species for re-introduction, as well as the density at which they can be stocked (Dekker et al. 1996). Failure to understand these factors has negative implications for both the animals themselves and the wider environment (Ferrar and Walker 1974). For instance, veld degradation and change in habitat quality in the Lowveld of South Africa can largely be ascribed to overstocking and/or poor management, resulting primarily from overestimation of the carrying capacity of the veld for various animal species (Bodenstein et al. 2000).

For African ungulates the main determinants of local migrations between habitats include forage availability, forage quality, water availability (Ben-Shahar and Coe 1992), predation (Sutherland 1996) and certain landscape features such as vegetation composition and structure, topography and soil types (Ben-Shahar 1995). Seasonal movements of animals may be attributed to climatic conditions, movements along the catena (Bell 1970) and the seasonal phenological development of forage and fire (Munthali and Banda 1992).

The spatial distributions of such biotic and abiotic assets on reserves are frequently recorded by wildlife managers, but, regrettably, these data are seldom used due to time constraints and insufficient personnel (Fabricius and Coetzee 1992). The advent of geographic information systems (GIS) offers an accessible and relatively rapid way of relating these data. A GIS is a computer program designed to store, manipulate and display data that are recorded according to geographic location (ESRI 1996). A GIS is capable of handling attribute or descriptive data about localities. Since natural resources are distributed spatially, i.e. in relation to localities, GIS is suitable for dealing with such data.

Habitat type, or vegetation community, has widely been shown to be the major influence on large mammalian herbivores' habitat selections (Vesey-FitzGerald 1960, Lamprey 1963, Keast 1968, Field and Laws 1970, Blankenship and Field 1972, Ferrar and Walker 1974, Pienaar 1974, Dekker et al. 1996). At Ithala Game Reserve, vegetation community has previously been described and entered into a GIS (Balcomb 1996), together with other pertinent environmental variables (surface water, soil types and degree of slope). The situation existed, therefore, where only the spatial position of the reserve's large herbivores was required, as an additional 'layer' of GIS information, to elucidate their habitat preferences by inter-relating the GIS layers. Determination of any variation in their position over the seasons would reveal seasonal habitat preferences. GIS has apparently been used in just one African ungulate, roan, to investigate the interrelationship of environmental determinants of habitat use (Perrin and Taolo 1999), whilst no studies have applied the technique across a guild of African ungulates.

However, numbers of animals occurring in a habitat type, on a certain soil type or a particular slope are, however determined, of little use in themselves as they may merely reflect the prevalence of that particular habitat type, soil or slope in the area sampled. Actual densities are required. In a reserve such as Ithala, characterised by steep valleys and large areas of tall, dense vegetation, spotting animals reliably, especially those of the browsing guild, from the air is difficult – and expensive. Transects by foot are equally impractical. Road transects allow a more thorough recording of large herbivores' positions, but rapid changes in visibility, due to topography, negate the assumptions of most techniques (Caro 1999) used to determine area sampled. This problem applies to the majority of reserves in this part of South Africa (Jachmann 2002). GIS again affords a solution in that it can be used to define the area sampled, from which densities, in relation to any of the variables entered into the system, can be easily determined.

Knowledge of the numbers of animals, and how they change over time, is a basic requirement for effective management of a reserve. Although widely used, aerial counts are generally believed to be inaccurate (Redfern et al. 2002). Specifically in Ithala, management also believed them to be inaccurate and that they were underestimating populations (Balfour pers.comm). Management therefore required an alternative, and more cost effective, method of censusing. Given that herbivores distribute themselves largely on the basis of habitat type, determination of numbers on the basis of their densities in each habitat type appeared to be logical. Since GIS, by using the vegetation layer of the whole reserve, could determine total area of each vegetation type in the reserve, total numbers for each species in the reserve could be determined.

Two factors operate separately or together to affect accuracy of a single count: imprecision (which may either increase or decrease the estimate) and bias (which consistently affects the estimate in the same direction) (Magin 1989). It is therefore necessary to determine, respectively, the level of replication and stratification required in a sampling technique to produce acceptable estimates. The existing population estimates in the reserve (including management's adjustments to aerial counts) served as a yardstick for this study's population estimates and therefore also, as they were based on the same data, for the habitat selection estimates.

Unless annual censuses are carried out over many years separating counting error from demographic change is not possible. If demographics are recorded annually however, a means of separating the two is provided. Previous studies (Wolf 1997, Adcock 2000, Openshaw 2000) had shown that certain herbivores' population growth in the reserve has been well below their potential, and management had current concerns as to the demographics of the reserve's population of the endangered tsessebe (Pillay 2004 pers.comm). There were also additional concerns as to the state and normality of certain herbivores' sex ratios and how this should relate to the reserve's removals programmes (Rushworth 2002 pers.comm). For these reasons management of the reserve required data on the demographics of the reserve's herbivores. Recording demographic data in the field adds very little time to the recording of position and numbers.

A snap shot of species habitat preferences, numbers and demographics is of limited use. They should be determined repeatedly over a time frame which will pick up any trends, which are central to the management and conservation of animal populations (Mason 1990b). The author of this dissertation was already collecting raw numbers and demographics data on four species over 2001 and 2002 for the reserve's management, when he was approached to expand the project to include positional data on a wider range of herbivores, with a view to a GIS based approach to determining absolute numbers and habitat preferences. Hence numbers and demographics data on giraffe, kudu, wildebeest and impala were collected over four years (2001 to 2004), whilst for 2003 and 2004 the same data were collected on all the reserve's large herbivores, together with positional data.

Knowledge of animals' habitat preferences, numbers and demographics is, therefore, central to their effective management and conservation. Data required for these three subjects may be collected, as described above, virtually simultaneously in the field and, additionally, their likely underlying environmental determinants, namely habitat quality, competition and predation, are similar. Consequently the three topics lend themselves to a single study.

The broad aims of the study were to determine Ithala Game Reserve's large mammalian herbivores' habitat occupancy, to investigate the feasibility of road strip counts as a census method for the same herbivores and to produce estimates of their absolute abundance, to determine their demographics, and to establish what environmental factors influence habitat occupancy, numbers and demographics.

The specific objectives were:

1) To determine the general habitat occupancy of the different herbivore species, and their different social groups, and to show any changes in this occupancy over the wet/dry seasons.
2) To devise and assess a vehicle based technique for determining acceptable estimates of population numbers of the different herbivore species, and to

3) determine their absolute population numbers and show any changes over time. The technique should be applicable to other, similar reserves.
4) To determine the demographics of the different herbivore species and show any changes over time.
5) To explain the above findings and any changes in terms of relevant environmental determinants.
6) To compare and explain similarities/differences between the above findings and results from other conservation localities.

Study Area

Ithala Game Reserve (29,653 ha) is situated in northern KwaZulu Natal, South Africa (27°30′S, 31°25′E). Elevation ranges from 350 m a.s.l. on the Pongola River, forming the northern boundary, to 1550 m a.s.l. on the southern escarpment plateau. Long term annual rainfall is 791mm, falling mainly during the summer (October to March) (Fig1.1). Summers are warm to hot (daily average of 18-30°C), with winters being warm to mild (15-25°C) (Porter 1983). Frosts do not occur but low (near freezing) temperatures are known during cold windy spells on winter nights. Vegetation, usually in valley bottoms in riverine forest, may be scorched at such times (Porter 1983).

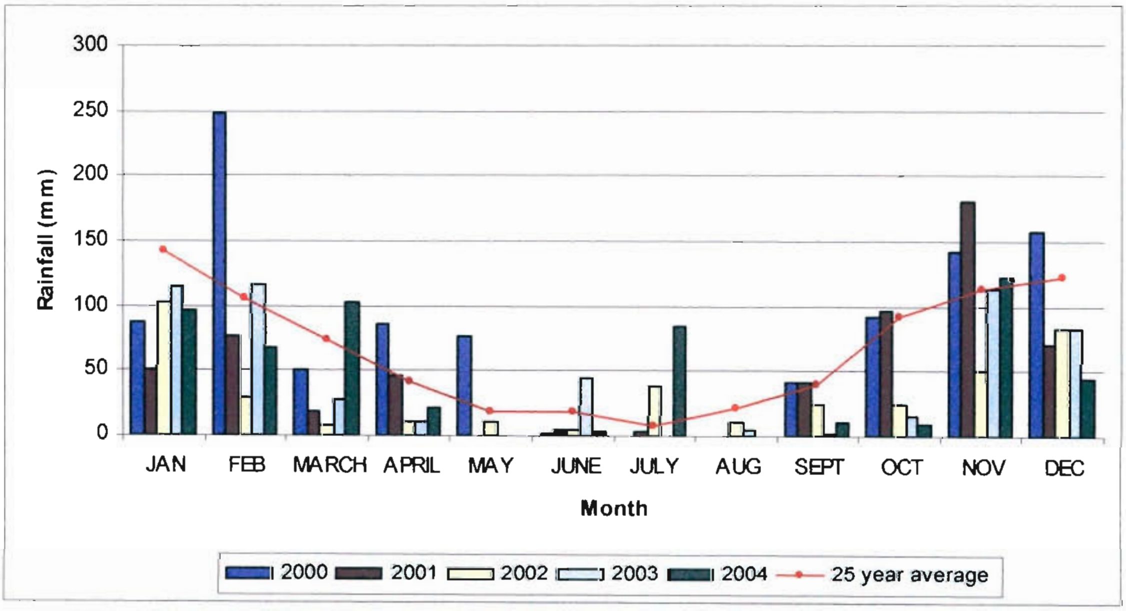

Fig 1.1: Monthly rainfall, Ithala Game Reserve (Thalu) 2000 to 2004, with 25 year average (up to 2003). Data from Ithala Game Reserve research centre.

The reserve is located in steep, dissected terrain, interspersed with broad grassy plains. Gradients exceed 40° on 20% of the reserve, making access difficult to 5884 ha for larger mammals (Le Roux 1985). It is bounded by a major river in the north, into which six main perennial streams drain. Many small annual drainage channels flow into these streams. A few small seasonal pans occur on the tops of hills. There are no artificial water points in the reserve (Fig 1.2). Geology includes Archaean granite exposures, sandstones, shales and mudstones of the Karoo system, and igneous dolerite dykes and sills (Porter 1983) (Fig 1.3). Correspondingly, soil types are as varied, although shallow, rocky (lithosols) of the Mispah form (Group 1991) predominate (Turner 1980) (Fig 1.4).

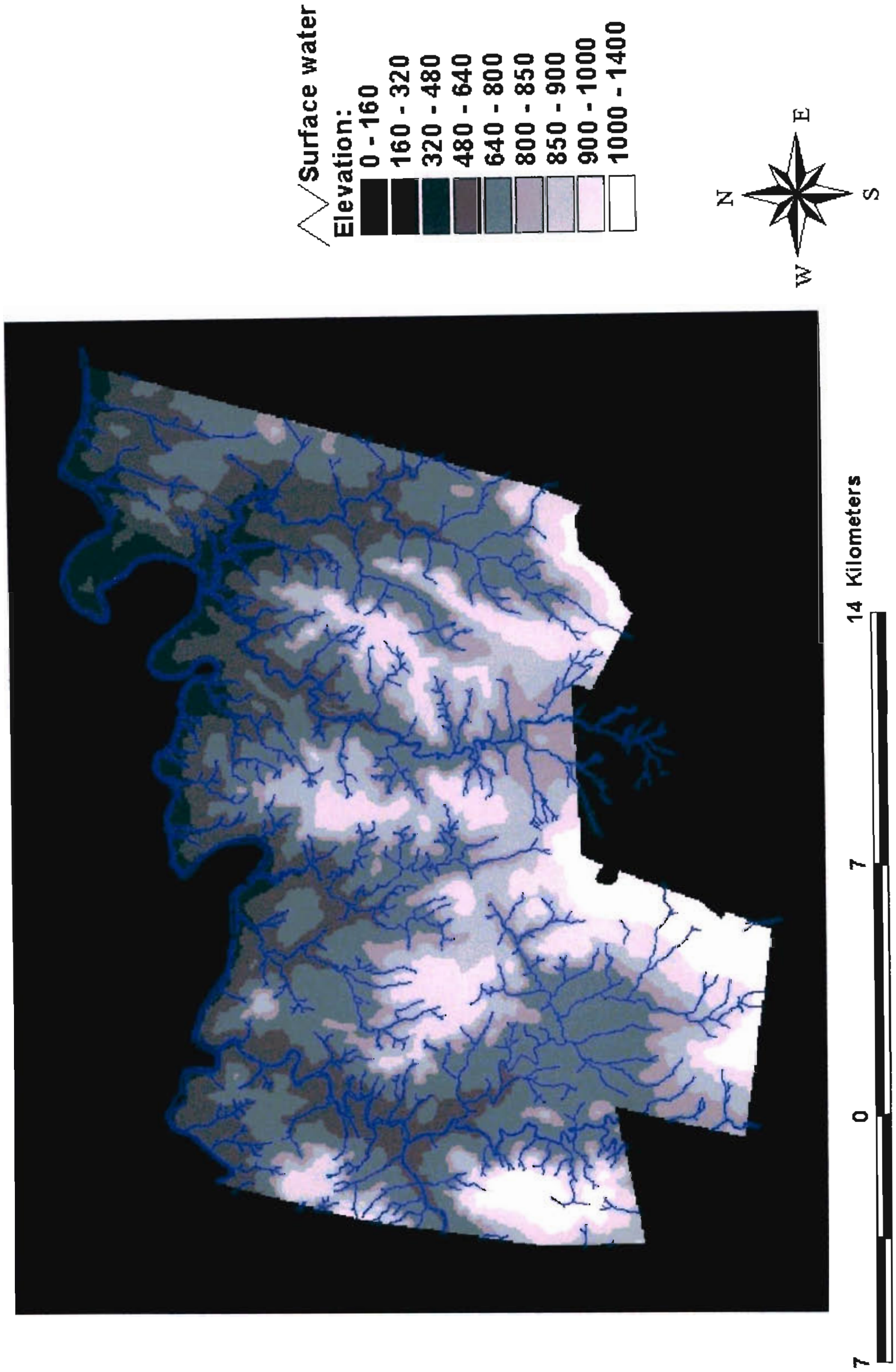

Fig 1.2: Elevation map (in metres above sea level) of Ithala Game Reserve, with surface water. Data from Ithala Game Reserve research centre.

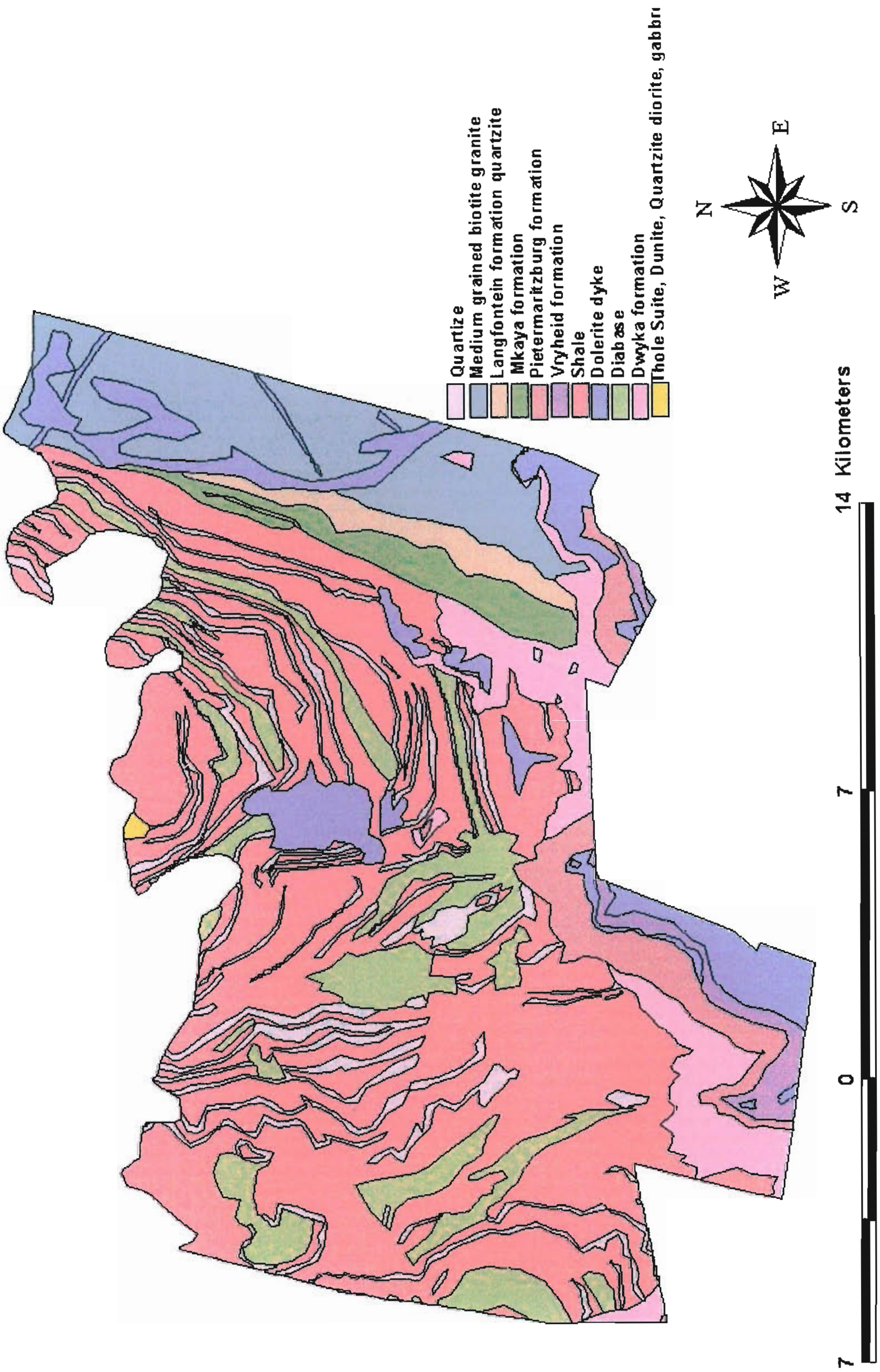

Fig 1.3: Geology map of Ithala Game Reserve. Data from Ithala Game Reserve research centre.

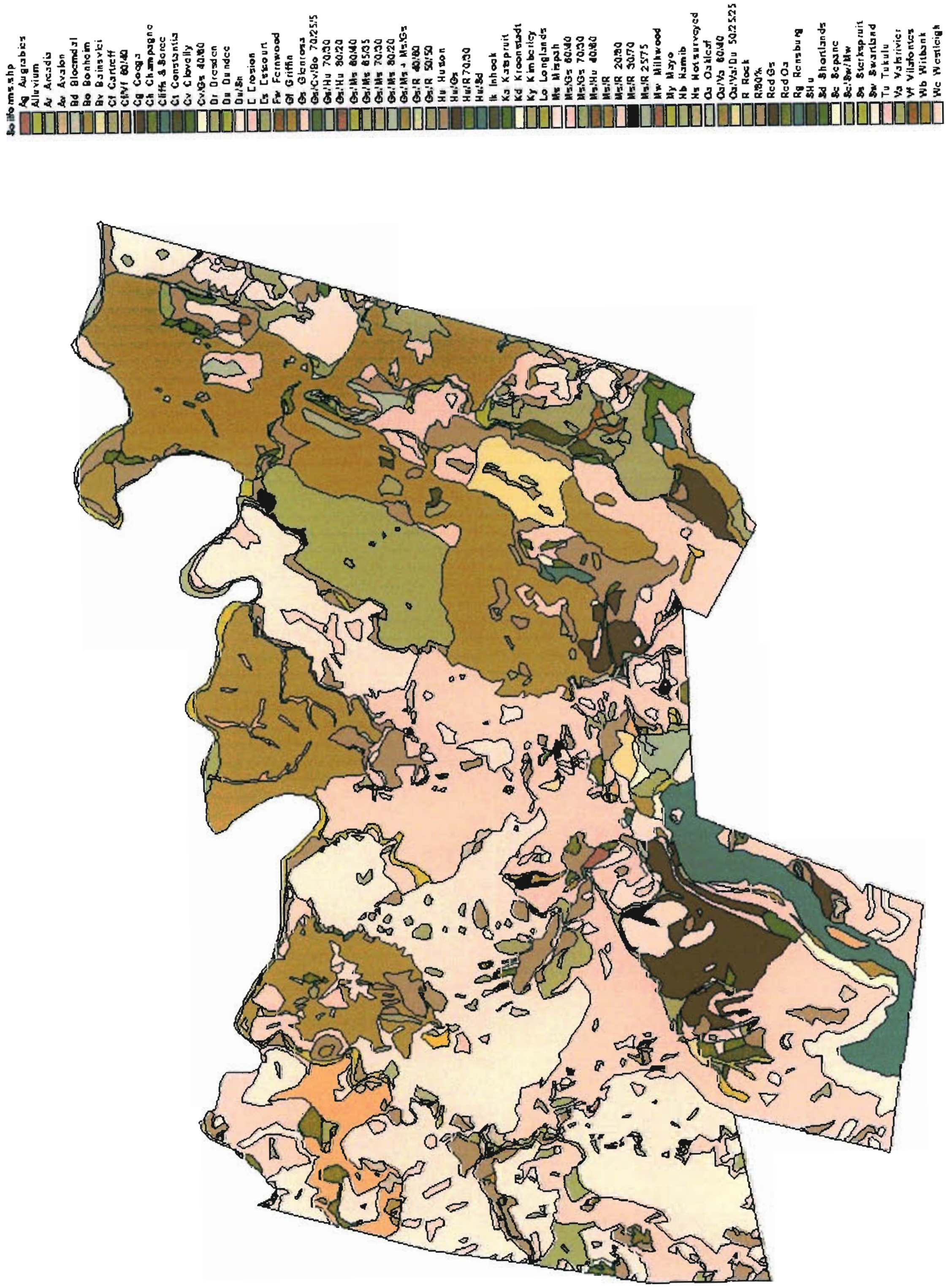

Fig 1.4: Soils map of Ithala Game Reserve. Data from Ithala Game Reserve research centre. Scale and orientation as per Fig 1.2.

The vegetation is a mix of north-eastern mountain grassland at high elevations, Natal central bushveld at mid-elevations and Natal lowveld bushveld at low elevations (Low and Rebelo 1996). Structurally it is a mosaic of grasslands, open savanna dominated by acacias and more or less closed thickets of broad-leaved shrubs and trees (Fig 1.5). The steep environmental gradients contain a varied flora, including a number of species endemic to the area (Scott-Shaw 1999). The vegetation communities may be described in more detail as follows, with physiognomy descriptions being based on Kotze (1990) (Appendix 1): (1) riverine and scree forest (continuous, riverine vegetation), (2) wetlands (sparse, wetland vegetation), (3) undulating tall grassland (sparse, old croplands not on flood plain, dominated by *Hyparrhenia* and *Hyperthelia* sp. with smaller areas of increaser 1 grass species dominated by *Themeda triandra*; where woody species present these include *Dichrostachya cinerea, Rhus lucida* and *Acacia nilotica*), (4) basin bushveld and thicket (closed, *Euclea racemosa*, *D. cinerea*, *A. nilotica*, *Faurea saligna*, *Euphorbia ingens* – very few *F. saligna* and *E. ingens* < 2.5m in height), (5) mixed thornveld (ranges from open, through continuous to closed; disturbed lands, often old kraal sites, *A. nilotica*, *Aloe marlothii*, *Maytenus heterophylla* and *Dombeya rotundafolia*), (6) sparsely wooded hill slopes (open, *Combretum apiculatum*, *D. rotundafolia*, *M. heterophylla*, *A. nilotica* - *C. apiculatum* seldom found at heights < 2.5m), (7) tall deciduous woodland (closed, *Acacia nigrescens*, *A. tortilis*, *A. robusta*, *Spirostachys africana*, *Maytenus senegalensis*), (8) woody rocky outcrops (ranges from open to closed; patchy unit composed of grassland with granite outcrops on which woodies found, *Terminalia phanerophlebia*, *Sclerocarya birrea* subsp. *caffra*, *A. nilotica*, *Lannea discolour*), (9) short mountain grassland (sparse, dominated by increaser 1 grass species, *T. triandra*, *Tristachya leucothrix*, *H. aucta*).

Indigenous animal populations had largely been destroyed by the 1950's in the reserve by a mixture of farming (since 1884), a rinderpest epidemic (1896) and hunting, including that to control tsetse fly (1919-1950) (Johnson 1990). The Natal Parks Board purchased the land in 1972, adding to it at various stages up until 1982, and stocked it with indigenous mammals typical of the south-eastern African savannas, including warthog (*Phacochoerus aethiopicus*), impala (*Aepyceros melampus*), black (*Diceros bicornis*) and white rhinoceros (*Ceratotherium simum*), zebra (*Equus burchelli*), buffalo (*Syncerus caffer*), wildebeest (*Connochaetes taurinus*), kudu (*Tragelaphus strepsiceros*), giraffe (Giraffa camelopardalis) and elephant (*Loxodonta africana*). Although historical records suggest that giraffe did not occur in this part of Africa (Goodman and Tomkinson 1987), giraffe were introduced in 1977 as they had thrived after introduction to similar reserves in the area (Hluhluwe-Umfolozi and Mkuzi). The reserve is entirely fenced except to the north where animal movement is limited by the substantial Pongola River. Consequently no significant immigration/emigration of animals occurs. Although there are small numbers of leopard (*Panthera pardus*), the reserve is not stocked with the major predators (lion, hyaena, cheetah and wild dogs) and, with the exception of cheetah (*Acinonyx jubatus*), these are unlikely ever to be re-introduced because of the small size of the reserve and the nature of its fencing, which is unlikely to restrain the larger predators. Populations have, in the absence of any significant predation and in the presence of fencing, increased to the point where changes in the vegetation are occurring and removals to preserve the reserve's biodiversity have become necessary (Bond and Loffell 2001, Wiseman et al. 2004).

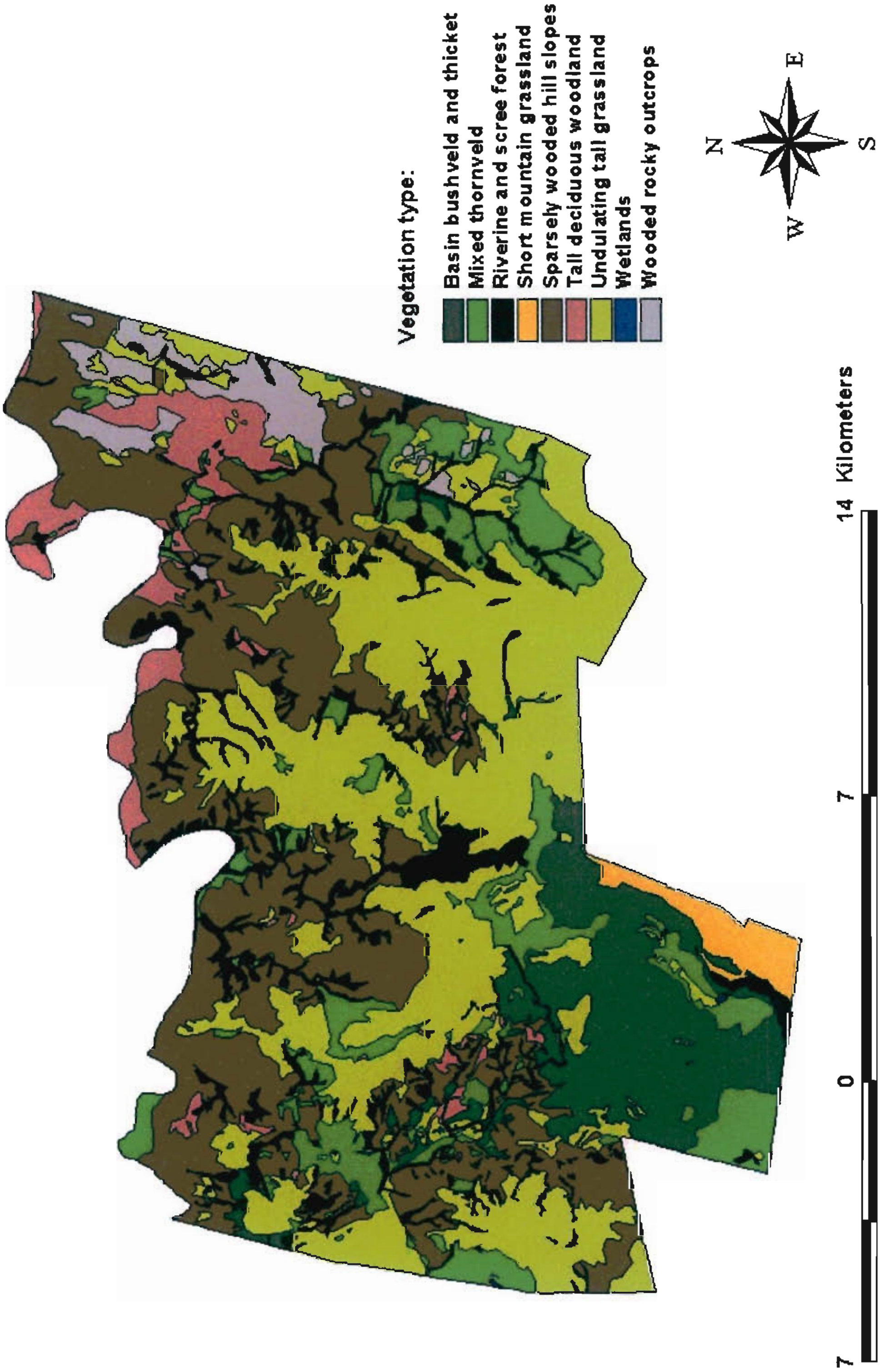

Fig 1.5: Vegetation map of Ithala Game Reserve adapted from Balcomb (1996) by Rushworth (Rushworth 2000).

General Methods

Data collection:

Field trips were conducted about once a month, with data collection taking four days per trip (Appendix 2).The reserve was divided into six routes on the basis that each route could be covered in a morning or afternoon (Fig 1.6 and Table 1.1). Routes were driven at the same time of day on each field trip, with midday being avoided. On each route all tourist and management roads were traversed by vehicle once; any sightings made while retracing a route were ignored. A powerful pair of binoculars (Bausch & Lomb 10 by 25) was used; spotting scopes were found to be too cumbersome and impractical. If there was dead (i.e. not visible) ground between the observer and the animals sighted, the sighting was ignored.

Table 1.1: Description of field routes at Ithala Game Reserve used in this study.

Route number	Route name	Route description	Route distance (km)	Average transit time (minutes)
1	Southern section Ngubhu Loop	Starting junction 11/grid k15, finishing junction 9/grid d17	14.8	149
2	Northern section Ngubhu Loop	Starting grid I12, via junctions 22-9-10-21-Thalu river-4 by 4 track return 22	26.0	196
3	Dakaneni circuit	Ntshondwe camp-junction 7-via 4 by 4 track linking Ngubhu Loop to Dakaneni circuit-Dakaneni Loop-junction 26	30.0	188
4	Bergvliet Loop	Junction 7/grid k14-junction 6-13-26-Bergvliet Loop	19.8	159
5	Mvunyane circuit	Junction 6-5-1-2-14-3-4	12.7	160
6	Mhlangeni/ Phongolo river	Junction 14 to Mhlangeni bush camp and north to Phongolo river using western management road only	44.2	296

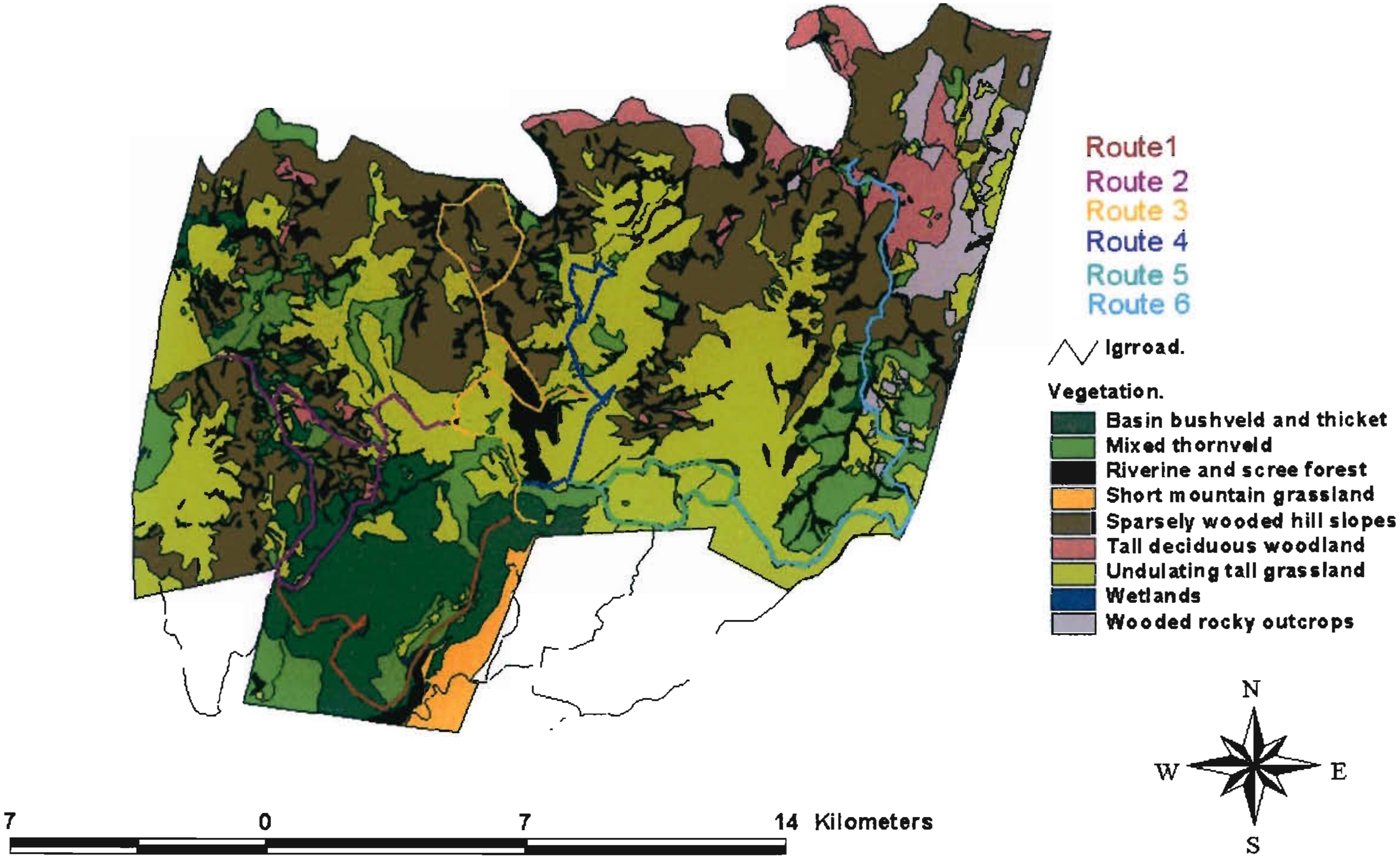

Fig 1.6: Route map, showing vegetation types through which routes travelled.

Once within a classifiable distance with an unobstructed view of the individual/group of herbivores, the total number of animals and then their age and sex were determined working from left to right or right to left. Where possible, the count was then retaken in the opposite direction. The longitude/latitude of the vehicle was determined and recorded using G.P.S. (Garmin 12XL) and the distance from the vehicle to the (approximate) centre of the herd by optical rangefinder (Topcon DM – 500). Since magnetic compasses do not give accurate bearings when near large metal objects (e.g. cars) but G.P.S. does give an accurate bearing for the direction being travelled, the bearing from the vehicle to the herd was determined by adding/subtracting the number of degrees, as indicated by a compass (M73), that the herd was in relation to the bearing indicated by G.P.S. For this technique to be accurate, the vehicle must have been travelling in a straight line long enough for the G.P.S. bearing reading to have 'stabilised'; in Ithala this was typically about 5 metres. Additionally, where possible, to minimise error the vehicle was driven until it was at right angle to the herd; in such cases (representing ~ 70% of observations) 90 degrees was simply added/subtracted to the bearing given by G.P.S. to give the bearing to the herd. These results, together with other pertinent observations, were recorded in the field on a data sheet (Appendix 3) and later entered manually into a database (Microsoft Access 2002).

During 2001/2002, numbers and other demographic data were collected for giraffe, kudu, wildebeest, and impala; during 2003/2004 these data, together with positional data, were collected on all large mammalian herbivores and ostrich (*Struthio camelus*). Time constraints in the field, combined with inter-species differences in ease of identifying age/sex classes, meant that not all aspects of all large herbivore species could be recorded. Consequently it was decided that those species occurring in greatest numbers and/or easily classified (giraffe, kudu, warthog, wildebeest, zebra and impala) would be studied in greatest detail, whilst those occurring in smaller numbers and/or difficult to classify (hartebeest (*Alcelaphus buselaphus*), reedbuck (*Redunca arundinum*), tsessebe (*Damaliscus lunatus*), waterbuck (*Kobus ellipsiprymnus*), white rhino, eland (*Tragelaphus oryx*), nyala (*Tragelaphus angasii*) and ostrich) would be studied in less detail. For example, whilst wildebeest and impala sightings were fully age (adult or yearling or juvenile) and sex classified, for hartebeest and tsessebe no sex classification was obtained and age categories were only adult (incorporating yearling) or juvenile. Within these broad guidelines differences do occur e.g. zebra, although occurring in large numbers, are notoriously difficult to sex classify (Smuts 1974), whilst reedbuck, although occurring in small numbers, are, due to bucks having horns, easy to sex classify. Ostrich, although they cannot chew or ruminate, have a digestive efficiency comparable with that of a large herbivorous mammal (Swart 1988). This, combined with their mobility and selectivity, makes them destructive to rangeland when stocked at high densities (Milton et al. 1994); hence it was decided to include ostrich in the project.

Warthog, wildebeest and impala are seasonal breeders and, as previously observed (Brooks 1985), usually lamb/calve at Ithala over a few weeks in November and December. Therefore, for convenience, 1st November was taken in these three species as the start of the breeding season, so that during that month animals will be either newborn, 12 months or 24 months and above i.e. animals classed as juveniles in October are automatically classified as yearlings from 1st November, and likewise yearlings become adults.

In the sole case of impala, due to the increasing difficulty (except at close range) in the second half of the breeding year to distinguish female juveniles from female yearling/adults, as of 1st May all females were counted together. For the period 1st May to 31st October, the number of juvenile females was taken to be the same as the number of juvenile males, as it seems reasonable to assume there is no significant difference in their mortality while both sexes remain within the herd.

The precise criteria for age and sex classification are as per Brooks 1985 (with modifications as outlined above).

CHAPTER TWO

HABITAT SELECTION OF LARGE MAMMALIAN HERBIVORES IN ITHALA GAME RESERVE

Introduction

Insight into the habitat use, habitat needs and potential competition among the different animals of a reserve, is essential to successfully maintain mixed ungulate populations without detriment to either habitat or animals (Scogings et al. 1990, Clark et al. 1993). Large herbivores prefer certain habitat types and, consequently, are not uniformly distributed while foraging (Ferrar and Walker 1974, Jarman 1974, Pienaar 1974, Hirst 1975, Winkler and Owen-Smith 1995). These preferences and the availability of optimal habitat will affect lifetime reproductive success (Melton 1987). For African ungulates day to day movement between habitats is determined by diverse factors including forage composition, availability and quality, water availability, topography, soil types, (Ben-Shahar and Coe 1992, Ben-Shahar 1995) and predation (Lima and Dill 1990, Grand 2002). Additional seasonal movements relate to climatic conditions, the catenary level (Bell 1970) and the effect of fire on vegetation (Crowe et al. 1981, Munthali and Banda 1992). The collection of data on all these variables is often difficult, expensive and/or time-consuming to gather. Where aspects of these variables have been studied and recorded by previous researchers, clearly the burden of data collection is reduced but collation of the different variables using traditional maps and overlaid grids is still a cumbersome and lengthy process. Entering the data into a Geographic Information System (GIS) creates spatial data bases that can be linked by overlay operations to address, in a relatively more accessible fashion, how habitat features are inter-related, spatially and temporally (Johnson 1990, Perrin and Taolo 1999). Although the potential of GIS to elucidate habitat preferences has been recognised (Haslett 1990, Johnson 1990) and its use in modelling has been explored (Fabricius and Coetzee 1992), it is mainly in North America that the system has been used in habitat selection studies (Clark et al. 1993, Mahoney and Virgil 2003); there appears to be only one example in the literature of it being used to investigate the interrelationship of environmental determinants of habitat use in an African ungulate (Perrin and Taolo 1999) and no studies applying the technique across a guild of African ungulates.

The aim of this part of the study was to determine habitat occupancy and establish from a list of pre-selected variables which environmental factors influence occupancy. The techniques and findings are intended to be applicable to other reserves.

Specific objectives were (1) to determine the habitat occupancy of the different herbivores, and their different social groups, and to show any changes in this occupancy over the wet/dry seasons of 2003 and 2004, (2) to explain this habitat occupancy, and any associated seasonal variation, in terms of (i) habitat/vegetation type, (ii) nutrient status of the different habitat types, (iii) grass flushes/burning regimes, (iv) distance to surface water, (v) soil type, (vi) slope, (vii) the influence of lack of predation and (viii) the influence of other herbivore species and (3) to compare and explain similarities/differences between the above findings and those from other conservation localities.

Methods

Data analysis:

Community or habitat type has been shown to be the principal influence on the distribution of large mammalian herbivores (Vesey-FitzGerald 1960, Lamprey 1963, Keast 1968, Field and Laws 1970, Blankenship and Field 1972, Ferrar and Walker 1974, Pienaar 1974, Dekker et al. 1996); this 'layer' of GIS data was available from previous work in the reserve (Balcomb 1996).

Absolute numbers observed in the field per vegetation type are of little use as they may merely reflect the relative areas of the different vegetation types being sampled; estimates of actual herbivore density, by vegetation type, are required.

Distance, a widely used software program developed for estimating abundance of biological populations, assumes that sighting visibility falls off gradually as distance from the observer increases (Buckland et al. 2001). Whilst this is valid in flat or gently undulating terrain, the varied topography in reserves such as Ithala frequently results in visibility being cut off abruptly, leading to areas of dead ground, where animals cannot be seen, between the observer and the limit of his vision. In such circumstances it seems likely that *Distance* will produce erroneous results. Instead a GIS approach was used. All records of sightings were imported into a GIS (Arcview GIS 3.2a, by ESRI) and overlaid onto the vegetation, road and surface water themes available for Ithala Game Reserve. Using the points thus displayed, each representing a sighting record (total number = 8,742), and guided by the underlying themes and the researcher's personal knowledge of the terrain along the various sampling routes (based on >1,000 hours in the field), estimated polygons of the areas sampled were drawn in Arcview 3.2 and then merged. Using the 'Geoprocessing Tool' ('Clip'), the vegetation theme as the 'input theme' and the sampled area polygon as the 'clip theme', the 'resultant theme' demarcated the area sampled by vegetation type. Additional polygons were also drawn of areas within the sampled area which were not visible; these were subtracted to produce the final area sampled by vegetation type (Fig 2.1). Of the herbivore species studied, giraffe were the only species that showed a markedly different visibility in terms of distance compared to the other species (i.e. they were regularly seen at greater distances) and, consequently, a separate polygon was drawn and processed for this species, producing larger values for areas of the different vegetation types sampled (Fig 2.2). The 'XTools' routine in ArcView 3.2 was then used to calculate the area sampled by vegetation type. The number of animals sighted in each vegetation type was determined from the database in Microsoft Access (using the query builder to summarise the habitat field by sum of the total field). With the number of animals per vegetation type and the area of that vegetation type sampled known, a density was obtained.

In order to avoid errors that might occur because of the mapping of the edges of vegetation types, animals were allocated to a vegetation type directly in the field. The errors in the mapping of the edges are thought not to affect the calculation of areas significantly.

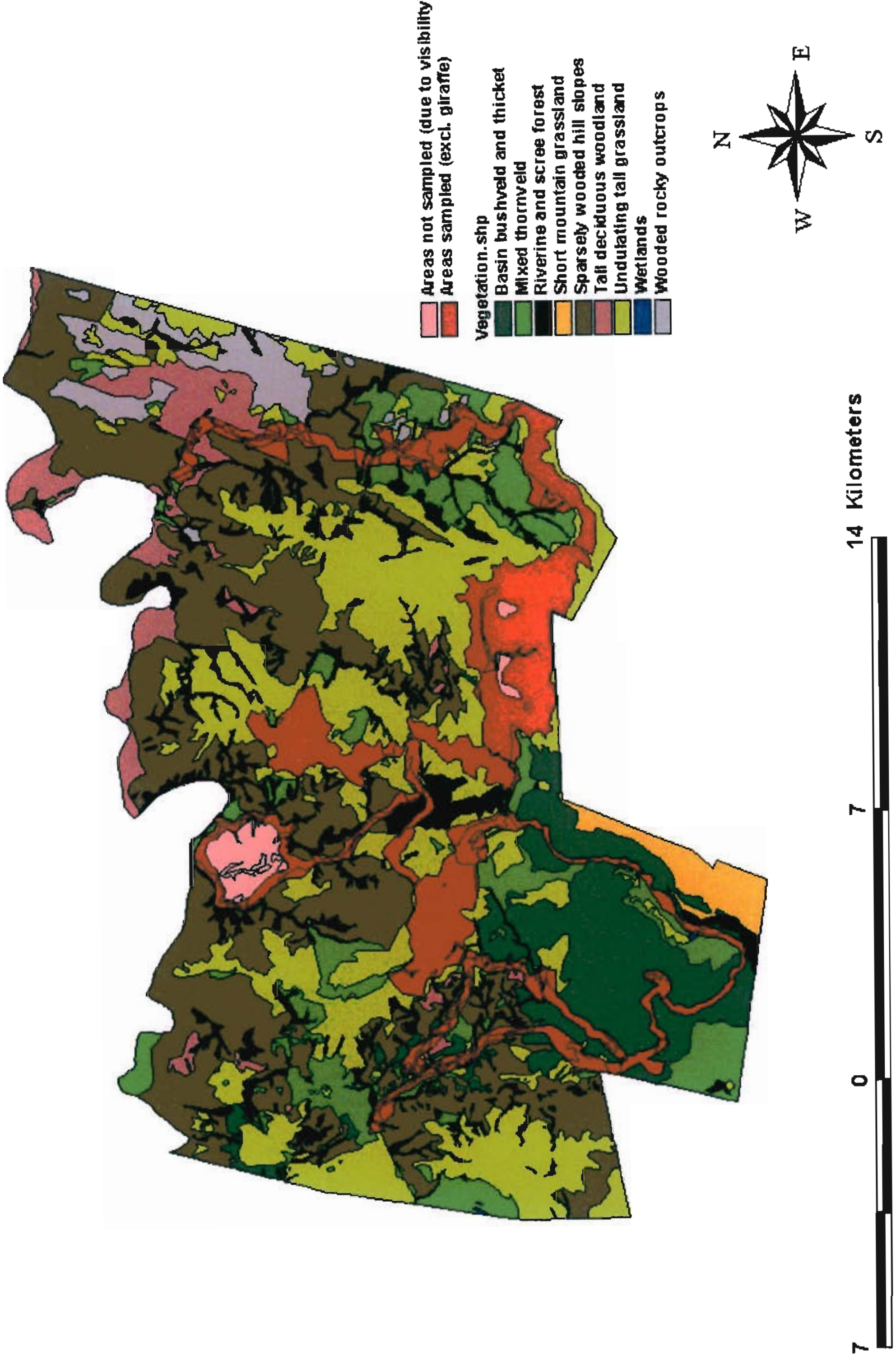

Fig 2.1: Area sampled for all species except giraffe. Areas in light pink, within the sampled area, were not visible and consequently were not sampled.

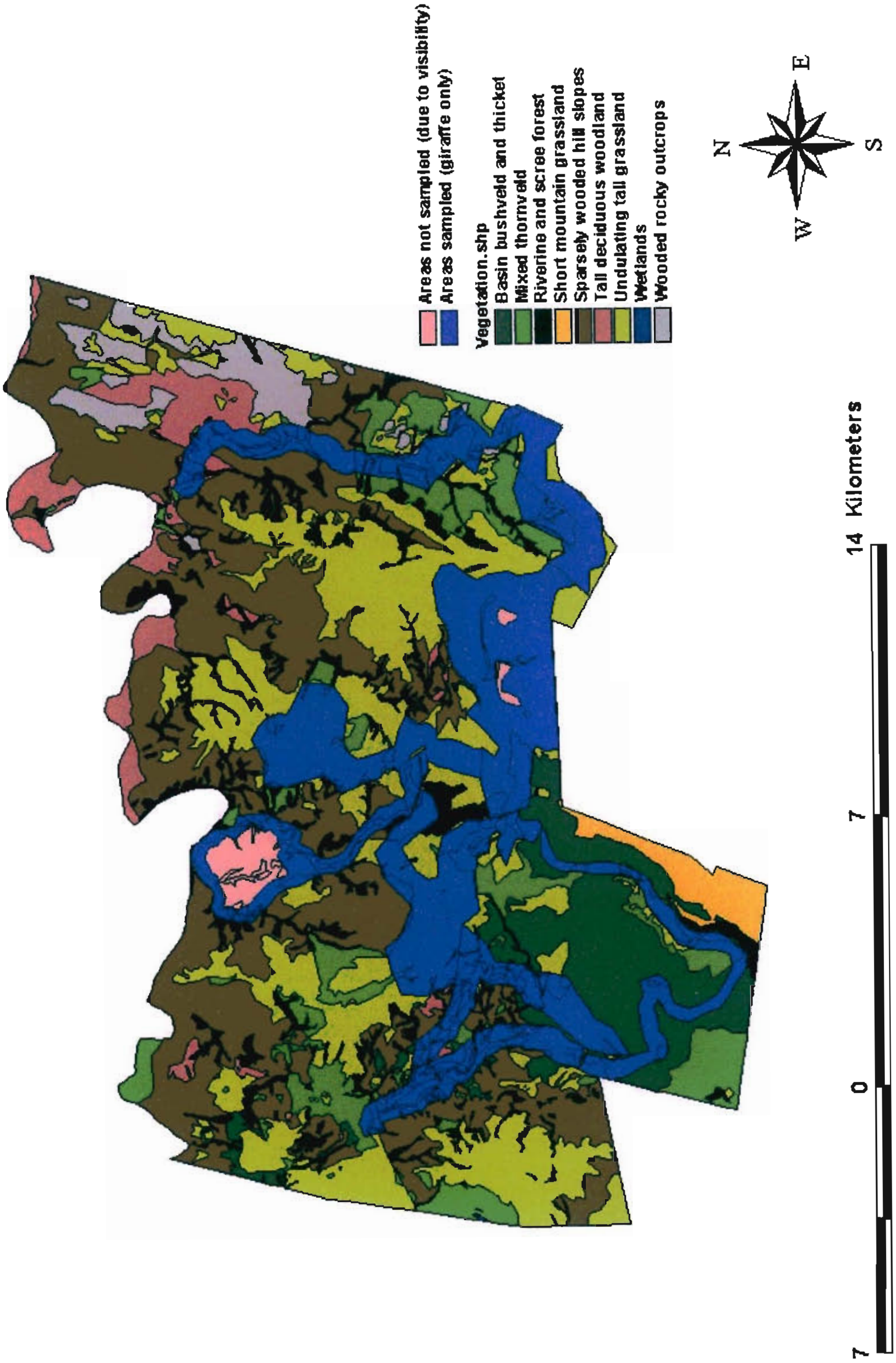

Fig 2.2: Area sampled for giraffe only. Areas in light pink, within the sampled area, were not visible and consequently were not sampled.

The availability of additional 'layers' of GIS material for Ithala Game Reserve provided the opportunity of investigating herbivore distribution in relation to variables other than vegetation type. The available layers deemed to be of possible relevance were: distance to nearest surface water, slope, and soil type. Although an elevation layer was also available, vegetation type was closely related to altitude and therefore elevation was not analysed. Results were obtained by overlaying herbivore location data separately onto each of these additional layers in Arcview 3.2 (i.e. performing spatial joins between the relevant attribute tables). A value for each of these parameters for each animal record was thus obtained. These parameters would be either impossible or difficult to measure using the data collection method used in this study as they are not obvious to the naked eye and therefore independent verification, unlike with vegetation type, was not possible. Degree of error will be related to distance to the animal(s), as described above, and the accuracy and scale to which the additional 'layer' was originally compiled. Such error is problematic to quantify. Additionally, inter-relating these different parameters is complicated by some being categorical (vegetation/habitat type, soil type) whilst others are ordinal (distance to surface water, slope). Various approaches to this problem of multivariate analysis have been used, including multiple regression analysis (Hirst 1975), discriminant function analysis (Ferrar and Walker 1974) and correspondence analysis (Beardall et al. 1984), but all have their drawbacks (Beardall et al. 1984) necessitating that, whatever the method used, it is important that results are evaluated in a qualitative manner to gain a broad holistic insight into the underlying structure and function of the system (Ferrar and Walker 1974). Such complex hypothesis-generating techniques (Scogings et al. 1990) were felt to be beyond the scope of this study. Instead Chi-square tests, a hypothesis-testing technique (Dorgeloh 1998) widely used to statistically compare resource use and availability (Thomas and Taylor 1990), were used to assess habitat/vegetation type selection and, with the other variables studied being supplemental, a broad overview is presented of the environmental determinants of species' habitat selection.

Herbivore selection of habitat type would be expected to vary by season (Bell 1970). Although the Zululand year may be divided into one wet and one dry season, including data at the margins of these periods might blur any distinction between wet/dry season habitat preferences. Equally, using data from too narrow a central period would result in too small a sample size. As a compromise, the consecutive three sampling periods that were the wettest in the summer and those that were driest in the winter were used to analyse seasonal differences in habitat selection. These were, respectively, December (02)/January/February and July/August/September for 2003 and January/February /March and June/July/August for 2004 (Table 2.1). For density results (vegetation, slope and soil type), the total number of animals seen on the subclass of that variant over these wet or dry sampling periods, was divided by the area of that subclass sampled and that in turn by the number of field trips (i.e. three) to give a density expressed as the number of animals per hectare per vegetation, slope and soil type, which was an average of the three sampling trips. Chi-square tests were applied to type of vegetative habitat selected results with the null hypothesis for the wet season (summer) being that animals showed a random distribution and *for the dry season (winter) that animals showed the same distribution as in the wet season.* Significant results were taken to be those where $P< 0.05$. Soil classes are very numerous with many covering small areas (Fig 1.4), and consequently results generated by overlay operations in Arcview which showed high densities on a rare soil type due to only a single sighting (whether a single animal or a herd), were rejected on the basis that they might be chance findings due either to animals passing over that soil type when observed, or to problems with the inter-relationship of accuracy of animals locations and the underlying scale/accuracy of the GIS theme as discussed above. For distance to nearest surface water, weighted averages (with one standard deviation) for the seasons were calculated. High standard deviations necessitated the construction of histograms to better determine underlying trends. Results for 2003 and 2004 are generally shown separately as combining results across years often hides/distorts trends (Schooley 1994); where there were no noticeable differences results were combined.

Table 2.1: Rainfall Ithala Game Reserve (Thalu), 2003 and 2004 (mm).

	Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	**Total**
2003	115	117	28	10	0	45	0	5	2	16	113	83	534
2004	96	68	102	22	0	3	84	0	11	9	122	44	561

An additional variable affecting herbivore distribution is the presence of a grass ‘flush’ following burning (Pratt 1967, Field and Laws 1970, Crowe et al. 1981, Shackleton 1992, Wilsey 1996, Dorgeloh 1998, Wilmshurst et al. 1999, Gureja and Owen-Smith 2002, Tomor and Owen-Smith 2002). Although management at Ithala Game Reserve attempts to record the areas they have burned and then digitally maps them into a GIS, this project highlighted major differences between these records and actual findings on the ground. It was therefore decided to ignore the management records and rely exclusively on direct observations as to whether an herbivore was situated on a flush. Taking a field trip where major flushes were observed and using the query builder in Arcview 3.2, all records where the sighting was situated on a flush were selected and converted to a separate shape file and added to the view. Polygons were then drawn, by eye, around each large concentration of herbivores on a flush and, by calculating the area of the polygon, density figures for each species on the flush were produced. These same polygons were then used to determine density figures on the same parcels of land for these same species one month (i.e. one field trip) before and one month after the appearance of this major flush. Results were then grouped into the broad vegetation/elevation classes that seemed to best explain the differential response of the various herbivores to flush. In the winter of 2003 burning occurred just prior to substantial winter rains, producing a marked flush, but in 2004 burning occurred well after winter rain resulting in very little flush. Consequently only herbivore species distribution in relation to grass flushes in 2003 was analysed.

Results and Discussion

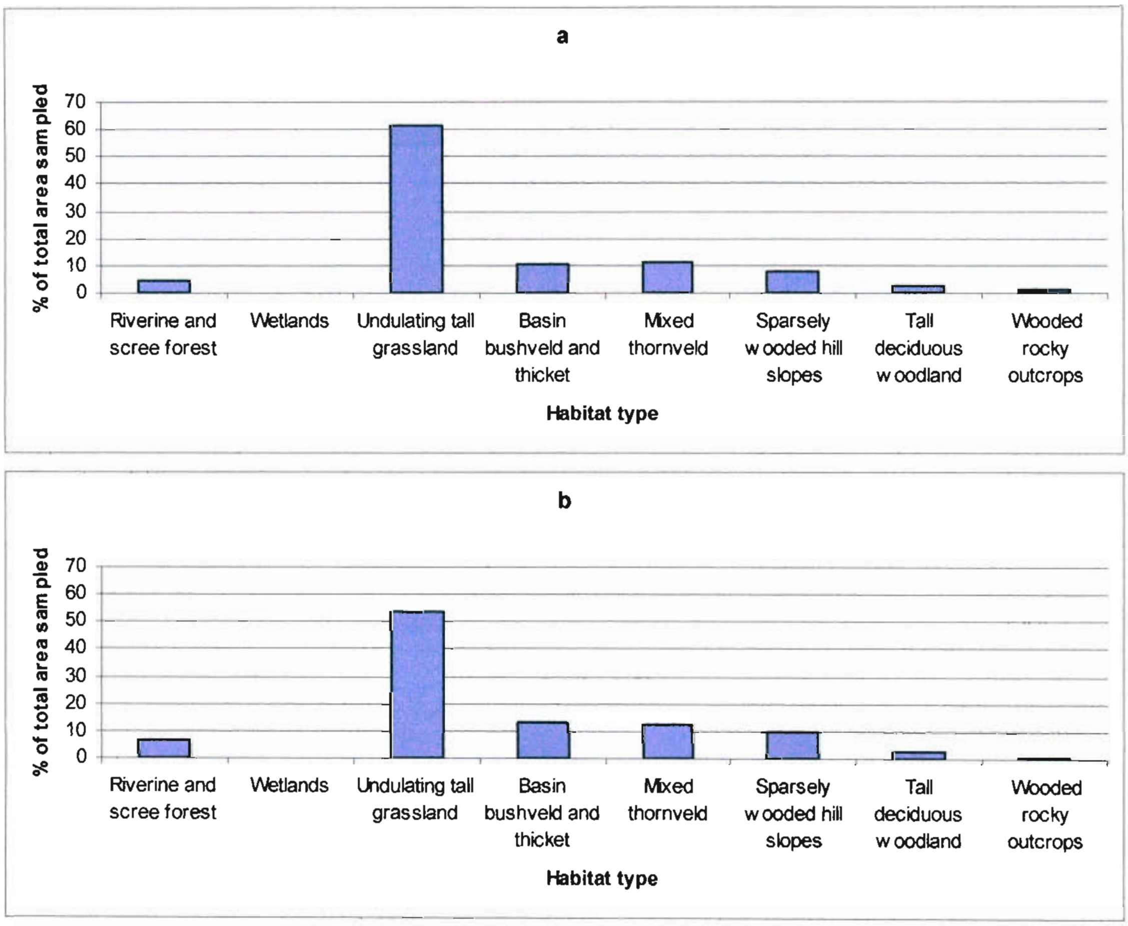

Fig 2.3: Habitat type as a percentage of total area sampled in the reserve for a) all herbivore species excluding giraffe and b) giraffe only.

Notes on maps and tables: 1) Maps that follow showing animal distributions overlaid on the reserve's habitats have been presented in landscape format and without legend, scale or orientation. The latter are all as per Fig 1.5 (page 9) and this presentation has been adopted solely to allow the actual maps to be of sufficient size on A4 paper to satisfactorily display the data presented. 2) 'Bachelors' = male-only groups in species with territorial males (number >1), 'breeding' = groups containing at least one female of breeding age (number ≥ 1) and 'terr. male' = adult males sighted alone and presumed to be territorial males

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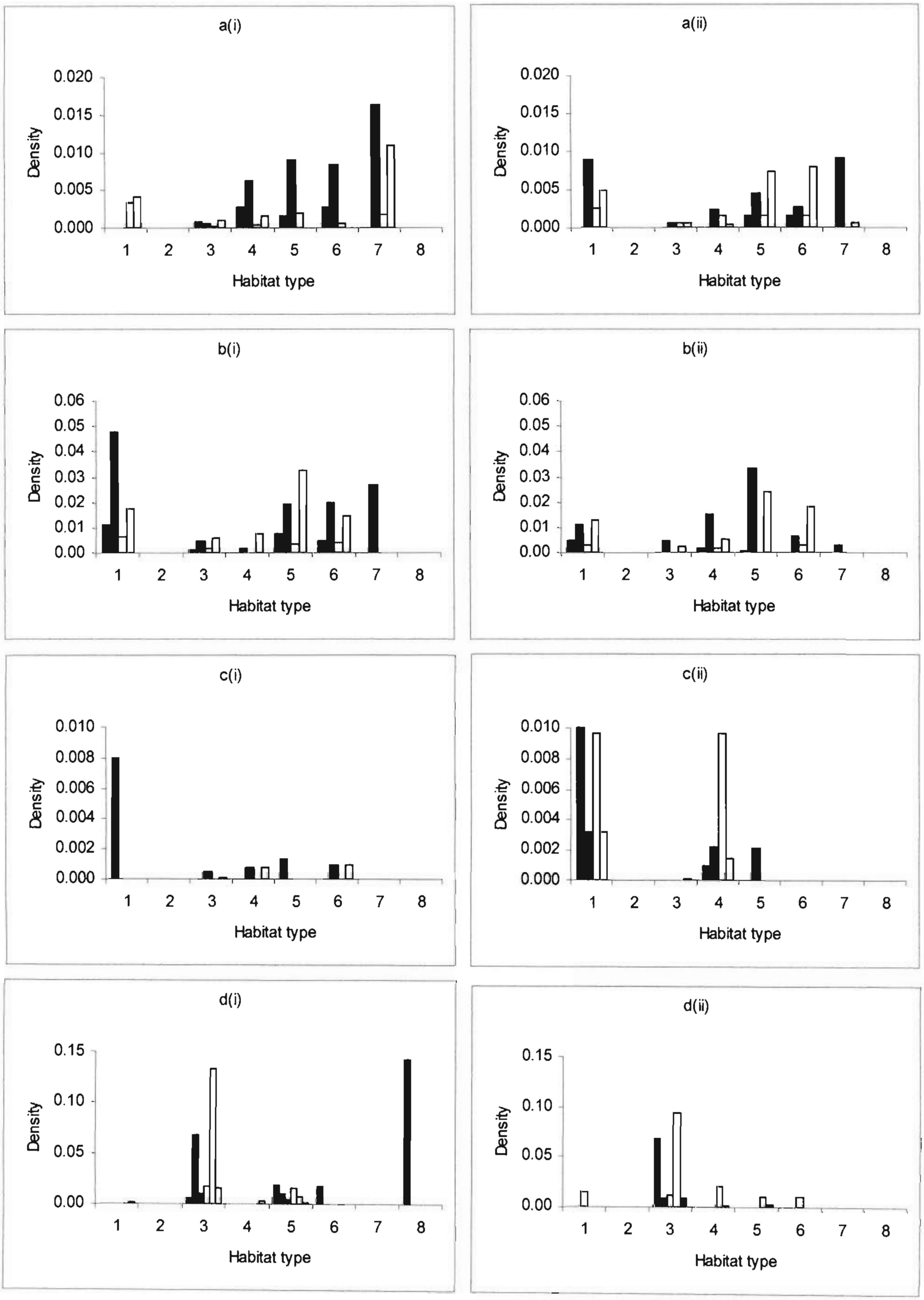

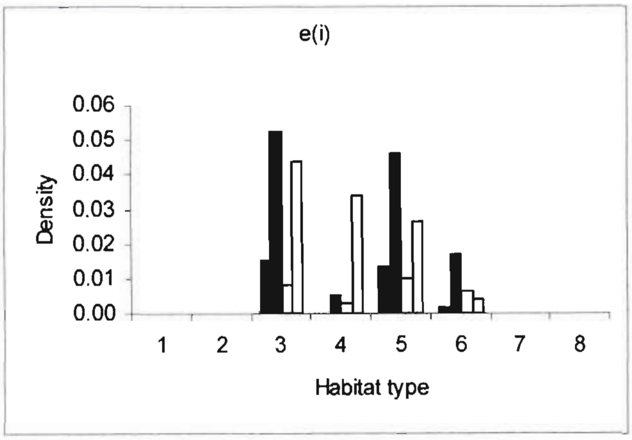
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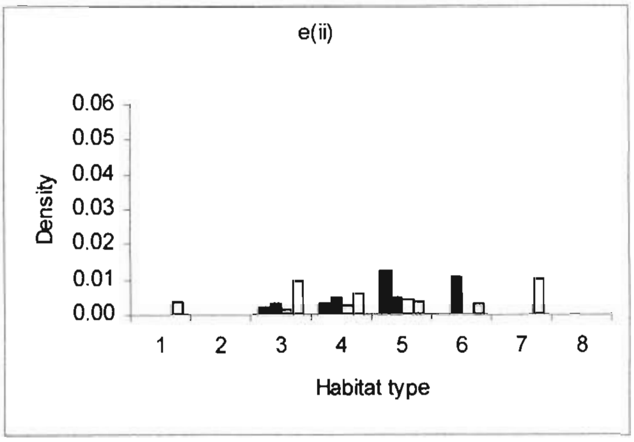
Habitat type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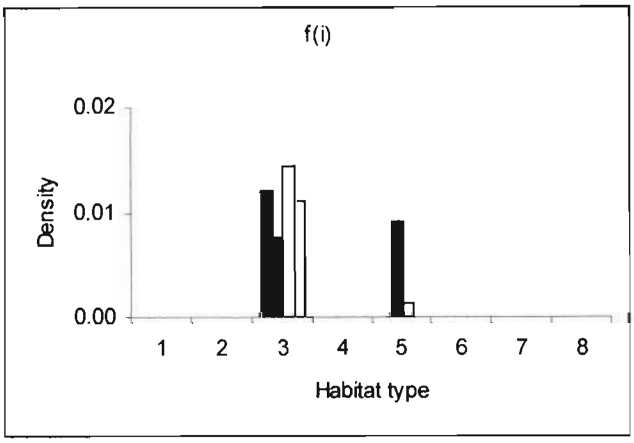
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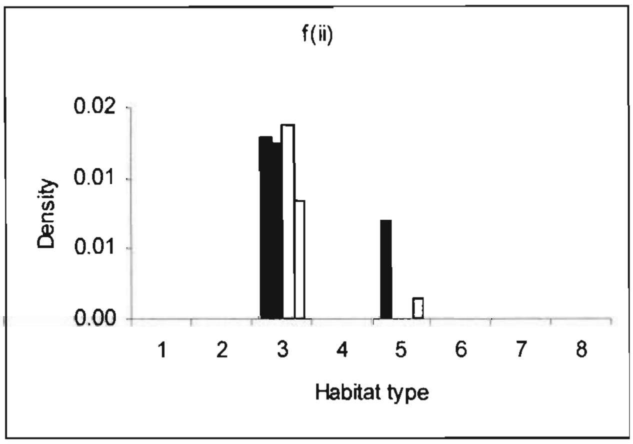
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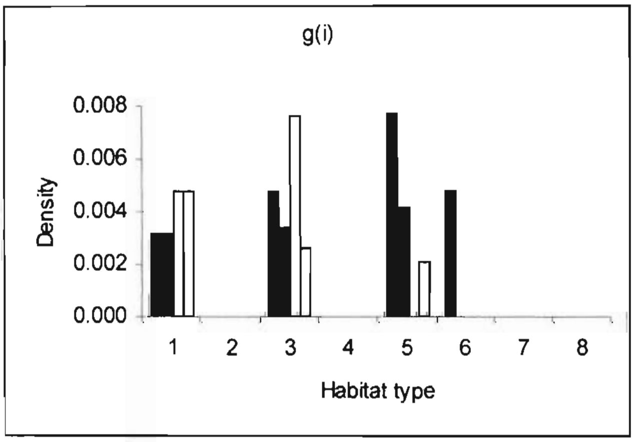
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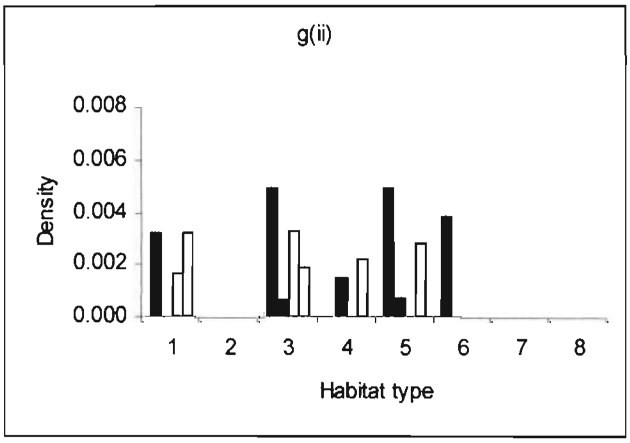
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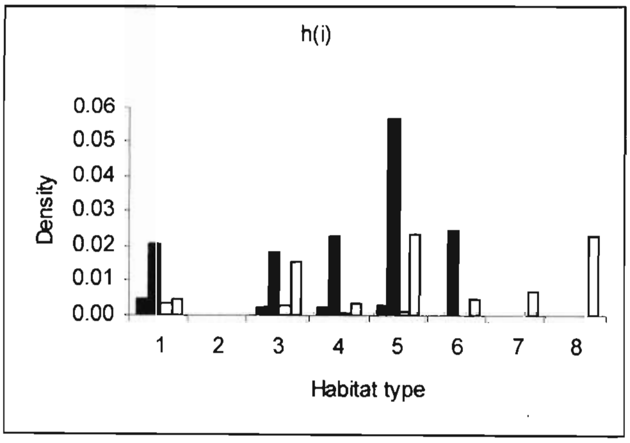
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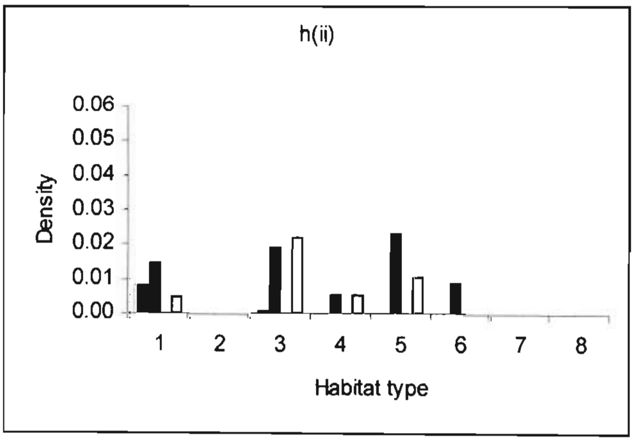
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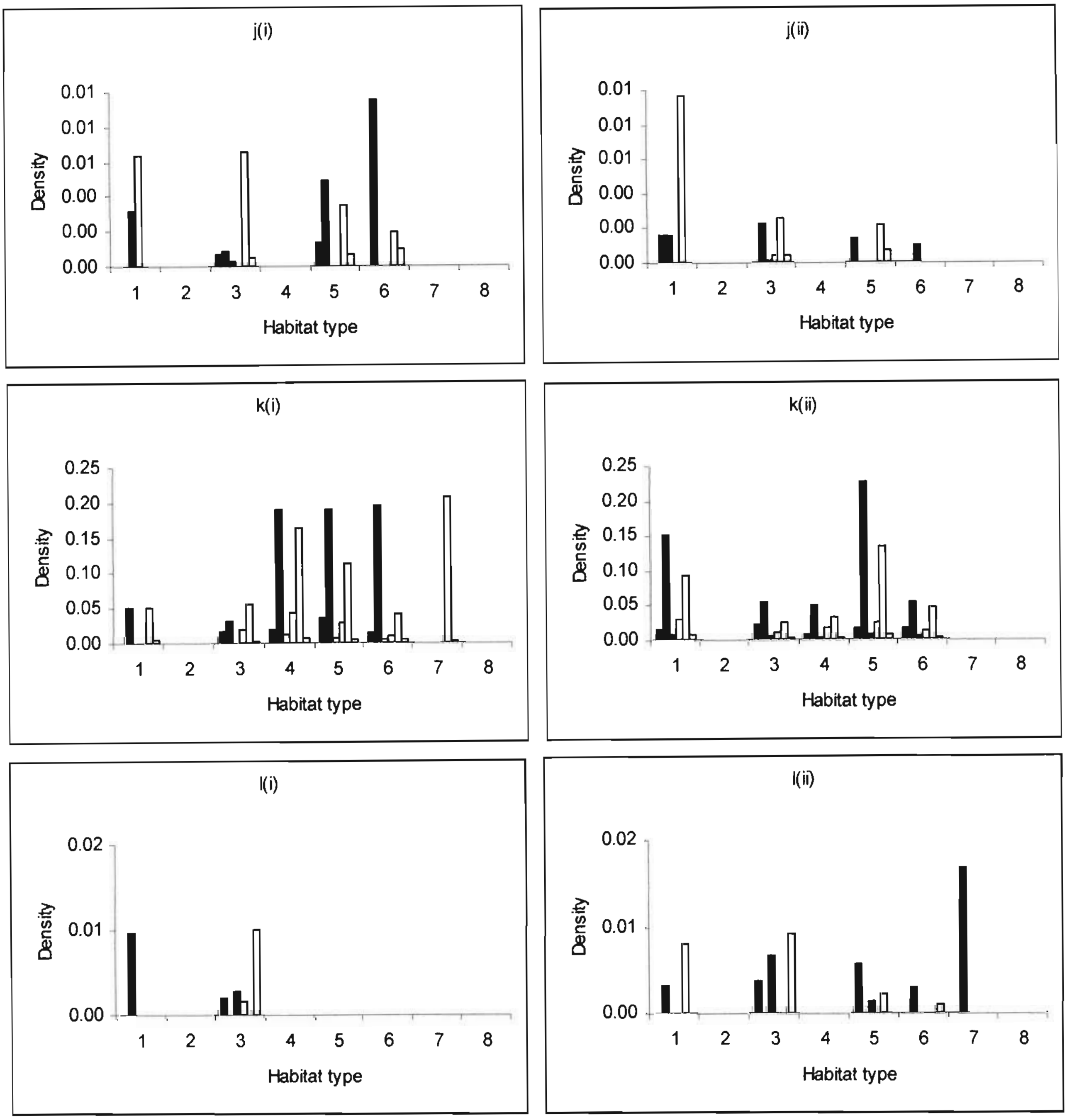


Fig 2.4: Habitat selection. (i) = wet seasons, (ii) = dry seasons. Solid bars = 2003, open bars = 2004. a = giraffe, b = kudu, e = zebra and h = warthog, with the sequence within each year/season being 'males only' and then 'breeding herds'. d = wildebeest, j = waterbuck and k = impala, with the sequence within each year/season being 'bachelors', then 'breeding herds' and then 'territorial males'. c = bushbuck and duiker, f = hartebeest and tsessebe, g = reedbuck and white rhino and l = eland, nyala and ostrich; with these species no sex categories were recorded and the sequence is as per the order of species given. Density = number of animals per hectare. Habitat types are: 1 = riverine/scree forest, 2 = wetlands, 3 = undulating tall grasslands, 4 = basin bushveld and thicket, 5 = mixed thornveld, 6 = sparsely wooded hill slopes, 7 = tall deciduous woodlands and 8 = wooded rocky outcrops. Statistics for the above data are presented in Tables 2.2 and 2.3.

Table 2.2: Habitat type selection, wet season densities. Bold type indicates significant (P<0.05) positive selection for that habitat type compared to random selection. 1 = riverine/scree forest, 2 = wetlands, 3 = undulating tall grasslands, 4 = basin bushveld and thicket, 5 = mixed thornveld, 6 = sparsely wooded hill slopes, 7 = tall deciduous woodlands and 8 = wooded rocky outcrops. Blank entry = no sightings.

			Densities (number of animals per hectare) per habitat type							
Species	**Group**	**Season**	1	2	3	4	5	6	7	8
Giraffe	Males only	wet 03			0.0007	**0.0027**	0.0016	0.0026	0.0018	
		wet 04	**0.0032**		0.0001	0.0004	**0.0020**	0.0005	0.0018	
	Breeding	wet 03			0.0006	**0.0062**	**0.0089**	**0.0084**	**0.0163**	
		wet 04	**0.0041**		0.0009	0.0015			**0.0109**	
Kudu	Males only	wet 03	**0.0112**		0.0011		**0.0077**	0.0048		**0.0151**
		wet 04	**0.0064**		0.0019		0.0035	0.0038		
	Breeding	wet 03	**0.0478**		0.0046	0.0007	**0.0195**	**0.0200**	**0.0267**	
		wet 04	**0.0175**	0.1094	0.0056	0.0073	**0.0327**	0.0143		
Bushbuck	All	wet 03	**0.0080**				0.0014			
		wet 04								
Duiker	All	wet 03			0.0005	0.0007	0.0010			
		wet 04			0.0001	0.0007		0.0010		
Wildebeest	Bachelors	wet 03	0.0048		0.0054	0.0022	**0.0181**	**0.0171**	0.0100	**0.1430**
		wet 04			**0.0176**		0.0153			
	Breeding	wet 03		0.0547	**0.0685**		0.0097	0.0029		
		wet 04			**0.1332**		0.0077			
	Terr. males	wet 03	0.0016		**0.0105**	0.0015	0.0049	0.0010		0.0075
		wet 04	0.0016		**0.0150**	0.0022	0.0014			
Zebra	Bachelors	wet 03			**0.0151**		0.0132	0.0019		
		wet 04			0.0081	0.0029	0.0097	0.0067		
	Breeding	wet 03	0.0048		**0.0523**	0.0051	0.0459	0.0171	0.0300	
		wet 04			**0.0439**	0.0335	0.0264	0.0038		
Hartebeest	All	wet 03			**0.0120**					
		wet 04			**0.0144**		0.0014			
Tsessebe	All	wet 03	0.0048		**0.0075**		0.0090	0.0010		
		wet 04			**0.0111**					
Reedbuck	All	wet 03	0.0032		0.0048		0.0077	0.0048		
		wet 04	0.0048		**0.0076**					
W. Rhino	All	wet 03	0.0032		0.0034		0.0042			
		wet 04	0.0048		0.0026		0.0021			
Warthog	Males only	wet 03	0.0048	**0.0821**	0.0020	0.0022	0.0028	0.0010		
		wet 04	0.0032	**0.0274**	0.0029	0.0007	0.0014			
	Breeding	wet 03	0.0207		0.0184	0.0226	**0.0564**	0.0248		
		wet 04	0.0048		0.0154	0.0036	**0.0237**	0.0048	0.0067	0.0226
Waterbuck	Bachelors	wet 03			0.0006		0.0014			
		wet 04	**0.0064**							
	Breeding	wet 03			0.0009		**0.0049**	**0.0095**		
		wet 04			**0.0065**		0.0035	0.0019		
	Terr. males	wet 03	**0.0032**		0.0003					
		wet 04			0.0005		0.0007	0.0010		
Impala	Bachelors	wet 03			0.0179	0.0189	**0.0369**	0.0152		
		wet 04			0.0181	**0.0430**	**0.0285**	0.0095		
	Breeding	wet 03	0.0510		0.0303	**0.1894**	**0.1907**	**0.1952**		
		wet 04	0.0510		0.0562	**0.1639**	**0.1127**	0.0419	**0.2067**	
	Terr. males	wet 03	0.0016		0.0010	**0.0109**	**0.0084**	0.0048		
		wet 04	0.0048		0.0031	**0.0080**	0.0049	0.0048	0.0033	
Eland	All	wet 03			0.0005					
		wet 04			0.0016					
Nyala	All	wet 03	**0.0096**							
		wet 04								
Ostrich	All	wet 03			**0.0028**					
		wet 04			**0.0103**					

Table 2.3: Habitat type selection, dry season densities. Bold type indicates significant (P<0.05) positive selection and italics significant negative selection for that habitat type when compared to the same habitat type in the preceding (i.e. same year) wet season. Blank entry = no sightings. Habitat types as per Table 2.2.

			Densities (number of animals per hectare) per habitat type							
Species	**Group**	**Season**	1	2	3	4	5	6	7	8
Giraffe	Males only	dry 03			0.0002	0.0004	0.0016	0.0016		
		dry 04	0.0024		**0.0006**	**0.0015**	0.0016	0.0016		
	Breeding	dry 03	**0.0089**		0.0005	0.0023	0.0045	0.0026	0.0091	
		dry 04	0.0049		*0.0006*	*0.0004*	**0.0073**	**0.0079**		
Kudu	Males only	dry 03	0.0048			0.0015	0.0007			
		dry 04	0.0032		0.0003	0.0015		0.0029		
	Breeding	dry 03	*0.0112*		0.0045	**0.0153**	**0.0334**	*0.0067*		
		dry 04	0.0128		0.0025	0.0051	0.0237	**0.0181**		
Bushbuck	All	dry 03	0.0096		0.0003	0.0007				
		dry 04	**0.0096**			0.0096				
Duiker	All	dry 03	0.0032			0.0022	**0.0021**			
		dry 04	0.0032		0.0001	0.0015				
Wildebeest	Bachelors	dry 03			**0.0121**		0.0118			
		dry 04	0.0144		0.0115			0.0095		
	Breeding	dry 03			0.0675		*0.0021*			
		dry 04			0.0931	**0.0204**	**0.0104**			
	Terr. males	dry 03			0.0094		0.0021	0.0010		
		dry 04			0.0093	0.0007	**0.0035**			
Zebra	Bachelors	dry 03	0.0016		*0.0020*	**0.0029**	**0.0118**	0.0010		
		dry 04			0.0009	**0.0022**	**0.0042**			
	Breeding	dry 03			*0.0028*	**0.0044**	0.0049	**0.0105**		
		dry 04	0.0032		0.0094	0.0058	0.0035	**0.0029**	0.0100	
Hartebeest	All	dry 03			0.0129		**0.0070**			
		dry 04			0.0138					
Tsessebe	All	dry 03		**0.1642**	0.0124		*0.0014*			
		dry 04			0.0084		0.0014			
Reedbuck	All	dry 03	0.0032		0.0049		0.0049	0.0038		
		dry 04	0.0016	0.0274	0.0033					
W. Rhino	All	dry 03			0.0006	0.0015	0.0007			
		dry 04	0.0032		0.0019	**0.0022**	0.0028			
Warthog	Males only	dry 03	**0.0080**		0.0006					
		dry 04			0.0003					
	Breeding	dry 03	0.0144		**0.0192**	*0.0051*	*0.0230*	*0.0086*		
		dry 04	0.0048		**0.0219**	0.0051	*0.0104*			
Waterbuck	Bachelors	dry 03					0.0014			
		dry 04			**0.0004**					
	Breeding	dry 03	0.0016		**0.0023**					
		dry 04	**0.0096**		0.0025		0.0021			
	Terr. males	dry 03	0.0016		0.0001			0.0010		
		dry 04			0.0004		0.0007			
Impala	Bachelors	dry 03	**0.0144**		**0.0220**	*0.0080*	*0.0160*	0.0181		
		dry 04	**0.0287**		*0.0089*	*0.0175*	0.0244	**0.0124**		
	Breeding	dry 03	**0.1515**		**0.0543**	*0.0474*	**0.2262**	*0.0533*		
		dry 04	**0.0925**		*0.0249*	*0.0321*	**0.1336**	**0.0457**		
	Terr. males	dry 03	**0.0064**		**0.0039**	*0.0022*	0.0077	0.0048	0.0033	
		dry 04	**0.0080**		0.0014	0.0022	**0.0070**	0.0029		
Eland	All	dry 03			0.0036	0.0007	**0.0056**			
		dry 04								
Nyala	All	dry 03	*0.0032*					**0.0029**	**0.0167**	
		dry 04	**0.0080**				**0.0021**			
Ostrich	All	dry 03			0.0066		0.0014			
		dry 04			0.0091			0.0010		

Giraffe, which are almost exclusively browsers (Owen-Smith 1988b), were seen in a wide range of vegetation types, generally showing avoidance of open vegetation types (Fig 2.4a). Estes (1997) suggested that sexual spatial separation occurred in giraffe because bulls browse high and females feed on regenerating trees and shrubs below two metres where a choice exists between high and low browse (Pellew 1984a), and also because males are less vulnerable (due to size and lack of parental responsibility) to predation in taller and denser woodland. Such a separation is not apparent from these results; indeed, females are seen to positively select tall woodlands. Giraffe density is, compared to a wide range of other reserves, very high in Ithala (Chapter 3) and this, together with them being alien species to the region (Goodman and Tomkinson 1987), has lead to severe depletion of the browse at giraffe browsing height (Bond and Loffell 2001, Wiseman et al. 2004). This reduction of browse and the virtual absence of predation in the reserve may thus explain this apparently anomalous situation. Shortage of appropriate browse would also explain the lack, for the most part, of avoidance of the grasslands as these contain small quantities of browse. No other patterns of vegetation selection, whether between seasons or years, are apparent from the vegetation category selection results.

Kudu, another nearly pure browser (Wilson 1965, Smithers 1983), was seen to select habitats rich in browse (Fig 2.4b). In a population of kudu in the Kruger National Park that was monitored for three years with radio telemetry (du Toit 1995), bulls maintained a preference for riverine habitat throughout the year with cows occupying open savanna habitat in the wet season and moving into riverine habitat in the dry season. Dorgeloh (2001) also found breeding herds utilising more open savanna habitat in summer in Nylsvley. Although in this study bulls were seen to significantly select riverine habitat in both years and in both seasons, cows, in contrast, in the wet season were also found to occupy riverine (significantly so in 2003) and to significantly avoid grasslands (i.e. open habitat). Du Toit (op. cit.) discusses how this female wet season behaviour may be a predator avoidance strategy; the lack of predation in Ithala may thus account for this finding.

Bushbuck are mainly browsers, live in denser habitats and are of a secretive nature (Jacobsen 1974, Odendaal 1983, MacLoed et al. 1996). Direct observation of bushbuck often does not, therefore, accurately reflect their habitat utilisation (Allen-Rowlandson 1985) or density. Few bushbuck were seen in this study, allowing little analysis of results; however they were seen to significantly select riverine and scree forest – a dense habitat – in all three seasons they were encountered and to avoid open grasslands, significantly so in one season (Fig 2.4c). Common duikers are also browsers and will live in any habitat affording concealment, they do not venture onto open plains (Kingdon 1982). Again, very few were seen but they did show significant avoidance of open grassland and significant selection for mixed thornveld (Fig 2.4c).

Wildebeest are pure grazers (Smithers 1983), favouring plains covered by colonial grasses which respond to grazing, trampling and manuring by rapid regrowth (McNaughton 1985). Wildebeest breeding herds and territorial bulls were seen to significantly select the grasslands throughout both years and both seasons (Fig 2.4d). Selection or avoidance of the other vegetative communities varies between the two years; in 2003 virtually every other community was significantly avoided in both the wet and dry seasons, but in 2004, whilst other communities were avoided in the wet season, in the dry season both breeding herds and territorial bulls significantly, to varying extents, selected the basin bushveld/thicket and mixed thornveld communities. Variation in rainfall, both monthly and annual, between the two years was minimal (Table 2.1, page 19) and would seem unlikely to be the explanation of this difference; a more likely explanation seems to be the presence or absence of green flushes. In 2003 management burning of selected areas, including substantial areas of grasslands, started on 8th May; substantial (for winter) rain fell following this burning in June promoting marked green flushes. In 2004, in contrast, burning did not start until 30th July after the only sizeable winter rains (in early/mid July); consequently no winter flush occurred. Wildebeest made marked use of this winter 2003 flush (Fig 2.11, page 49) which, since they were not seen to select any other habitat, presumably ensured the grasslands alone continued to provide sufficient nutrition throughout the winter months. In the winter of 2004, with the absence of any flush, wildebeest selecting additional communities implies the grasslands alone could no longer provide maintenance nutrition. Moving onto green flushes or down the catena into smaller areas (see below) are both examples of wildebeest being forced to respond to the resource limitations of winter by increasing their selectiveness, as is often the case with ruminants (Demment and Van Soest 1985, Beekman and Prins 1989) and is theoretically more likely with grazing ruminants as they are more dependant on the quality of their food (Owen-Smith and Novellie 1982).

The general avoidance of non-grassland communities by the Ithala wildebeest breeding herds and territorial bulls was in contrast to Attwell's (1977) and Robertson's (1993b) findings in the nearby Hluhluwe – Umfolozi game reserve. Although their findings of wildebeest large scale usage of habitat types significantly avoided in this study were undoubtedly consequent, as Attwell remarks, on them forming the vast majority of the available range, with grasslands forming only ~5% (as opposed to 62% of the study area in Ithala and 32% of the game reserve as a whole), the lack of their usage in Ithala suggests that either the wildebeest population had no need of them (i.e. its nutritional needs were being met entirely by the grasslands) or that they were being prevented from using them. The unusually high density of wildebeest in the reserve (Chapter 3) and their suffering decreased fecundity following slightly lower rainfall in 2002 (Chapter 4) suggests the latter was more likely. With the virtual absence of predators, inter-specific resource competition probably from impala (see below) seems to be the most likely explanation. In broad agreement with Attwell (1977) and others (Estes 1969), however, was the finding that bachelor herds differed in their habitat occupancy from breeding herds, with bachelor herds occupying more marginal habitats, both in terms of vegetative community (Fig 2.4d) and harshness of slope (Table 2.5, page 46). This spatial sexual segregation was seen (pers. obs.) to wane in the depths of winter as bull territorial behaviour declined, although social segregation remained. Although this observation is seen in the results between the summer and winter of 2003, it is not apparent in 2004. This may be because (a) the three month winter periods over which data is used did not totally coincide with periods of loss of territorial behaviour, leading to a dilution of the result and (b) the marked flush of 2003's winter would be expected to encourage bulls to abandon their territories to go to the flushes and also to attract bachelor groups, whose presence, in the absence of territorial behaviour, would be tolerated. Sexual segregation is discussed further elsewhere (Chapter 4).

Zebra, in contrast to the quality-dependent ruminating wildebeest, are hindgut fermenters (Bell 1971, Janis 1976) and during the dry season can compensate for their lower digestive efficiency by increasing intake of low quality foods (Gordon 1989, Okello et al. 2002). This difference between zebra and wildebeest has been demonstrated both at individual animal level (Bodenstein et al. 2000) and at a population level (Ben-Shahar 1991). Zebra would thus be expected to broaden their resource base (i.e. become less selective) during the dry season, in keeping with Rosenzweig's (op. cit.) model. This was the case in Umfolozi Game Reserve where zebra were shown to reduce their habitat type selectivity in winter (Melton 1987). Findings in this study were in agreement as selection of vegetation type (Fig 2.4e) generally broadened in winter, especially in 2004, and spatially zebra (see below) showed, in contrast to wildebeest, a broadening of distribution in the winter. Zebra barely utilised green flushes (Fig 2.11, page 49). Generalist feeders should consume different foods in relation to their abundance, specialists should select a diet that optimizes a mixture of nutrients irrespective of availability (Westoby 1974, Belovsky 1981). Although varying levels of resource depletion for different ungulates in different environments will differentially affect the empirical findings expected from these principles (Melton 1987), zebra vegetation type selection should therefore show throughout the year a closer correlation to underlying abundance than wildebeests'; this is the case (Figs 2.4d and 2.4e, compared to Fig 2.3, page 20). In Hluhluwe Game Reserve, Robertson (1993a) found little evidence of habitat selection by zebra. Although stallions vigorously defend their females in oestrous, they do not defend a territory (Klingel 1969, Smuts 1974) and thus, unlike the situation with wildebeest, there is no patchwork of territories tending to drive bachelor herds into sub-optimal habitats. Consequently bachelor habitat type selection was similar to that of the breeding harems.

Hartebeest and tsessebe, both members of the *Alcelaphini* tribe, are typical plains antelope sympatrically inhabiting open grasslands and tree savanna; both are pure grazers (Lamprey 1963, Pienaar 1974, Smithers 1983). Vegetation type selection results (Fig 2.4f) confirmed this preference, with both species selecting the grasslands; with tsessebe, however, this was only significant in 2004. In the summer of 2003 they also showed a greater preference for mixed thornveld than hartebeest; other researchers found hartebeest to enter denser bush grassland more readily than tsessebe, although this was Coke's Hartebeest as opposed to the red hartebeest (Gosling 1974). Only hartebeest were observed on the green flushes of the winter of 2003 (Fig 2.11, page 49). Tsessebe were attracted to flushes in the Kruger National Park but only those within easy reach of their small home ranges/territories (Joubert and Bronkhorst 1977). In the Nylsvley Nature Reserve they made relatively limited use of green flushes possibly due to the burnt areas being outside their ranges (Tomor and Owen-Smith 2002). Burning at Ithala did occur well away from the main concentration of tsessebe in the south-easterly portion of the reserve, thus possibly accounting for their lack of usage of the flush, but since tsessebe had been observed in the areas of the flushes before burning, their apparent avoidance of it, especially since they appear to be in trouble (see below), is puzzling.

Reedbuck, a grazing ruminant, can subsist on grasses that are either inaccessible or unpalatable to most other antelopes, venturing into tall grasslands or onto steep slopes

(Jungius 1971b, Hofmann 1973). Here reedbuck showed usage of a wide range of habitat types, positively selecting grasslands in 2004 (Fig 2.4g). Although not actually seen on green flushes (Fig 2.11, page 49), the increase in distance to water in the winter of 2003 (see below) suggests burning did have some influence on their distribution.

Although a non-ruminant, the white rhino has a preference for bulk grazing on short, quality grass (Owen-Smith 1973, Pienaar et al. 1992, 1993). This apparent violation of the principle that non-ruminants utilize coarser, lower quality forage is explained by Owen-Smith's (op. cit.) observation that white rhinos are poor digesters (Page and Walker 1978). However, rhino were not seen to show an obvious preference for the grasslands, occurring in comparable densities in closer vegetative communities such as mixed thornveld and basin bushveld and thicket (Fig 2.4g). Perrin and Brereton-Stiles (1999) observed rhino feeding on fibrous senescent grasses in areas of low food availability and Owen-Smith (op. cit.) recorded rhino utilising such grasses during the worst period of the dry season. The marked usage by the Ithala rhino of vegetative communities not associated with extensive short grass plains, and their notable reduction in range during the winter (see below) may thus suggest that resources are generally limited for them; as wildebeest are their main competitors for short grass, one may speculate that the high density of wildebeest present in the reserve (Chapter 3) may be the causal factor. White rhino were not seen to utilise green flushes (Fig 2.11, page 49).

Warthog, non-ruminants, are predominantly grazers favouring short grass but during the dry season they broaden their diet to include a much larger proportion of graminaceous plant material, shovelled from beneath the soil surface with the snout (Mason 1982). Exploitation of grass rhizomes, tubers, bulbs and corms of other plants becomes particularly important to warthogs when the grass cover has been reduced to sparse, short stubble due to overgrazing by ungulates (Mason 1990a). In Ithala warthog were not seen to particularly favour the grasslands, instead showing use of a wide range of vegetation types and significantly avoiding (2003) or not selecting (2004) grasslands in the summer (Fig 2.4h). Such a relatively unselective use of habitat types implies resources were scarce (Rosenzweig 1985) and may, again, be related to the high density of wildebeest and pressure on available grazing. In the winter they were seen to positively select grasslands in both years. In 2003 this is undoubtedly related to their attraction to green flushes (Fig 2.11, page 49) but these did not occur in 2004. In the Kruger National Park, Mason (op. cit.) observed that warthogs rooted in the dry season for material mainly on grass lawns and terraces; this may explain the apparent attraction of warthogs back to the grasslands in the winter. However, whether due to fire or lack of soil moisture and/or cold weather, reduction in grass height and thickness, resulting in increased visibility compared to the summer, occurs on the grasslands over the winter – in all probability producing an erroneous rise in grassland density figures for warthog. This type I error may thus be distorting habitat selection results. The short-comings of the field data collection technique in relation to warthog visibility, grass height and burning are discussed further elsewhere (Chapter 3).

Waterbuck, principally grazers, are possibly the most water-dependent of all antelopes (Taylor et al. 1969) and are limited to habitat within a few kilometres of water (Spinage 1982). In Ithala, however, due to the wide availability of water throughout the year, this physiological/behavioural restriction is unlikely to influence habitat selection. Most dispersed in the wet season when females with calves tend to frequent woodlands, they spend more time in open grassland during the dry season while concentrated near water (Kiley-Worthington 1965, Hanks et al. 1969). Results in 2003 (Fig 2.4j) agree with these observations; breeding herds positively selected woodland in the summer and positively selected grassland in the winter. Additionally, spatial data (see below, Fig 2.7) clearly shows a wider dispersion in the wet season. In 2004, however, grasslands were positively selected for in summer as well as winter, and summer use of woodlands was less marked. Waterbuck were not seen to use burns (Fig 2.11, page 49); this is in contrast to others' findings (Tomlinson 1981). However, burning occurred mainly in areas well removed from the majority of waterbuck locations and it is known to be a fairly sedentary antelope (Hanks et al. 1969).

Impala are classified as intermediate or mixed feeders (Lamprey 1963, Hofmann 1973, Blankenship and Qvortrup 1974). Although they feed on a wide range of grasses, herbs, shrubs and trees, they prefer to graze (Dunham 1980, Monro 1980, Wronski 2003). Poor grass quality in the dry season usually enforces less time spent grazing and more browsing (Wronski 2002). An increase of browse over grass in the diet of impala in the dry season is widely reported in the literature (Stewart 1971, Rodgers 1976, Hansen et al. 1985, Meissner et al. 1996). As well as changing its diet between seasons, the impala can adapt to different habitats by being mainly a grazer in one area and a browser in another (Smithers 1983, Sponheimer et al. 2003). They thrive in areas where overgrazing has degenerated the natural vegetation (Dasmann and Mossman 1962a) and they have been shown to optimise their diet (Meissner et al. 1996).

In this study, although no direct measurement of grass versus browse consumed by impala was made, relative occupation of habitats consisting mainly of grass or of browse is an acceptable, although clearly less rigorous, stand-in. To this end, given that large areas of both grass and browse are available in Ithala, one would expect impala to occupy mainly grasslands in the wet season and move to browse habitats (mixed thornveld etc) in the dry season (Jarman 1972). This was not found to be the case (Fig 2.4k). Instead, impala consistently, in both wet and dry seasons, favoured browse communities. The only exception was in the winter of 2003 when they significantly selected grasslands – this was consequent on the marked green flush at that time which strongly attracted impala (Fig 2.11, page 49). This unexpected favouring of browse communities is, however, a shift in emphasis rather than a reversal of the more usual situation as reported by most others; impala still showed a significant increase in selection for browse (mixed thornveld) in winter compared to summer in both years, and in the winter of 2004, where green flushes didn't 'distort' results, there was significant avoidance of the grasslands compared to that summer. For this shift in emphasis to exist, grasslands must have become less desirable and/or browse communities more desirable. The unusually high density of wildebeest in the reserve (Chapter 3) might be expected to result in a shortage of their preferred food, namely short grass, and this may well make the grasslands less attractive habitats for those herbivores that have a choice. The intuitive concept that animals do not forage in patches independent of risks of predation is widely supported both theoretically, as a branch of optimal foraging theory (Brown 1988, Lima and Dill 1990, Brown 1992, Kie 1999, Grand 2002, Morris 2003), and empirically (Underwood 1982, Eshelman and

Cameron 1996, Mysterud et al. 1999, Owen-Smith 2002a, Mahoney and Virgil 2003). Although all predators prey on impala to a greater or lesser extent (Skinner and Smithers 1990), leopard have the greatest impact (Hirst 1969, Pienaar 1969, Le Roux and Skinner 1989, Cronje et al. 2002). As leopard hunt in closer habitats (Mills and Biggs 1993), the very low level of predation in Ithala would be expected to make denser habitats (e.g. browse communities) less dangerous. A combination of the effects of a high density of wildebeest and of minimal predation may thus be the explanation for the Ithala impalas' strategy.

Impala in southern Africa limit vigorous territorial behaviour to the few months around the rut (Anderson 1972, Murray 1982b). Anderson (op. cit.) recorded in Hluhluwe that bachelor herds maintained clear spatial separation from the breeding herds and continued to occupy sub-optimal habitat (shrubland versus flood plain/river terrace) even after territorial behaviour had declined outside of the rut. Jarman (1972) also recorded, although not to the same extent, differential habitat selection by male versus female impala in the middle Zambezi Valley outside of the rut. This was not the case in Ithala, where bachelor herds outside of the rut occupied broadly the same range of habitat as the breeding herds (Fig 2.4k); slight differences are apparent from the vegetation type selection results but the overwhelming impression in the field was of the two groups occupying the same habitats. Conversely, the marked impression during the rut and pre-rut was that they occupied different habitats and this is supported by vegetation selection data specifically from that period (Figs 2.5 and 2.6). Lack of predation, and how it relates to differing male and female reproductive strategies, may again be the underlying cause of this lack of habitat separation outside of the rut. Social sexual segregation, as opposed to spatial, was, however, observed throughout the year; sexual segregation is discussed further elsewhere (Chapter 4).

Eland are generally classified as mixed feeders (Hofmann 1973, Buys 1990) but can vary their diet from location to location, being predominantly grazers in some (Underwood 1975) whilst predominantly browsers in others (Watson and Owen-Smith 2000). Few were seen but in the summer they occurred mainly on the open grasslands and in winter moved (significantly so in 2003) into mixed thornveld (Fig 2.4) – presumably to utilise the browse. This seasonal shift is in accordance with the findings of others (Fabricius and Mentis 1990). Nyala, another mixed feeder, are found in low-lying, densely wooded habitat generally near water and their habitat preference overlaps with, amongst others, bushbuck (Anderson 1978). In an attempt to boost bushbuck numbers it has been management policy for a number of years in Ithala to kill nyala on sight – not surprisingly few were seen. Those that were spotted conformed to expected habitat choices, showing positive selection for riverine and scree forest and wooded habitats, with avoidance of open grasslands (Fig 2.4). Ostrich forage in patches of green vegetation, feeding on a wide range of plant species (Williams et al. 1993). Here they significantly selected grassland in all seasons, occurring in other habitats rarely (Fig 2.4).

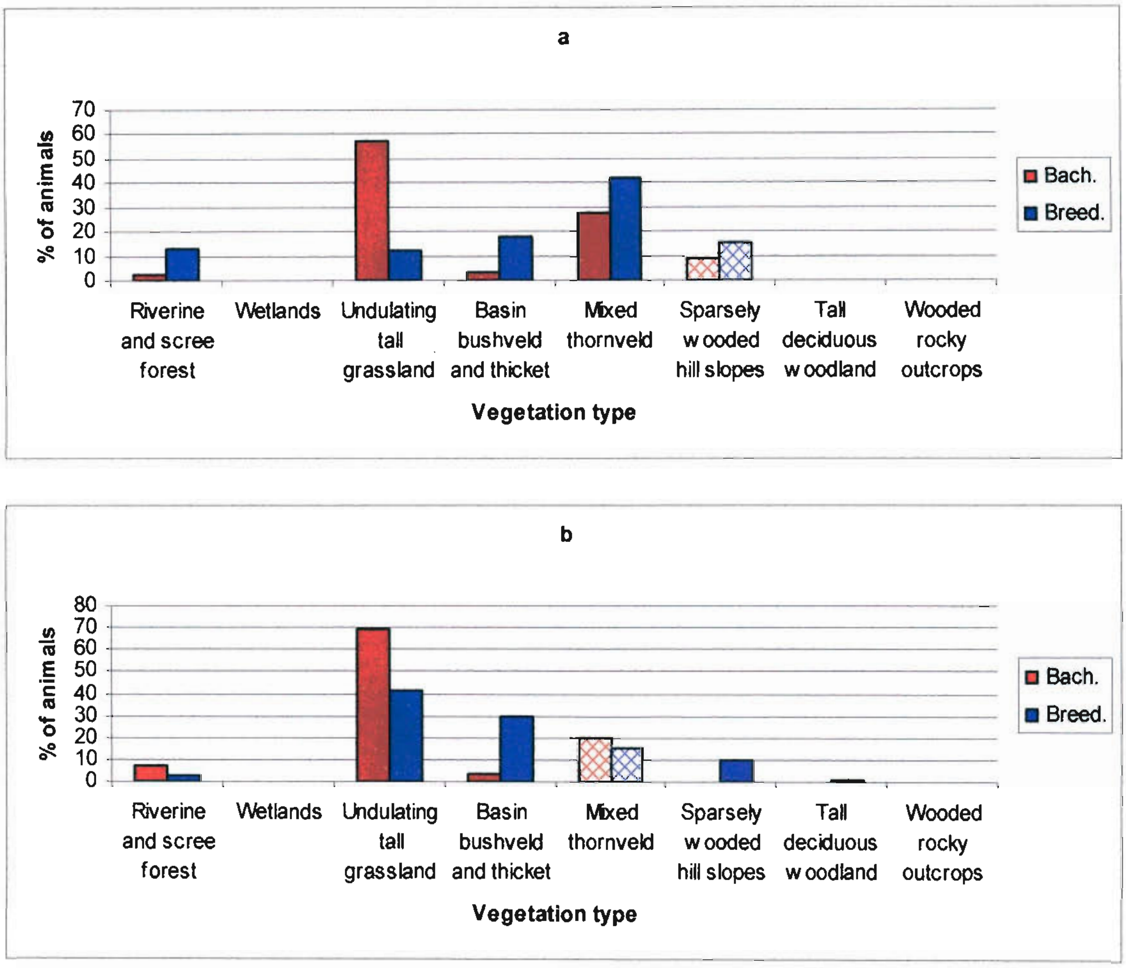


Fig 2.5: Impala, vegetation selection by bachelor and breeding herds during the rut of 2003(a) and 2004 (b). Differences in vegetation selection between bachelor and breeding herds within each year were significant (P<0.05), unless indicated by cross-hatching.

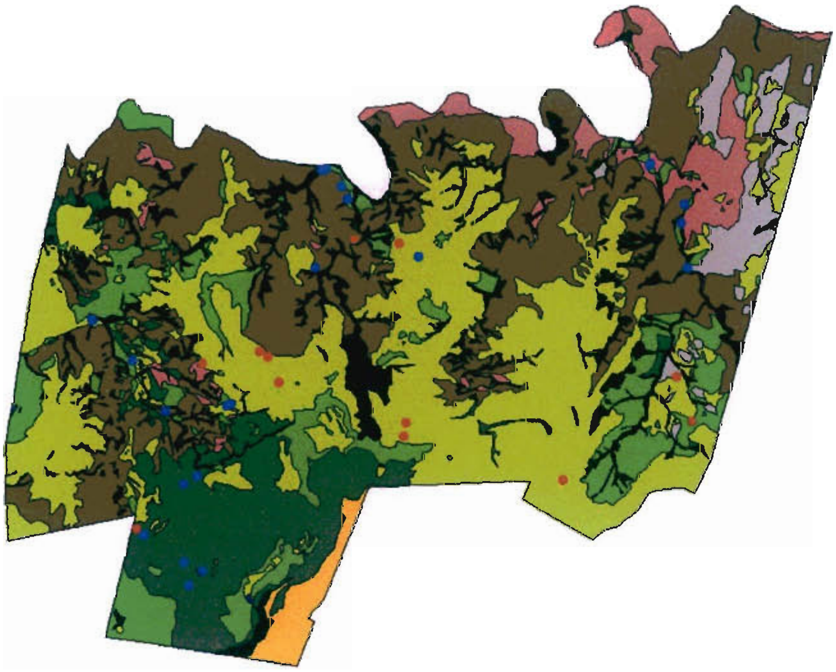
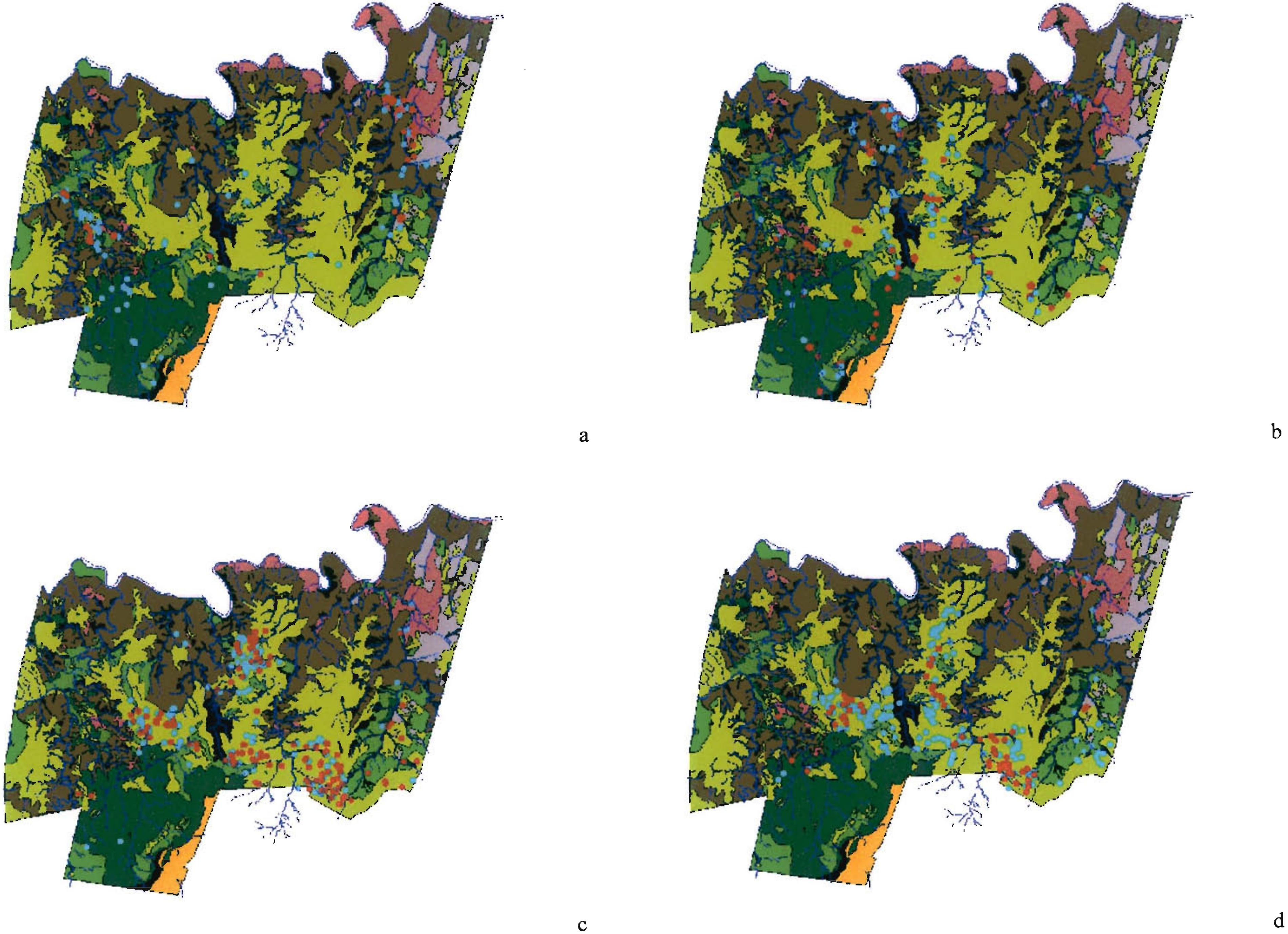


Fig 2.6: Impala, vegetation selection by bachelor and breeding herds during the rut (2003/2004 combined). Red dots = bachelor herds, blue dots = breeding herds. Vegetation legend, scale and orientation as per Fig 1.5, area sampled as per Fig2.2.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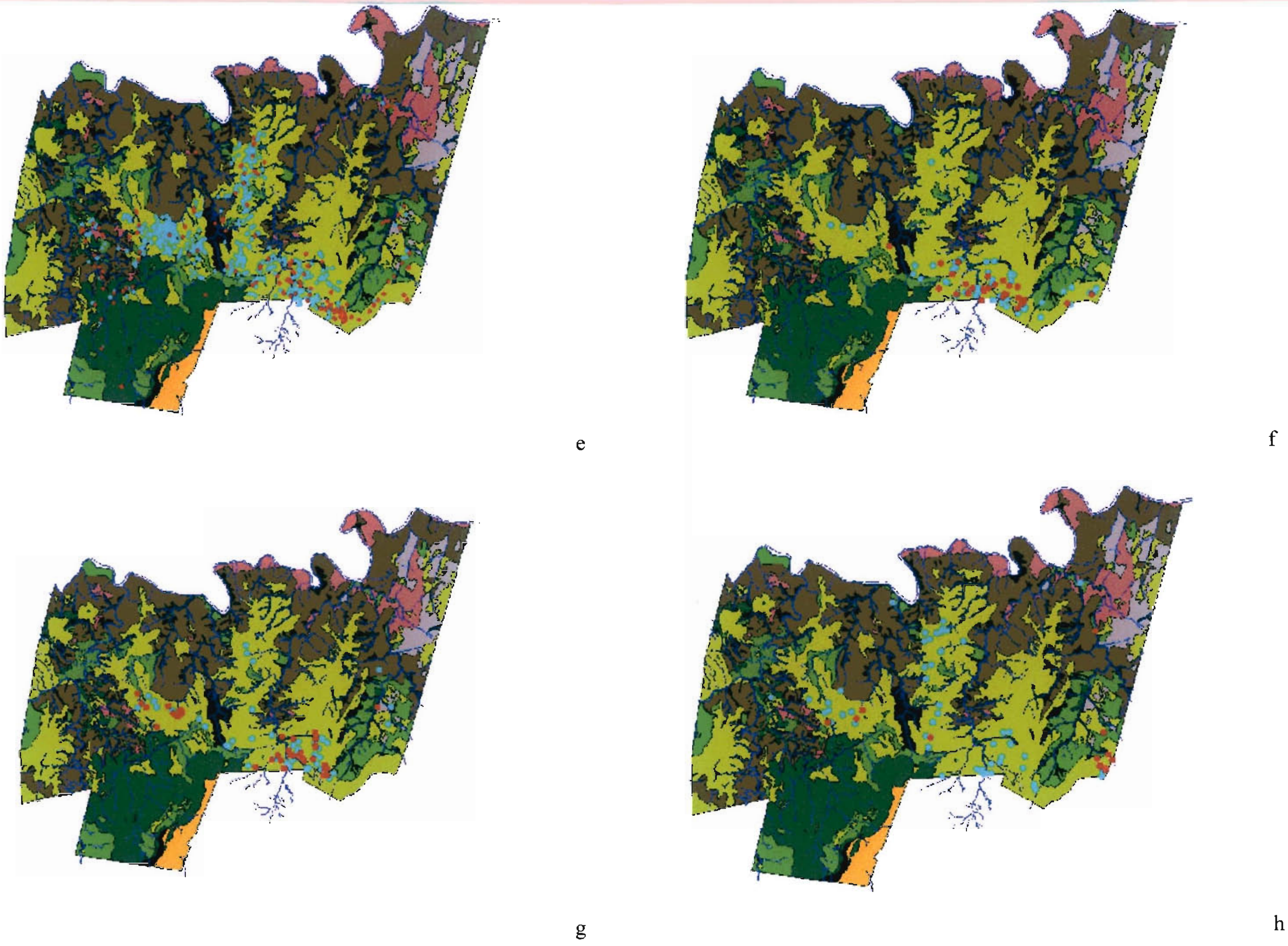
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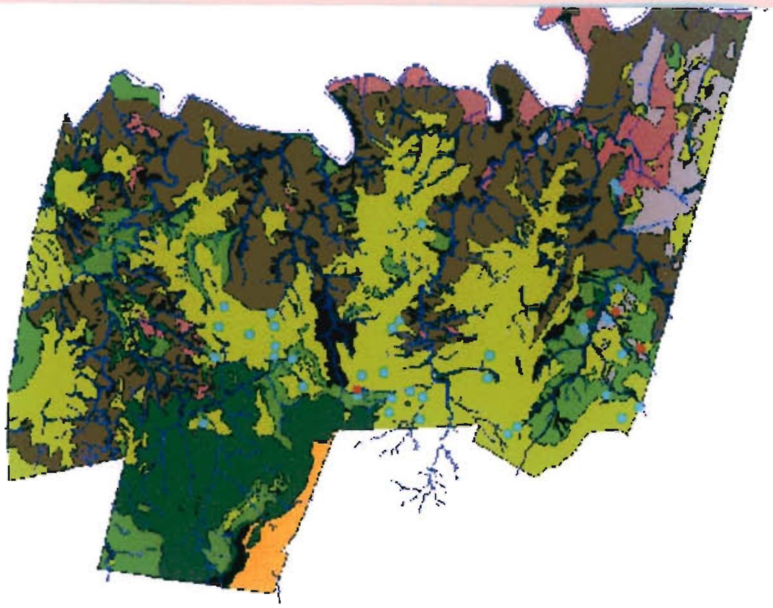

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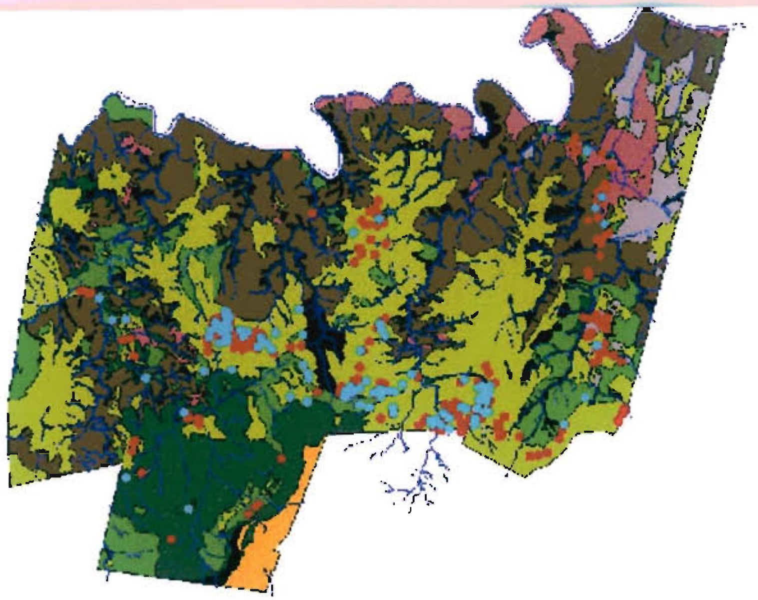

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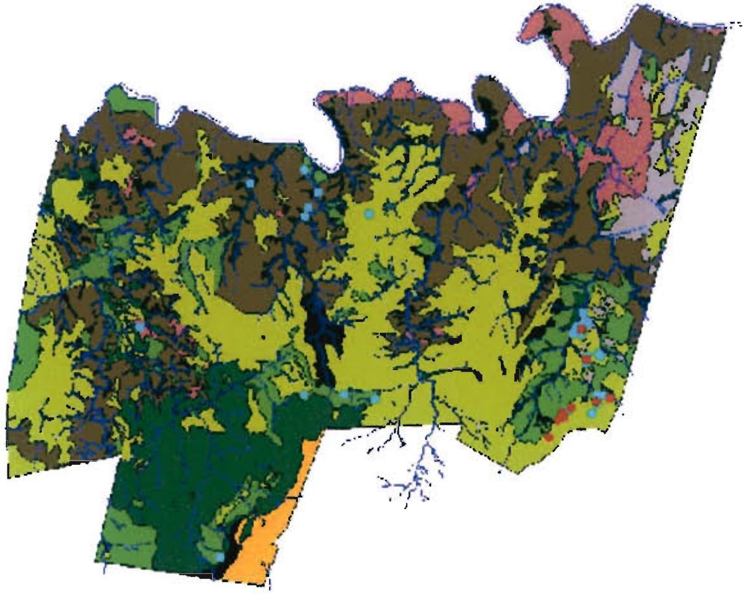

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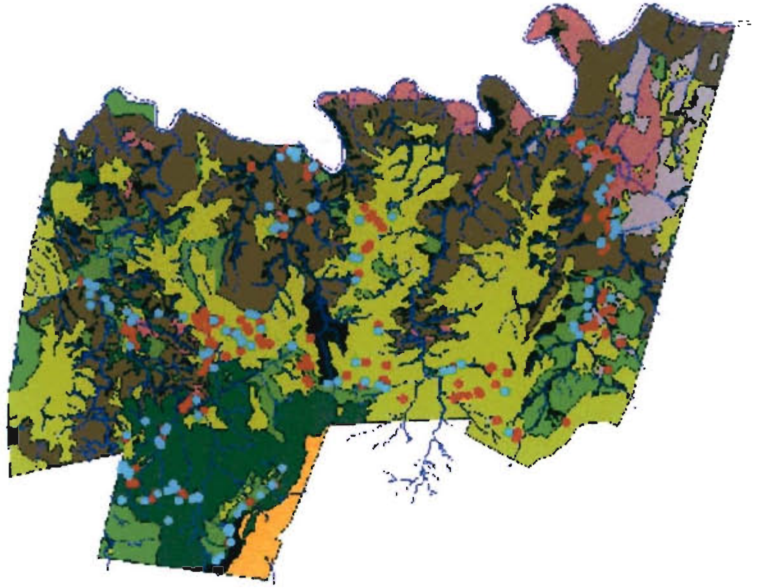

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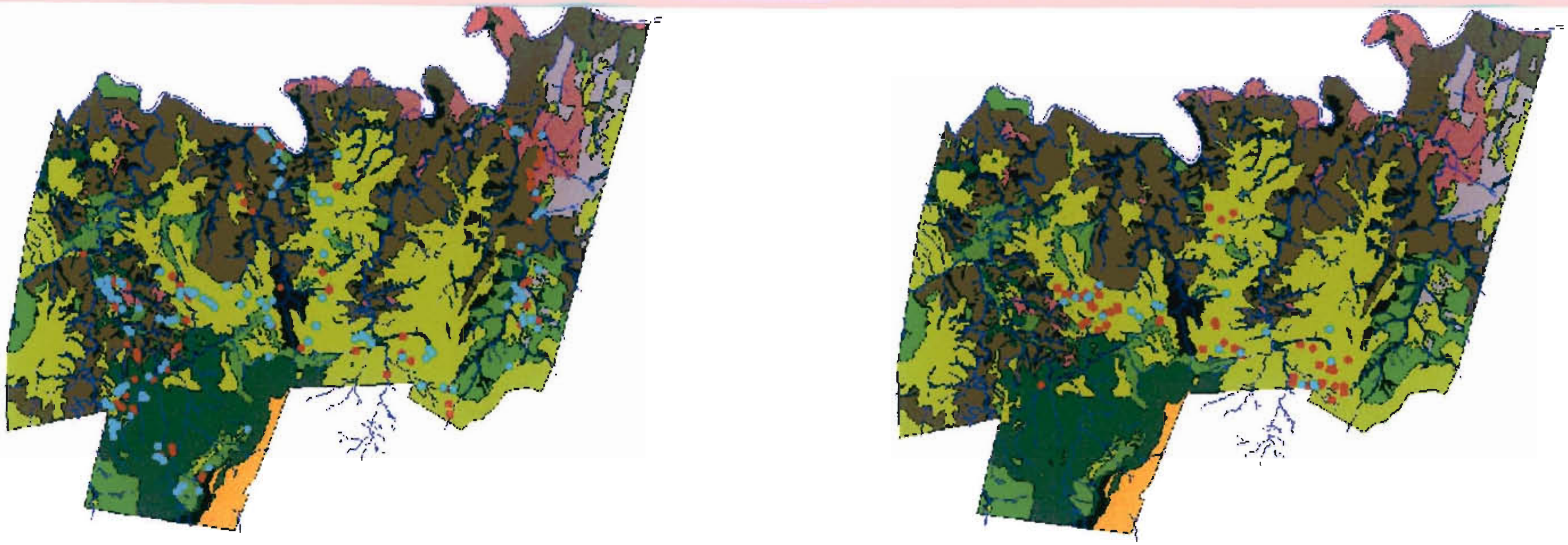


n

o

Fig 2.7: Seasonal distribution. Blue dots = wet season, red dots = dry season. Vegetation legend, scale and orientation as per Fig 1.5, area sampled as per Fig 2.2. Dark blue lines indicate surface water. 2003 and 2004 combined, except for wildebeest and impala where 2003 and 2004 are shown on separate maps. a = giraffe, b = kudu, c = wildebeest 2003, d = wildebeest 2004, e = zebra, f = hartebeest, g = tsessebe, h = reedbuck, j = white rhino, k = warthog, l = waterbuck, m = impala 2003, n = impala 2004 and o = ostrich.

Considering spatial, rather than categorical, data shows (Fig 2.7a) giraffe more widely dispersed in the wet seasons whilst concentrating along watercourses in the dry seasons. This is in keeping with others' findings (Leuthold 1978, Pellew 1984a) and is explained, in proximate terms, by giraffe moving down-slope as forage is lost at higher, and drier, elevations first and persists for longer closer to the drainage lines. Pellew (1983a) showed that quarterly rates of production of *Acacia* browse show a significant, sustainable production of new shoots in the valley-bottom woodland types throughout the dry season, as production rates fall to very low levels in the drier ridge top areas. This seasonal movement across the catena is thus the equivalent of similar movements demonstrated for grazing ungulates (Anderson and Talbot 1965, Bell 1970, Anderson and Herlocker 1973, Andere 1981); protein content has been shown to be higher in grasses growing on bottom-land illuvial soils (Downing 1979). Rosenzweig (1981, 1985) clarified habitat selection theory's position within optimal foraging theory, hypothesising that a single species should be less selective in its use of habitat types as resources become limiting. Pimm *et al* (1985) extended this to include the presence of other potentially competing species and Owen-Smith and Novellie (1982) further incorporated consideration of digestive rate limitations, hypothesising that whilst an optimally foraging ungulate should become less selective initially as food availability declines, once nutrient intake falls below maintenance levels animals will once again become more selective. In addition they hypothesised ruminants, due to more severe gastric limitations on the rate at which they can process forage, are more likely to be affected than non-ruminants, and grazers, for whom food quality is more likely to be important, more than browsers. However, other responses (e.g. to predators, water etc.) may obscure any habitat selectivity predicted by these theories, as may factors (e.g. individual differences, habitat variation, evolutionary lag) combining to make it unlikely that any animal will be perfectly adapted to a niche (Melton 1987). The marked restriction in area used by giraffe in the dry season compared to the wet season, characterised by their movement into the watercourses, can thus be explained, at a functional level, in terms of nutrient intake outside of these lower lying areas falling below maintenance.

Owen-Smith and Novellie (1982) found that kudus tendered to widen their diet in the dry season, and Dorgeloh (op. cit.) observed herds to be more widely distributed in that season. Here, although there is no evidence of an actual widening of diet (probably consequent on the spatial scale of vegetative category used in this study), there is no restriction in the area used by kudu in the dry compared to wet season and they are not seen to move into the watercourses (Fig 2.7b). This suggests that kudu in Ithala are not so resource limited in the dry season as to have to restrict themselves to comparatively small areas of acceptable/maintenance quality, as appears to be the case with giraffe, but rather continue to roam widely in search of food. Indeed, Owen-Smith and Novellie (op. cit.) suggested that kudu were limited by quantitative availability rather than by the effects of low quality food on digestion rates. Browsers exhibit feeding height stratification (du Toit 1990) and the acceptable condition of the intermediate browse, versus the upper browse, in Ithala (pers. obs.) would support this comparative interpretation of the state of dry season resource limitation for kudu as compared to giraffe. In contrast, a study in Rhodesia (Simpson and Cowrie 1967) showed kudu to move down the catena and restrict their habitat choice in the dry season; however the density of kudu in that reserve was four times that in Ithala and it suffered from low rainfall – factors which would suggest that kudu there were more likely to be severely resource restricted.

As the flushes of winter 2003 were on parts of the summer grasslands, wildebeest seasonal differences in spatial usage were more noticeable in 2004, with a marked reduction in area used in the winter of 2004 (Figs 2.7c/d). Melton (1987) recorded a significant winter reduction in area usage (i.e. increased selectivity) by wildebeest in nearby Umfolozi reserve. Spatially zebra (Fig 2.7e) showed, in contrast to wildebeest, a broadening of distribution in the winter.

Wildebeest, also *Alcelaphines*, had a considerably wider distribution in the reserve compared to hartebeest and tsessebe despite their occurrence on the same vegetation type (Figs 2.7c/d/f/g). Areas favoured by tsessebe (and hartebeest) were also not favoured by wildebeest and vice-versa (Fig 3.8, page 71). The possible manner in which the wide-mouthed wildebeest can 'capture' vegetation at a sward height below that tolerated by the narrow-mouthed (Schuette et al. 1998) tsessebe/hartebeest, and tsessebe/hartebeest can reduce the leafy component to a level below that tolerated by wildebeest (Murray and Illius 2000), is discussed later (Chapter 3) in connection with the poor performance of the tsessebe population. Such a situation may also explain the inter-species spatial difference. Both hartebeest and tsessebe showed a reduction in area used in winter (Figs 2.7f/g), tsessebe marginally more so, possibly relating to the inter-play between hartebeest having relatively low energy intake and slow growth rate (Arman and Hopcraft 1975, Murray 1993) and tsessebe, as shown by their considerably poorer performance as a population (Chapters 3 and 4), being under greater resource pressure.

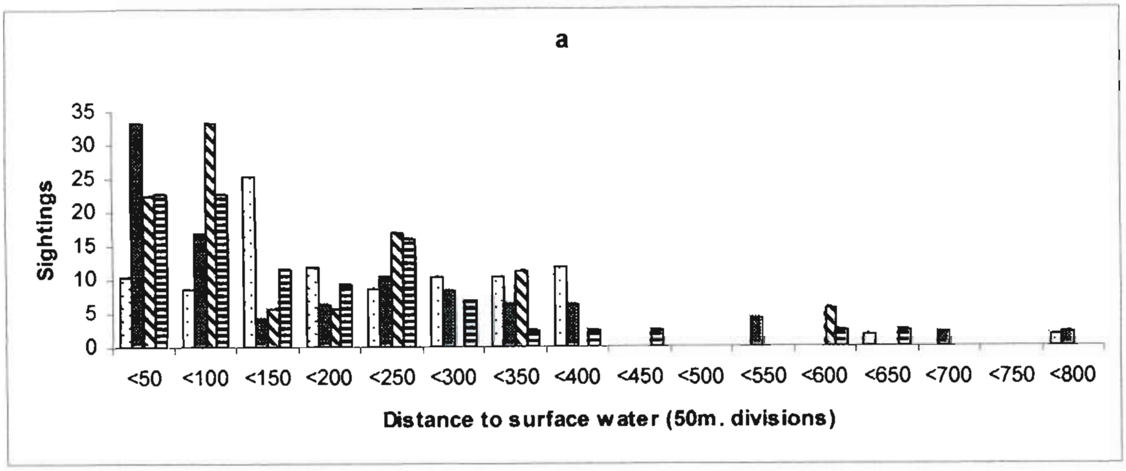
Spatially, reedbucks are seen to have a much reduced distribution in the winter (Fig 2.7h), suggestive of marked resource limitation at that time. The poor performance of the species in Ithala is discussed in later chapters.

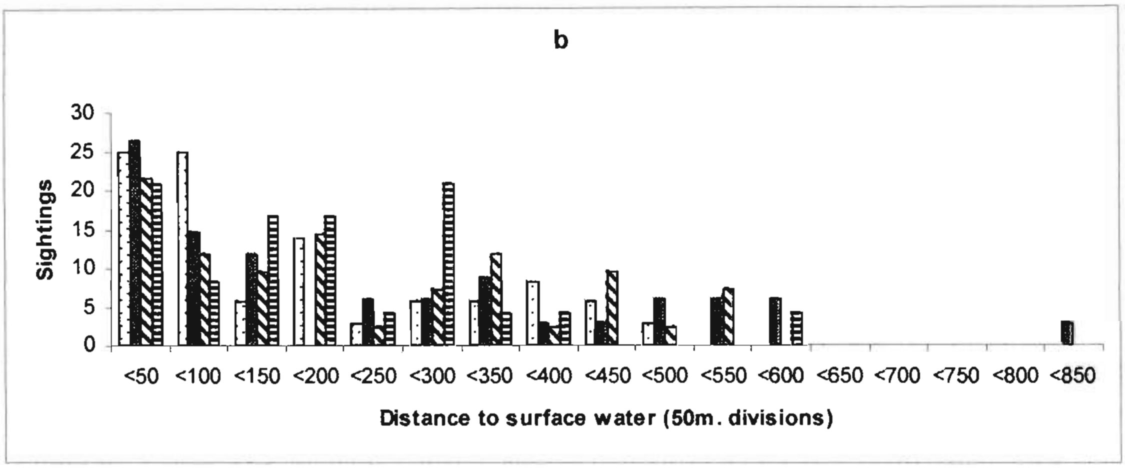
It would be expected (see above) for white rhino to be affected more in the manner of a grazing ruminant by food restriction i.e. to be dependant on quality rather than quantity. Perrin and Brereton-Stiles (1999) found that they moved to valley bottoms in the dry season in Hluhluwe-Umfolozi; white rhinos near the White Nile also used to concentrate in wetlands in the dry season and migrate to higher ground during the rains (Foster 1967). In this study rhino, in both winters, showed a marked move down-slope into the watercourses occupying a much more restricted area (Figs 2.7j).

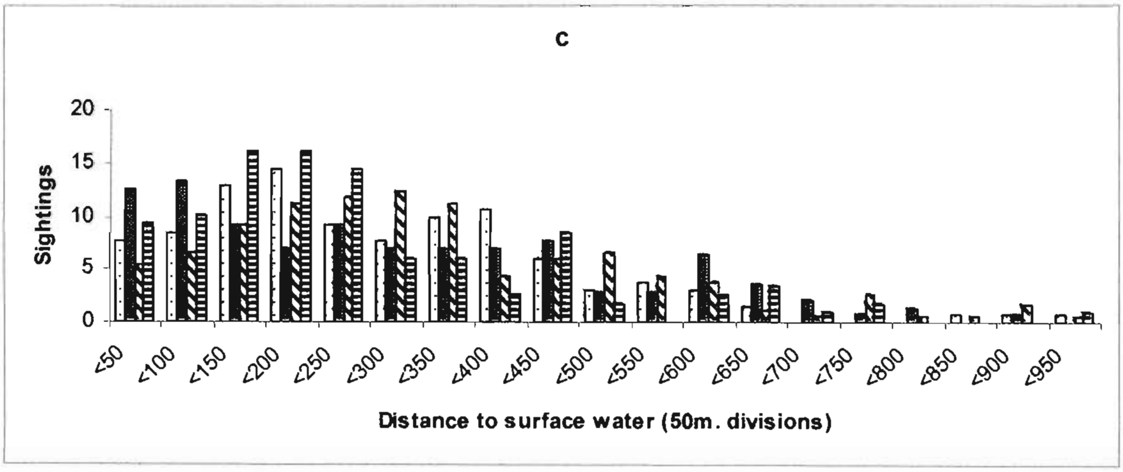
Spatially (Fig 2.7k) warthog appeared to show a mild widening (certainly no narrowing) in distribution in winter compared to summer; a similar widening in habitat type was not seen but since warthog can exploit a different resource in the same habitat type in different seasons due to their rooting, simple records of habit type used, with no direct measurement of food type consumed, would not be expected to show such a result.

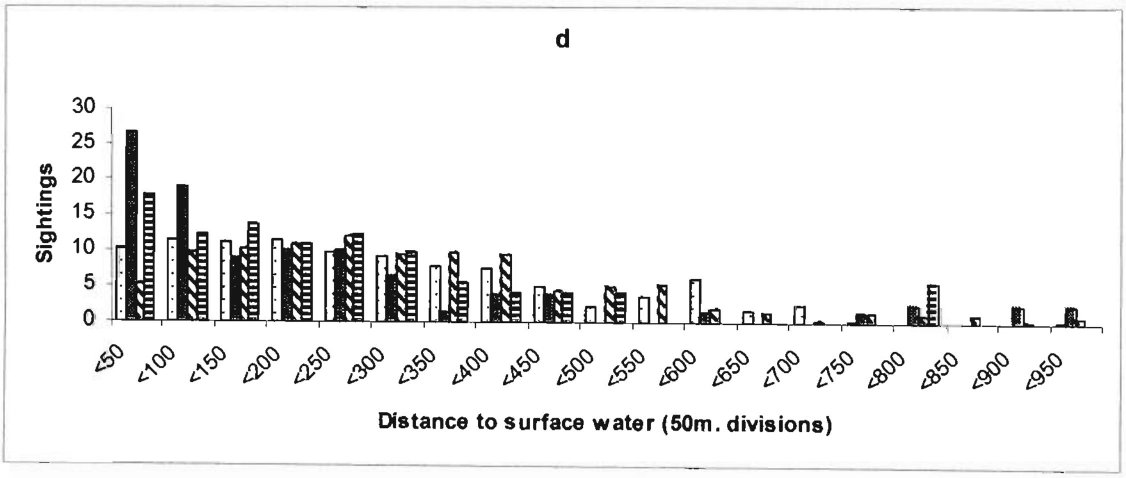
In Umfolozi Game Reserve impala were seen to be both more habitat and area selective towards better resources in the dry season (Melton 1987). A trend is apparent from the vegetation selection results (Fig 2.4k) towards animals' densities being spread across fewer categories in the dry season and, as remarked on above, these categories are rich in browse, a better resource at that time. A trend towards increased area selectivity is not obvious visually (Figs 2.7m/n), although there is possibly an overall reduction in the winter. The reduction is certainly not as obvious as with wildebeest, but not as non-existent as with kudu; thus there appears to be no evidence from these findings of marked resource limitation, as is the case with wildebeest, but equally impala in this reserve do not seem to be as quality independent, and quantity dependant, as perhaps kudu are in winter (Owen-Smith and Novellie 1982). Impalas' position as an intermediate feeder would fit in with these tentative suggestions.

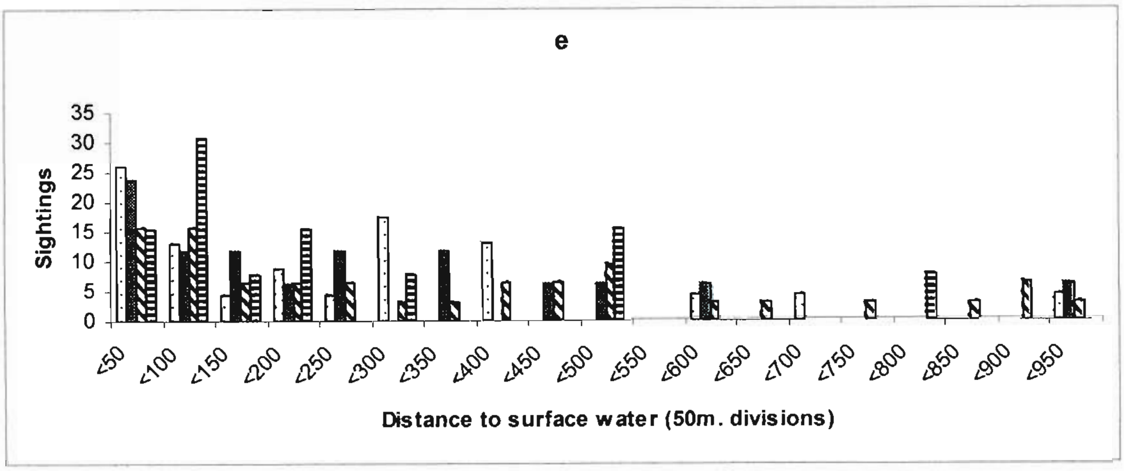
Distance to water:










e
Sightings
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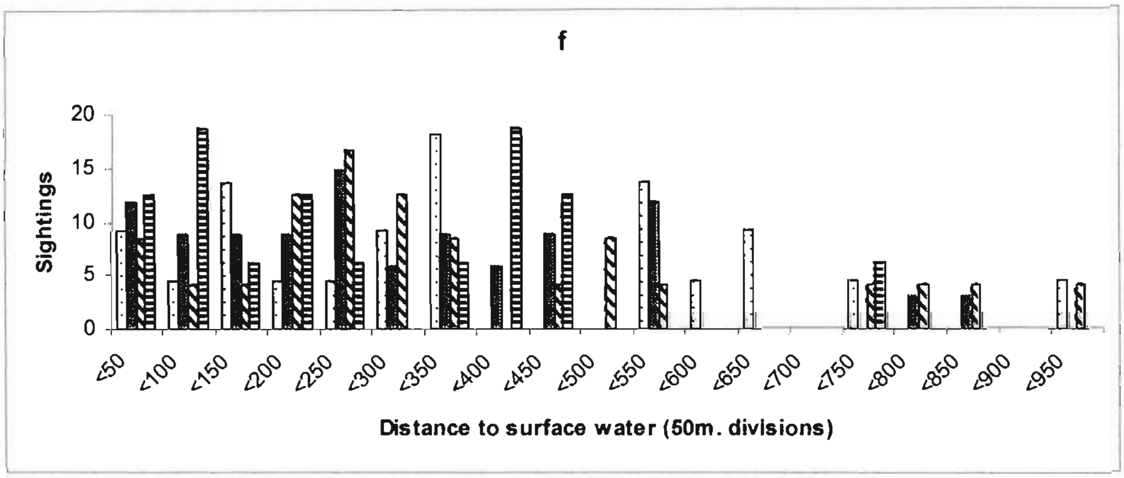
Distance to surface water (50m. divisions)


f
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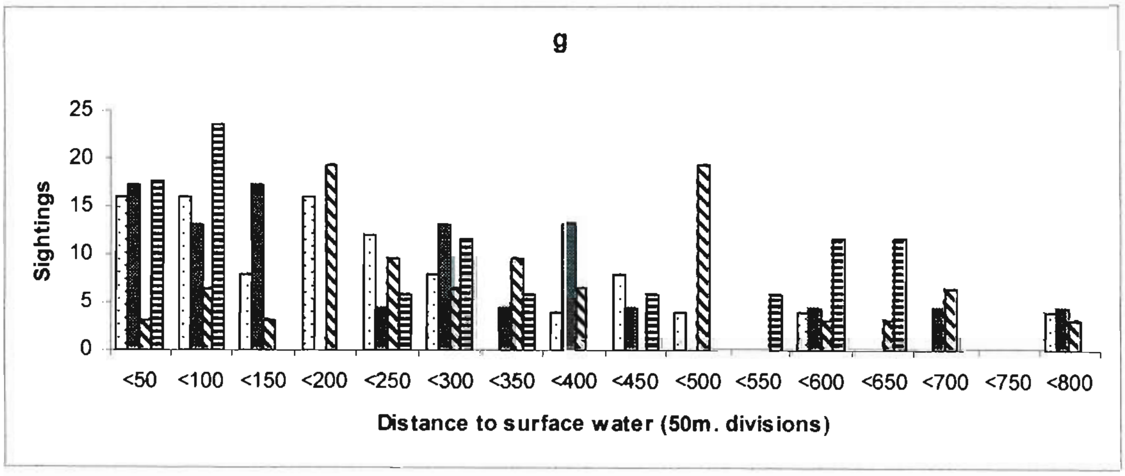
Distance to surface water (50m. divisions)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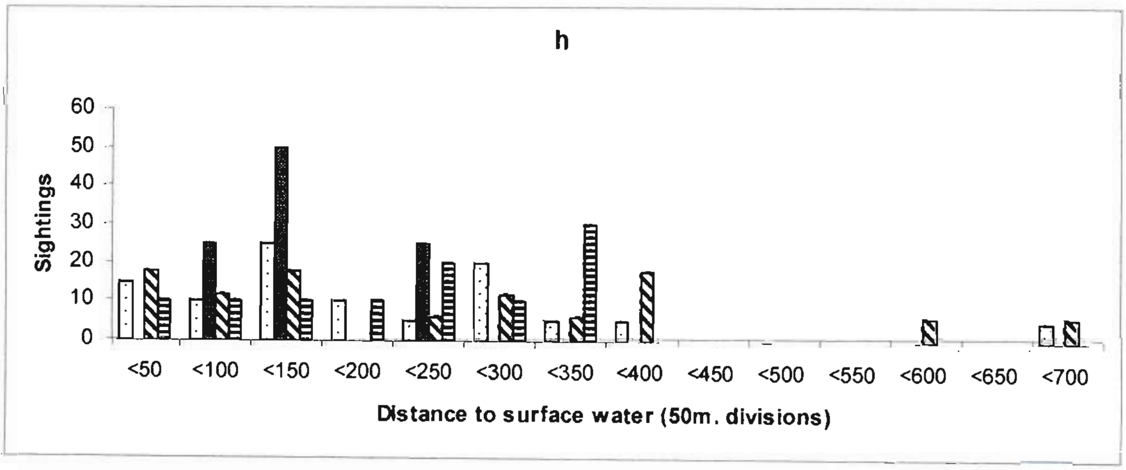
Distance to surface water (50m. divisions)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Sightings
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Distance to surface water (50m. divisions)

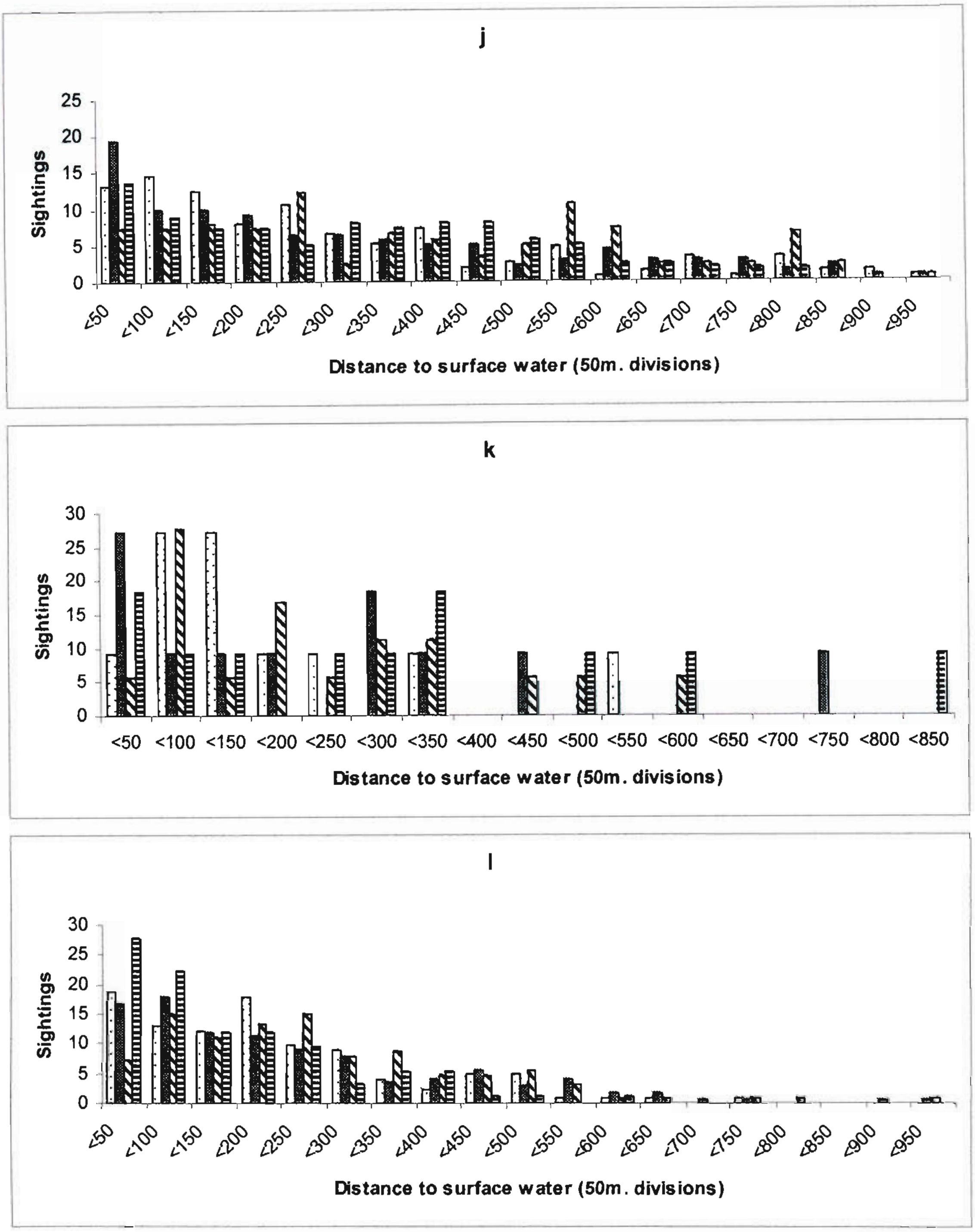


Fig 2.8: Distance to surface water. Sparse dots = wet season 2003, close dots = dry season 2003, diagonal strips = wet season 2004 and horizontal strips = dry season 2004. Sightings = number of sightings expressed as a % of total number of sightings. a = giraffe, b = kudu, c = wildebeest, d = zebra, e = hartebeest, f = tsessebe, g = reedbuck, h = white rhino, j = warthog, k = waterbuck and l = impala.

Table 2.4: Average distance to water by season. Increases in the dry season compared to the wet season are shown in bold type. Italics indicate a very small sample.

Species		Average distance (metres) to surface water by season					
		2003			2004		
		wet 2003	dry 2003	dry as a % of wet	wet 2004	dry 2004	dry as a % of wet
Giraffe	all	212	146	69	146	**174**	**119**
	males only	202	188	93	151	**157**	**104**
	breeding	217	152	70	134	**177**	**132**
Kudu	all	154	**270**	**175**	213	176	83
	males only	215	*52*	*24*	177	***201***	***114***
	breeding	137	**289**	**211**	221	173	78
Hartebeest	all	233	222	95	370	258	70
Reedbuck	all	223	**259**	**116**	353	299	85
Tsessebe	all	362	264	73	421	257	61
Warthog	all	253	**275**	**109**	390	326	84
	males only	229	**249**	**109**	284	*164*	*58*
	breeding	242	**271**	**112**	410	360	88
Waterbuck	all	219	**240**	**110**	216	**376**	**174**
	breeding	225	**277**	**123**	232	**405**	**175**
White Rhino	all	227	147	65	216	196	91
Wildebeest	all	272	**303**	**111**	310	234	75
	bachelor	220	**235**	**107**	196	125	64
	breeding	284	**367**	**129**	335	246	73
	terr. Male	274	**289**	**105**	345	270	78
Zebra	all	274	189	69	304	237	78
	bachelor	281	120	43	258	***292***	***113***
	breeding	290	265	91	364	291	80
Impala	all	169	**213**	**126**	221	128	58
	bachelor	293	268	91	236	158	67
	breeding	141	**193**	**137**	217	119	55
	terr. Male	155	**247**	**159**	252	132	52

The relationship between animals distance to surface-water and the season will vary according to the interplay between topography and water availability. Animals will remain within reach of water, according to their varying temporal requirements, and therefore if sources are restricted animals will occur in higher concentrations in their vicinity than elsewhere. In such cases declining quality and quantity of forage available during the dry season will force animals to forage further away from the water, leading to an increase in average distance of animals to surface water (Redfern et al. 2003); this will especially be the case in flatter regions where catena effects, which lead to better resources down the catena (i.e. closer to water), will be minimal. At the other extreme, if water is freely available and places no restriction on animal range, animals will be distributed irrespective of surface water. How seasonal shortages affect the situation will vary according to topography; flat areas would be expected to show little change in animals' ranges but in hilly areas animals would be expected to move down the catena i.e. closer to water and to lower elevations. Consequently in areas where water is freely available with markedly varied topography, as is the case in Ithala, average distances to surface water (and elevation) would be expected to decrease in the dry season.

Average distance to surface water (Table 2.4) for giraffe did show a decrease, corresponding to movement down the catena, in the dry season of 2003 but an unexpected increase in the dry season of 2004. Distances to water histograms (Fig 2.8a) confirm this finding. However in both winters giraffe locations were in the valleys along the watercourses (Fig 2.7a); the avoidance of lower areas in the dry season of 2004 compared to the preceding wet season was perhaps due to permanent damage to the upper browse (a phenomenon seen widely in the reserve, pers. obs.) in those areas from previous over grazing. As kudu were seen to seasonally maintain a wide distribution and not move into the watercourses (see above), average distance to water would not be expected to show any particular seasonal trend. The fairly marked increase in 2003 and decrease in 2004 (Table 2.4), which is shown by histograms (Fig 2.8b), is thus unexpected.

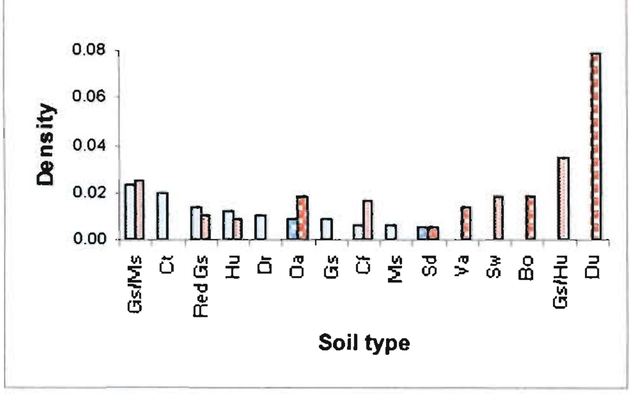
Grasslands burnt, partially due to the topography of the reserve and partially due to the location of tourist routes, were generally on higher ground and this accounts for the finding that in winter 2003 there was an overall increase in wildebeest distance to surface water, whilst in winter 2004 there was the more expected decrease in this measurement (Table 2.4 and Fig 2.7c), consequent on movement down the catena (Andere 1981). It is of interest that Zulu herders of yesteryear practiced this same seasonal movement, moving their Nguni cattle as the summer progressed down the valley sides to the sweeter grasses of the valley floors in the winter (Guy 1980, Poland et al. 2003). Zebra were also seen to reduce their average distance to water (Table 2.4 and Fig 2.7d) in winter, in keeping with a general move down the catena. The extent of this move, reflected in these results, accounts for the large reduction in sightings of this species in winter, as vehicle routes used tend to be on higher ground. The use of the flush most probably accounts for hartebeest moving further away from water in the dry season of 2003 - otherwise both hartebeest and tsessebe showed a mark move towards water in the dry seasons (Table 2.4 and Figs 2.7e/f), commensurate with their increasing their area selectivity and moving down the catena.

Reedbuck distance to water increased in the winter of 2003, possibly due to grass flushes affecting their distribution (see above), but decreased in 2004 (Fig 2.7g) commensurate with a move down the catena. White rhino moved nearer to water in both winters (Table 2.4 and Fig 2.8h). Consequent on their attraction to green flushes (located on higher ground), warthog showed an increase in distance to water in the winter of 2003 but a decrease, corresponding to a move down the catena, in the winter of 2004 (Table 2.4 and Fig 2.8j). Waterbuck showed puzzling increases in distance to water in both winters (Tables 2.4 and Fig 2.8k). In a ruminating grazer that selects and requires a diet rich in protein (Taylor et al. 1969), this lack of a move down the catena in winter is unexpected. It may be that the behaviour of moving to grasslands in the dry season (see above) is the cause, as these tend to be higher in Ithala, but this would imply that waterbuck are obtaining sufficient nutrition on the (higher) grasslands in winter – this seems unlikely. The weaknesses of the data collection technique when applied to waterbuck are discussed elsewhere (Chapter 3); these same weaknesses may be the underlying explanation for these unexpected findings.

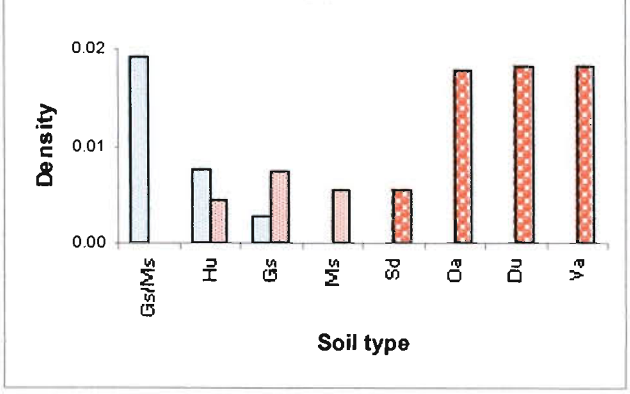
Impala have been shown to move down-slope in the dry season in the middle Zambezi Valley (Jarman 1972) and in the Serengeti (Jarman 1979). Here a reduction in average distances to water, commensurate with such a move, are seen in the 2004 dry season (Tables 2.4 and Fig 2.8l); the reverse is seen in 2003 due to the marked move to green flushes on higher ground. This difference is also discernable visually from animal distribution maps (Figs 2.7m/n).

Soil selection:

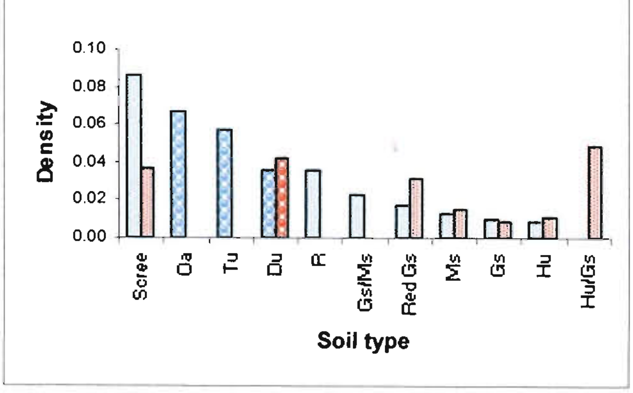
a(i)



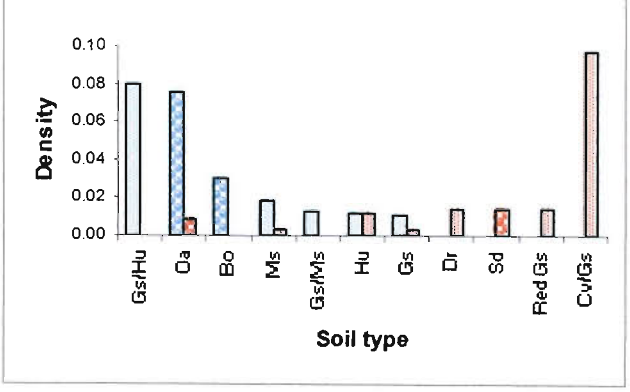
a(ii)



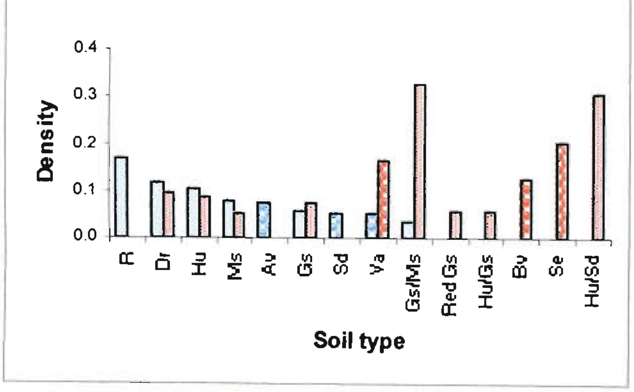
b(i)



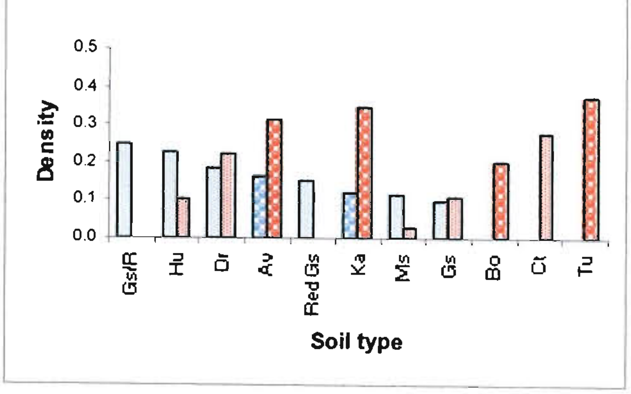
b(ii)



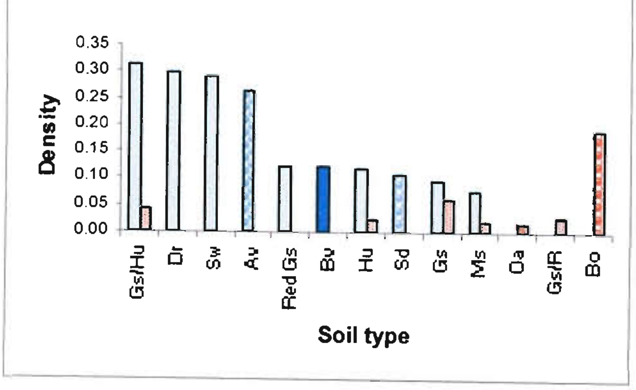
c(i)



c(ii)



d(i)



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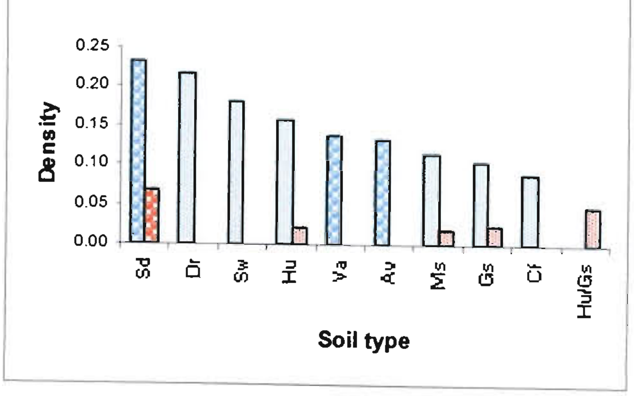


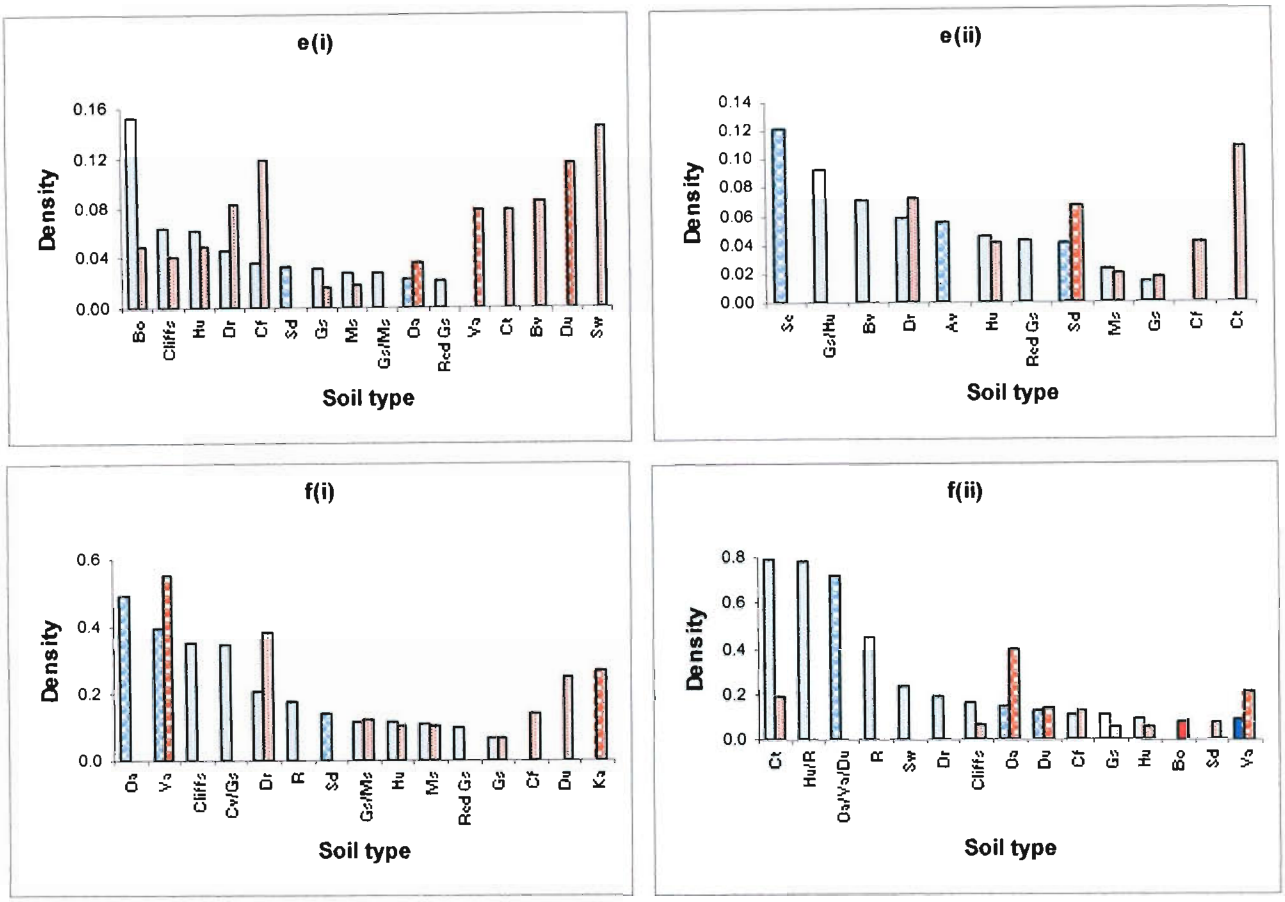


Fig 2.9: Soil selection. (i) = 2003, (ii) = 2004. Blue = wet season, red = dry season. Small dots = light soils, large dots = heavy soils; see Appendix 4 for full description of soil characteristics. a = giraffe, b = kudu, c = wildebeest, d = zebra, e = warthog and f = impala.

Bell (1970) explained movement down the catena in the dry season in terms of the heavier, more nutrient rich and water retentive bottom-soils supporting vegetative growth for longer in that season, versus the light, sandy, nutrient poor soils, with little water holding capacity, typically found higher up the catena. Soil type selection by giraffe (Fig 2.9a) showed this increased selection for heavy soils in the dry season. The lack of any apparent selection for heavier soils in the dry season by kudu (Fig 2.9b) is in agreement with their maintaining a wide distribution and not moving into the watercourses in the dry season.

Wildebeest showed selection of heavier, water and mineral retaining soils in the winter of 2004, but not, consequent on the green flushes being generally on higher ground, in the winter of 2003 (Fig 2.9c). The lack of any evidence of zebra moving onto heavier soils in winter (Fig 2.9d) possibly suggests that they, although generally moving down the catena, are not obliged to seek out and compete with ruminant herbivores for the localised areas of heavier soil, supporting superior quality forage. Warthog appeared to show no selection for heavier soils in the winter of 2004 compared to 2003 and their respective summers (Fig 2.35). The general picture for warthog is thus similar to that of zebra – another non-ruminant – in that both appeared to broaden their distribution in the winter, move down the catena closer to water but not onto the heavier soils.

Impala soil selection results (Fig 2.9f) do not show any obvious trend, although there is perhaps greater proportional selection of heavy soils in the winter of 2004 than 2003 compared to their respective summers; this would agree with their move down the catena.

Sample numbers for the other herbivores studied were too small to relate to underlying soil types.

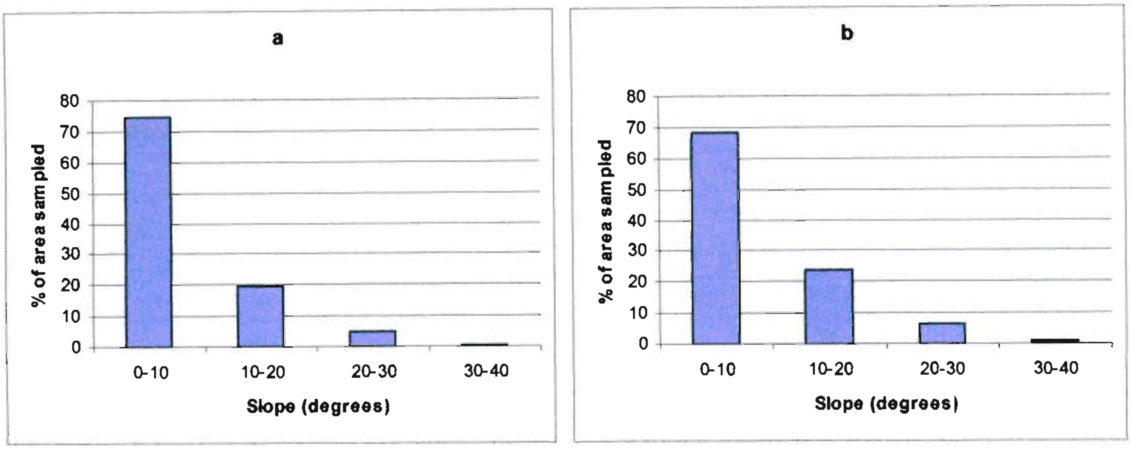
Slope selection:

Table 2.5: Slope, showing densities (number of animals per hectare) of species on each slope category (slope categories in degrees). Entries in italics indicate less than five observations were made of that species/sex group in that season. Blank entry indicates no sightings in that habitat type. The proportion each slope category contributes to the total area sampled is shown, as a percentage, in Fig 2.10 at the end of the table.

Species	Group	Season	Density (number of animals per hectare) by slope category			
			0 - 10	10 - 20	20 -30	30 -40
Bushbuck	All	wet 03	*0.0016*	*0.0024*		
		dry 03	0.0022	0.0012	0.0049	
		wet 04				
		dry 04		*0.0036*	*0.0049*	*0.033*
Duiker	All	wet 03	*0.0012*	*0.0024*		
		dry 03	0.0012		0.019	
		wet 04	*0.0003*	*0.0024*		
		dry 04	*0.0009*	*0.0024*		
Giraffe	Males only	wet 03	0.0042	0.0033	0.0024	
		dry 03	0.0023			
		wet 04	0.003			
		dry 04	0.0042	0.0007	0.0024	
	Breeding	wet 03	0.0122	0.0098	0.0024	
		dry 03	0.0083	0.0046		
		wet 04	0.0016	0.0098	0.0048	
		dry 04	0.0083	0.0046	0.0073	
Kudu	Males only	wet 03	0.006	0.008	0.02	
		dry 03	*0.001*	*0.002*		
		wet 04	0.0068	0.0071		
		dry 04	0.0022	0.0024		
	Breeding	wet 03	0.025	0.021	0.127	
		dry 03	0.022	0.037	0.088	
		wet 04	0.03	0.043		
		dry 04	0.023	0.016		
Hartebeest	All	wet 03	0.022	0.0059	0.0147	
		dry 03	0.034	0.0048		
		wet 04	0.034	0.0083	0.0098	
		dry 04	0.034			
Reedbuck	All	wet 03	0.015	0.008		0.033
		dry 03	0.008	0.023		
		wet 04	0.016	0.01	0.02	
		dry 04	0.007	0.006		
Tsessebe	All	wet 03	0.02	0.015		
		dry 03	0.031	0.008		
		wet 04	0.025	0.0083		
		dry 04	0.021			
Warthog	Males only	wet 03	0.009	0.002		
		dry 03	0.003			
		wet 04	0.008	0.004		
		dry 04	*0.001*			
	Breeding	wet 03	0.072	0.073		
		dry 03	0.06	0.02	0.01	
		wet 04	0.053	0.002		
		dry 04	0.052	0.023	0.015	

Species	Group	Season	Density by slope category 0 - 10	10 - 20	20 -30	30 -40
Waterbuck	Bachelors	wet 03	*0.0022*			
		dry 03	*0.0002*			
		wet 04	*0.0012*			
		dry 04	*0.0009*			
	Breeding	wet 03	0.0047	0.0095	0.0049	
		dry 03	0.0012	0.0028		
		wet 04	0.015	0.0036	0.044	
		dry 04	0.0019	0.0178	0.0391	
	Terr. males	wet 03	*0.0009*	*0.0012*		
		dry 03	*0.0003*			
		wet 04	0.0009	0.0012	0.0098	
		dry 04	*0.0009*	*0.0012*		
Wildebeest	Bachelors	wet 03	0.014	0.056	0.015	0.63
		dry 03	0.022	0.042	0.029	
		wet 04	0.031	0.058	0.064	
		dry 04	0.03	0.017		
	Breeding	wet 03	0.15	0.073		
		dry 03	0.13	0.144		
		wet 04	0.27	0.22	0.054	
		dry 04	0.23	0.052		
	Terr. males	wet 03	0.025	0.012	0.024	
		dry 03	0.022	0.009	0.005	
		wet 04	0.035	0.014	0.005	
		dry 04	0.021	0.013	0.01	
Wh. Rhino	All	wet 03	0.009	0.007		
		dry 03	*0.002*	*0.0024*		
		wet 04	0.007	0.004		
		dry 04	0.007			
Zebra	Males only	wet 03	0.039	0.012	0.02	
		dry 03	0.008	0.01		0.005
		wet 04	0.02	0.021		
		dry 04	0.004	0.002		
	Breeding	wet 03	0.14	0.05	0.024	0.02
		dry 03	0.008	0.02	0.015	
		wet 04	0.12	0.048	0.034	
		dry 04	0.025	0.017	0.015	
Eland	All	wet 03				
		dry 03	0.01	0.0048		
		wet 04	*0.0037*	*0.0012*		
		dry 04				

Species	Group	Season	Density by slope category 0 - 10	10 - 20	20 -30	30 -40
Impala	Bachelors	wet 03	0.06	0.052		
		dry 03	0.063	0.04		
		wet 04	0.075	0.01	0.015	
		dry 04	0.033	0.059	0.024	
	Breeding	wet 03	0.22	0.29	0.28	
		dry 03	0.24	0.16	0.05	0.03
		wet 04	0.24	0.238	0.054	
		dry 04	0.16	0.03		
	Terr. males	wet 03	0.01	0.01	0.01	
		dry 03	0.013	0.015	0.005	
		wet 04	0.012	0.013	0.005	
		dry 04	0.01			
Nyala	All	wet 03	*0.0019*			
		dry 03	*0.0031*			
		wet 04				
		dry 04	*0.0025*			
Ostrich	All	wet 03	0.004	0.011		
		dry 03	0.016	0.005		
		wet 04	0.024	0.005		
		dry 04	0.023			



2.10: Slope gradient categories as a percentage of total area sampled a) for all species except giraffe and b) for ıffe only.

hough there appears to be no particular trend in giraffes use of different slope categories, apart from them widely ising slopes up to the 20 to 30 degree category, the noticeable increase in their density on the steeper, and sumably less desirable, slopes in the winter of 2004 (Table 2.5) compared to the winter of 2003 may be further lence of worsening resource depletion. Kudu were generally seen in higher densities on steeper slopes mplimenting their preference for browse habitats), but no seasonal or sexual pattern was apparent. This finding ees with that of Mason (1973) in the Transvaal. Not surprisingly in view of their preferred habitat, bushbuck urred in highest density on steeper slopes.

ldebeest generally occupied gentler slopes, with bachelor herds showing higher densities on harsher slopes. A shift zebra towards the use of steeper slopes in the winter was apparent in both years, possibly reflecting their adening of habitat selectivity in that season. Both hartebeest and tsessebe were found mainly on gentler slope egories and both showed a shift to the most gentle in the winter. Reedbuck generally utilised steeper slopes than er antelope, with the exception of waterbuck. White rhino were, not surprisingly in view of their vegetation ferences and bulk, seen mainly on gentler slopes. Warthog, especially males, tended to use the gentler slopes with seasonal pattern apparent. Waterbucks' use of steeper slopes, which showed no seasonal pattern, was marked.

ala showed a general reduction in steepness of slope used in winter compared to summer, especially with eding herds.

Green flushes following burns:

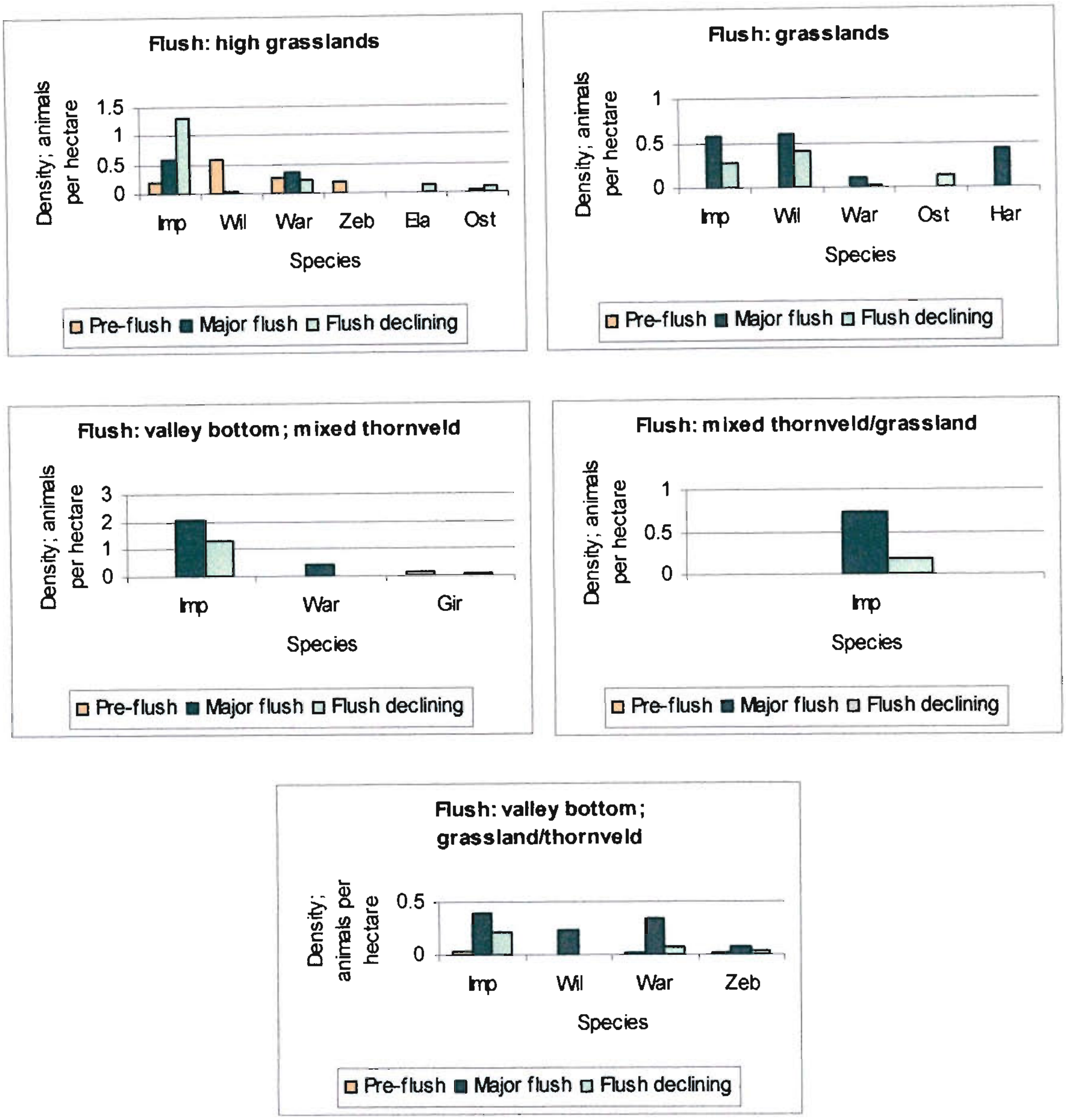


Fig 2.11: Flush, showing densities of herbivores on area of flush approximately one month before (pre-flush), during (major flush) and approximately one month after (flush declining) appearance of grass flush, in various habitats following winter burning in 2003.

As mentioned above, certain herbivores' habitat selection in Ithala is heavily influenced by flushes of fresh green grass following winter burning. Although started and controlled by management in the reserve, fire is a natural and integral part of savanna ecosystems (Scholes and Walker 1982). A few days after burning the residual tufts of grass drive out new growth, triggered by the fire induced 'heat shock', provided enough soil moisture is available (Sturm 1993). As plants age, their concentration of protein decreases whilst the proportion of relatively indigestible crude fibre increases – the young grass is thus high in protein and easily digestible, giving it high nutritive value (McDonald et al. 1987) especially as elsewhere in the dry season food availability is low and grass quality poor (Huntley and Walker 1982). Additionally, fire reduces canopy leaf mass of browse plants within its reach (Rutherford 1981) and for mixed feeders this may make the new grass doubly attractive. This attractiveness of newly burnt areas to large herbivores is widely recognized (Rowe-Rowe 1982, Moe et al. 1990) and has been investigated in terms of inter-species comparative utilisation of the resource (Wilsey 1996, Tomor and Owen-Smith 2002). Wilsey (op. cit.) proposed that relative use of green flushes following burns among African ungulates was related to body size; larger animals utilising them less due to their ability to survive on relatively lower quality foods (Demment and Van Soest 1985, Illius and Gordon 1992), consequent on the inter-relationships between body size, energy (Hungate et al. 1959) and protein turnover (Brody et al. 1934) and gut capacity (Illius and Gordon 1992). However, his own results from the Serengeti showed only a weak ($r^2 = 0.29$) linear regression between body size and use of burned sites, with wildebeest, one of the larger species, showing paradoxically marked use of flushes. Tomor and Owen-Smith (op. cit.) did not find this relationship between body size and use of flush.

In Ithala, impala, wildebeest and warthog made most use of the flush (Fig 2.11), with hartebeest also showing a fairly marked move onto the burnt areas. These findings agree with those of others (Field and Laws 1970, Crowe et al. 1981, Shackleton 1992, Wilsey 1996, Wilmshurst et al. 1999, Gureja and Owen-Smith 2002, Tomor and Owen-Smith op. cit., Wronski 2003). The relatively little use by zebra of flushes observed in this study agrees with Wilsey's (op. cit.) findings. White rhino were not seen on the flushes. This differential pattern of usage, whilst partially agreeing with Wilsey's body size hypothesis, suggests that the missing part in his proposal is the influence of gut morphology; namely ruminant versus non-ruminant. Ruminants, being more dependent on quality of forage than quantity, are likely to be more attracted during times of resource scarcity to flushes than non-ruminants, who can cope with such conditions by increasing their intake of lower quality forage. Clearly non-ruminants would be expected to still desire the quality new grass in the depths of winter, but ruminants desire would be greater as they have no easy alternative i.e. zebra are being competitively displaced from the flushes. Even where zebra have been seen on flushes to a more marked extent, they were observed to be the least restricted in their occupation of the different vegetation zones apparent in the flush area (Tomor and Owen-Smith, op. cit.) – again likely to be due to their more generalised, non-ruminant taste. White rhino, although non-ruminants, are considered, due to their poor digestion (Owen-Smith 1973), to behave digestively more like ruminants; however, their shear bulk requires large quantities of forage each day which short grass flushes are unlikely to provide.

The results for Ithala have been presented by broad habitat type and it is noticeable that on the high grasslands wildebeest, whilst occurring prior to the burning, do not appear on the grass flush after burning– in marked contrast to the situation on lower grasslands. This is most probably because burning occurred round about the time wildebeest were seen to abandon the higher elevations; even so it is interesting that for a species renowned at detecting and travelling large distances for fresh grass growth (Talbot and Talbot 1963), they did not travel back up the catena to utilise this resource.

Interactions between species:

Possible competition, in the form of resource competition, between some of the herbivores and the effect this may be having on their habitat selection has been discussed above. Thus the high density of wildebeest may be instrumental in the under-utilisation of the grasslands by impala, and the restricted range of hartebeest and tsessebe, year round, and of white rhino in the winter. Impala may be restricting wildebeest use of woodland and thicket.

Minimal predator/prey interactions may also be influencing species' habitat selection – such as impala favouring closer, browse habitats even in the summer, female giraffe utilising tall woodlands and kudu breeding herds not favouring open grasslands in the early breeding season.

Lamprey (1963) interpreted the formation of mixed (i.e. interspecific) herds in the Tarangire Game Reserve, Tanganyika as being protective to one or both species; it is thus an example of a facilitative interaction between species. Sinclair (1985a) concluded that in general predation (causing animals to associate) appears to play as much a role as interspecific competition (causing animals to disperse), in structuring the ungulate community in the Serengeti-Mara region. Although no formal analysis was carried out on this aspect of behaviour, which clearly relates to habitat selection, it was noticeable that whilst large herds (say greater than ~ ten individuals) were very rarely seen to associate with large herds of another species, smaller herds and individuals were frequently seen in the company of larger herds of other species. Thus lone territorial bulls were often seen to associate with larger groups of other species in their territory (Appendix 5 Plate 1), and those species typically in small groups (e.g. zebra, warthog) often associated with larger interspecific herds; findings in agreement with Sinclair (op. cit.). It would seem, therefore, that ungulates are applying a cost/benefit analysis when assessing whether to associate with another species or not; if there are too few of them interspecific association brings protection (in numbers) from predation which outweighs loss of resources from resource competition, but once above a certain number anti-predation advantages of association are outweighed by loss of resources. Species whose social structure strategy results in small family groups, such as zebra and warthog, are thus compensating for the increased risk of predation inherent in such behaviour by interspecific association. That such behaviour still exists so markedly in predator-free Ithala, suggests it is an anti-predator behaviour that is deep rooted and not lost quickly in the absence of predators (Blumstein 2002). The same principles might be expected to apply to intraspecific association between herds of varying size, although here the picture would be complicated by complete niche overlap, hierarchies and competition for another resource – mates. It is note worthy that the ungulate generally regarded as exhibiting the least overt male sexual competition, zebra (Klingel 1974, Estes 1997), was also the species were association between intraspecific groups occurred most freely (pers. obs.).

It has been suggested that grazers become browsers in the thicket biome (De Graaff et al. 1973). Evidence has been presented in this study suggesting that grazing is markedly limited for some species in Ithala, especially in the winter. If such dietary shifts were possible, it seems reasonable that they would therefore occur in this reserve; no such observations were made, supporting others' rejection of De Graaff *et al*'s hypothesis (Landman and Kerley 2001).

Summary

Preference for different habitats by different herbivores was demonstrated. Not surprisingly more data, and consequently more in-depth results, were obtained on the most numerous and visible species. A paucity of data on rarer (for the reserve) and/or cryptic species prevented either a detailed analysis (bushbuck, duiker, eland and nyala) or any analysis at all (buffalo and elephant). The virtual failure to sight elephants, numbering approximately sixty individuals at the time of the study, was unexpected and is probably explained by the reserve's population being extremely wary of man, possibly because the adults are survivors of a cull in the Kruger National Park.

Statistically significant selection, both positive and negative, for a range of habitat types by herbivores was shown, with species preferences generally corresponding to well established patterns. Outside of these patterns, namely of browsers occupying habitats rich in browse, grazers those rich in grass and mixed feeders selecting both types of habitat, the influences of other herbivores and the lack of predation possibly accounted for non-seasonal details of habitat occupancy. Thus the high density of wildebeest may be restricting habitat available both to other grazers (hartebeest, tsessebe and white rhino), resulting in these species having an unusually restricted range, and to impala, resulting in their unexpected under-utilisation of grasslands. Impala's year round attraction to browse habitats may be related to very low levels of predation and may in turn be depriving wildebeest of grazing in closer habitats. Lack of predation may also account for atypical habitat selection by giraffe and kudu breeding groups.

Differences in habitat selection between certain species' social groups were also shown, most noticeably in the case of wildebeest bachelors (outside of the depths of winter) and impala bachelors (over the rut).

Statistically significant changes in habitat selection between wet and dry season were demonstrated; changes in species' range between seasons were also apparent. Lower rainfall in winter led to a reduction in quality of herbivory forcing animals to adjust their habitat occupancy. The extent and nature of these changes appeared to correlate with the species dependence on quality versus quantity of forage during times of resource limitation. Thus non-ruminants (zebra) showed a broadening of both habitat types and the total range occupied, ruminant browsers (kudu) showed an unchanged dispersion, whilst ruminant grazers (hartebeest, tsessebe, reedbuck and wildebeest) showed markedly increased selectivity, mainly in the total range occupied. These findings are in general agreement with current models for ungulates of optimal foraging. Exceptions to these trends were explained by species behavioural, digestive or situational idiosyncrasies; thus warthog, although categorised as non-ruminant grazers, mitigate dry season shortage by utilising resources from beneath the surface, white rhino, although also non-ruminant grazers, require atypically (for their size) high quality forage and thus behave more like ruminant grazers, exhibiting markedly increased area selectivity, whilst giraffe, ruminant browsers, showed marked reduction in area selectivity compatible with their marked resource limitation in Ithala in general.

In general species showed a dry season movement down-slope and into the water-courses, where habitats of higher nutrient status would be expected at that time of year.

In some cases (giraffe, wildebeest and possibly impala) movement onto heavier, nutrient rich soils in winter was directly shown.

Certain species (hartebeest, warthog, wildebeest and impala) were strongly attracted to grass flushes following winter burning. As these only occurred in 2003, this attraction appeared to account for differences between the two years of study in these species' dry season habitat occupancies; namely that since flushes generally occurred on higher ground, they were associated with a move up the slope.

Apart from the association between distance to surface water and movement down-slope, relating to nutrient status of underlying soils, surface water in itself did not, due to the extensive network of rivers and streams available throughout the year in the reserve, influence species' habitat occupancy.

Results from this study were broadly in agreement with those from other conservation localities and where differences existed explanations were suggested relating to the high density of wildebeest and/or lack of predation in Ithala Game Reserve.

It is reasonable to assume that the G.I.S. based techniques used here would be applicable to other reserves.

Findings may thus be summarised:

1) Gross vegetative selection by herbivores was broadly in keeping with their established preferences, with browsers concentrating in open and closed woodlands and grazers on grasslands.
2) Deterioration in habitat quality in the winter, consequent on lower rainfall, generally led to changes in habitat selection. The extent and nature of these changes appeared to correlate with the species dependence on quality versus quantity of forage during times of resource limitation.
3) Generally species showed a move down-slope in the dry season moving, in some cases, onto heavier soils.
4) Surface water did not directly influence herbivore distribution.
5) Hartebeest, warthog, wildebeest and impala were strongly attracted, zebra less so, to grass flushes following winter burning.
6) Slope use broadly reflects the species vegetative preferences; there is some evidence of harsher slope use being related to low availability of resources on gentler slopes (e.g. giraffe in winter of 2004, bachelor wildebeest).
7) The high density of wildebeest, via inter-specific resource competition, may be having an adverse effect on other grazers, principally tsessebe, hartebeest and white rhino. It may also be instrumental in the unexpected under-utilisation of the grasslands by impala in summer; by the same mechanism impala may be depriving wildebeest of grazing in closer habitats.
8) Lack of predation in the reserve may also be contributing to impala's year round attraction to closer, browse habitats and additionally may be affecting giraffe and kudu breeding herds' habitat choice.
9) Giraffe showed marked reduction in area selectivity in the dry season, suggesting marked resource limitation. This is compatible with both their high

density and their destruction of large segments of the upper browse found by others.

Implications for conservation management are as follows:

1) A relatively easily replicable G.I.S. technique for determining large mammals' densities by habitat type, and seasonal variations in these occupancies, has been developed and implemented.
2) Individual species' habitat occupancies and associated seasonal changes have been elucidated.
3) The importance of varied topography and varied vegetative communities in providing areas of reserve forage for herbivores during periods of resource limitation (i.e. the dry season) have been demonstrated.
4) In view of the importance of mid-winter flushes for certain species and since winter rainfall in the reserve is sporadic and unpredictable, burning should be spread over the winter and not bunched at the end, otherwise flushes will be absent during those months where grazing is at its poorest (as occurred in 2004).
5) Consideration should be given to reducing the reserve's population of wildebeest to ease pressure on other ruminant grazers, especially the rare tsessebe.
6) Introduction of predators (a subject frequently mooted by management) would be expected to affect herbivores' habitat preferences. Leopard in particular, as they hunt in closed habitats, would be expected to shift impala preferences out into the grasslands thus putting further pressure on this resource.
7) Evidence of giraffe suffering severe resource restriction, a finding compatible with previous workers' findings of excessive giraffe densities and consequent damage to the upper browse, suggests consideration should be given to markedly reducing their numbers.

CHAPTER THREE

NUMBERS OF LARGE MAMMALIAN HERBIVORES IN ITHALA GAME RESERVE

Introduction

An annual census provides insight into herbivore population trends (Redfern et al. 2002). Such regular surveys determine whether populations are increasing, decreasing or remaining relatively constant in size, and are particularly useful for monitoring threatened species and for surveying game species (Johnson 1989).

If the objective of censusing is the determination of trends in animal numbers rather than absolute abundance, counting error is acceptable provided the survey is regularly repeated under similar conditions (Eiselen 1994, Reilly 2002). If however the aim is determination of absolute abundance, errors in counting need to be quantified and corrected for (Jolly 1969).

Although light aircraft have been used since the mid-1950's to census wildlife on the African continent, the accuracy of aerial counts has been overrated (Jachmann 2001, Redfern et al. 2002). A variety of techniques have been suggested to correct bias in such counts (Caughley and Goddard 1972, Cook and Jacobson 1979) but these techniques are generally impractical and expensive (Barnes et al. 1986). The only theoretically sound and practical method is the double count technique based on the concept of the mark-recapture model (Caughley 1974a), usually incorporating an adaptation of the Petersen estimate (Caughley 1994). However, the correction factors in this technique apply only to a single animal species, in a particular count. Additionally, no allowance is made for visibility bias (Jachmann 2002). For obtaining repeated counts across a guild of herbivores amongst the steep, dissected terrain and rugged topography, characterised by wooded valleys, thick bushveld and grass-dominated plateaus, of Ithala, such a technique is therefore inappropriate.

Amongst denser vegetation, such as riverine, rainforest and certain types of woodland, some ground survey methods have been used (Stearns 1969, Caro 1999) including strip transects in the Tarangire Game Reserve, Tanganyika (Lamprey 1963), drive counts in the Ngorongoro Crater, Tanzania (Runyoro et al. 1995) and dropping counts in north-eastern Gabon (Barnes et al. 1991). However, most of these techniques and associated software programmes, such as *Distance* (Buckland et al. 2001), assume that visibility in a given vegetation type (which, combined with distance travelled, give area sampled and hence animal density) declines in a smooth, increasing manner with distance from the observer. Amongst the steep topography of reserves such as Ithala, visibility is frequently abruptly cut off (for example on slopes of deep ravines closest to the observer) invalidating this assumption. These same techniques, if they are to produce meaningful estimates of animal densities within vegetation types that show wide intraspecific variation in visibility (e.g. basin bushveld and thicket), necessitate the capture of considerable amounts of field data. The constraints imposed on these techniques, by the twin problems of abrupt and varied changes in visibility on both a landscape and vegetation scale, are overcome if the actual, rather than the assumed, area sampled can be determined. Geographic Information Systems (GIS) offer a relatively accessible way of accomplishing this.

To date, censusing at Ithala has consisted purely of an annual, fixed wing aerial survey. Both management and scientific staff believe this survey is consistently underestimating numbers (Balfour 2003, Pillay 2004, pers. comms.) and it is also very expensive.

A snap shot in time of population numbers is also of limited use; reliable information on trends is central to the conservation and management of game populations (Mason 1990b). Consequently, numbers need to be repeatedly determined over a time frame likely to pick up any such trends. For the large mammals in Ithala this means that at least annual counts are required. The costs of aerial methods preclude this. A reliable and cost effective alternative is thus required.

The aims of this part of the study were (1) to investigate the feasibility of determining whether replicated road strip counts are able to provide accurate and/or precise (low variability) estimates of numbers and (2) to determine what level of stratification and replication was required for the large mammalian herbivores in Ithala Game Reserve and to produce estimates of their absolute abundance. The techniques and findings are intended to be applicable to other appropriate reserves.

KZN Wildlife, the statutory body who administer Ithala Game Reserve, specifically requested that presentation of the road count method and consequent population estimates should be combined with discussion of trends in numbers and comparison of species' densities with other reserves; consequently these subjects are, somewhat unusually, partially separated from presentation and discussion of other demographics (Chapter 4).

The specific objectives were (1) to devise and assess a vehicle based method for determining acceptable estimates of absolute population numbers of the larger herbivores in Ithala Game Reserve, that is both cost effective and applicable to other, similar reserves, (2) to determine absolute population numbers of the larger herbivores in the reserve, and to show and explain any changes in these numbers over time (2001 to 2004 for giraffe, kudu, wildebeest, impala; 2003 and 2004 for the remainder) and (3) to compare and explain similarities/differences with the above findings to results from other conservation localities.

Methods

Data analysis:

Variance is sample size dependant and generally decreases with increasing sample size. One method is to establish when variance stabilises.

To determine the minimum replication required to estimate the numbers in the reserve accurately, as well as estimate precision in trends in numbers between summer and winter and in successive years, the sample size (number of counts/trips) at which the variance in the total number of individuals counted per trip was reduced to a minimum (or stabilised) was determined by calculating the variance in total numbers in successive months (i.e. cumulative standard deviations), starting with 2 samples then 3, 4, 5 and 6. Six months was the longest time span over which it was believed that seasonal change, in itself, would not cause variation in numbers. Mostly 3 or 4 successive counts provided a minimum or stabilised variance (Appendix 6).

The average (mean), with one standard deviation, for each block of three consecutive field trips was used to remove noise in determining changes in numbers between seasons (summer and winter) and from one year to the next.

Study results showed (Chapter 2) habitat selection by species and thus a habitat/G.I.S. approach was used to produce estimates of the density and maximum absolute abundance of herbivores in the reserve. The manner in which area sampled, by vegetation type, was obtained using G.I.S. has been described (Chapter 2); here 'XTools' was additionally used to calculate the total area of each vegetation type in the reserve.

The maximum estimate of numbers for each species in the reserve were calculated by using values for the month with the highest count in each of the three month sampling blocks. The number of animals sighted in each vegetation type was determined from the database using the query builder. With the number of animals counted in each vegetation type and the area of that vegetation type sampled known, a density per vegetation type was obtained and from that, using the total area of that vegetation type in the reserve, an estimate of the maximum number of animals in the reserve obtained. It is expected that mortality of individuals, particularly newborn, should produce differences in numbers between summer and winter, especially if the contrast between hot and wet and cold and dry is large. Additionally, habitat selection varied, for most species, between seasons affecting numbers sighted (Chapter 2). For these reasons these maximum estimates (four in each full year) were averaged for the year, to provide an overall annual estimate of maximum numbers in the reserve.

The estimates from using the above method were evaluated by comparison with total aerial counts and management's estimates.

Where significant numbers of animals had been removed by management over the period of study, as was the case with giraffe and kudu, adjusted raw totals per field trip are also presented. These were calculated by cumulatively incorporating 90% (thus allowing for an assumed 10% mortality per annum (Balfour pers. comm.)) of animals removed at the end of the previous year (removals are done over October/November) into the subsequent year's monthly raw totals. The effectiveness of the method was also assessed by its ability or otherwise to pick up management removals.

Results

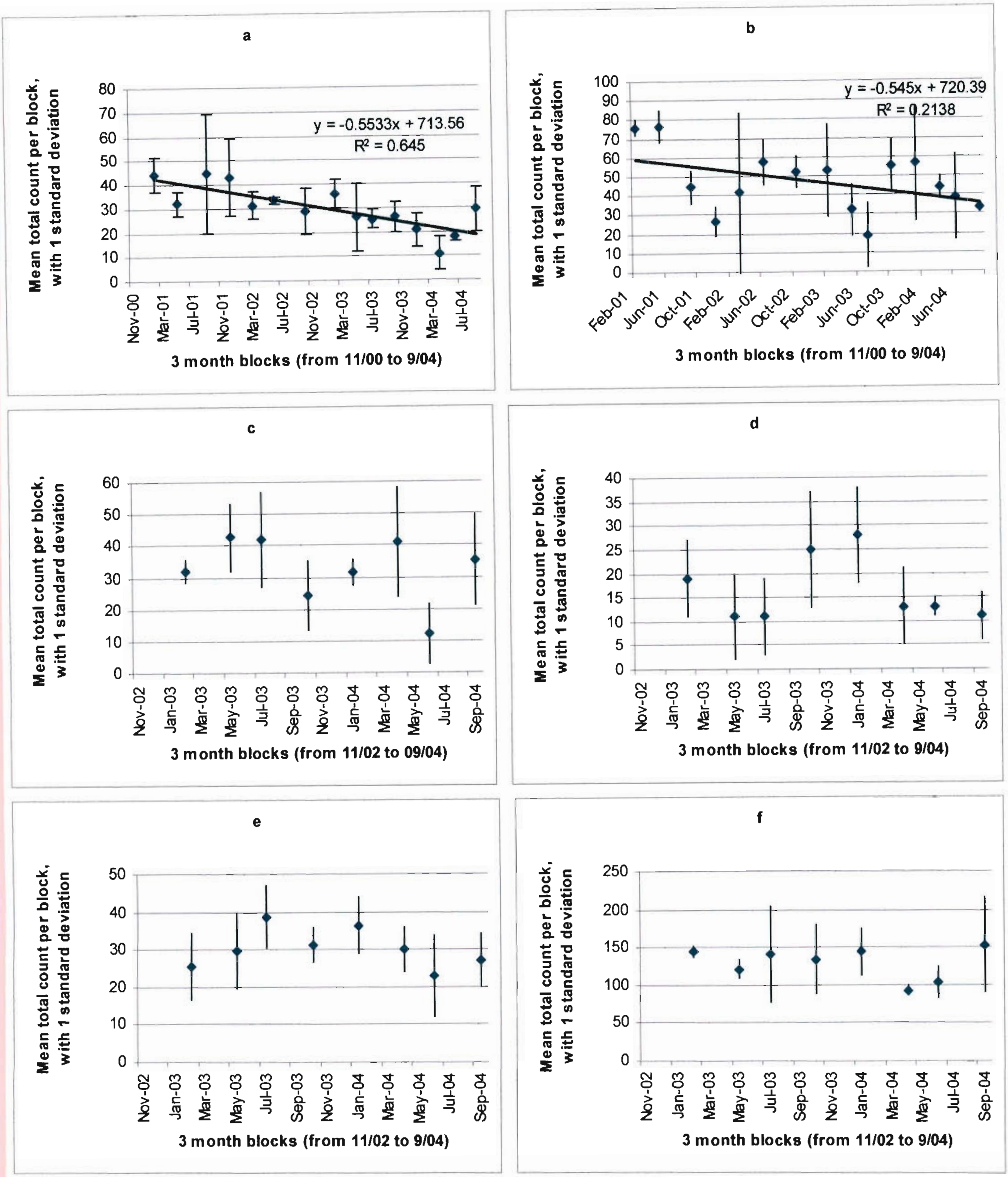


Fig 3.1: Changes in numbers counted, shown as the mean total count per three month block, with +_ one standard deviation. a = giraffe, b = kudu, c = hartebeest, d = reedbuck, e = tsessebe and f = warthog. Marked decreases are seen in giraffe and kudu numbers over the study period; less obvious decreases are apparent in the case of reedbuck and tsessebe. Management removals principally occurred over October (giraffe 2002 n=53, 2003 n = 49, kudu 2002 n = 181, 2003 n = 201).

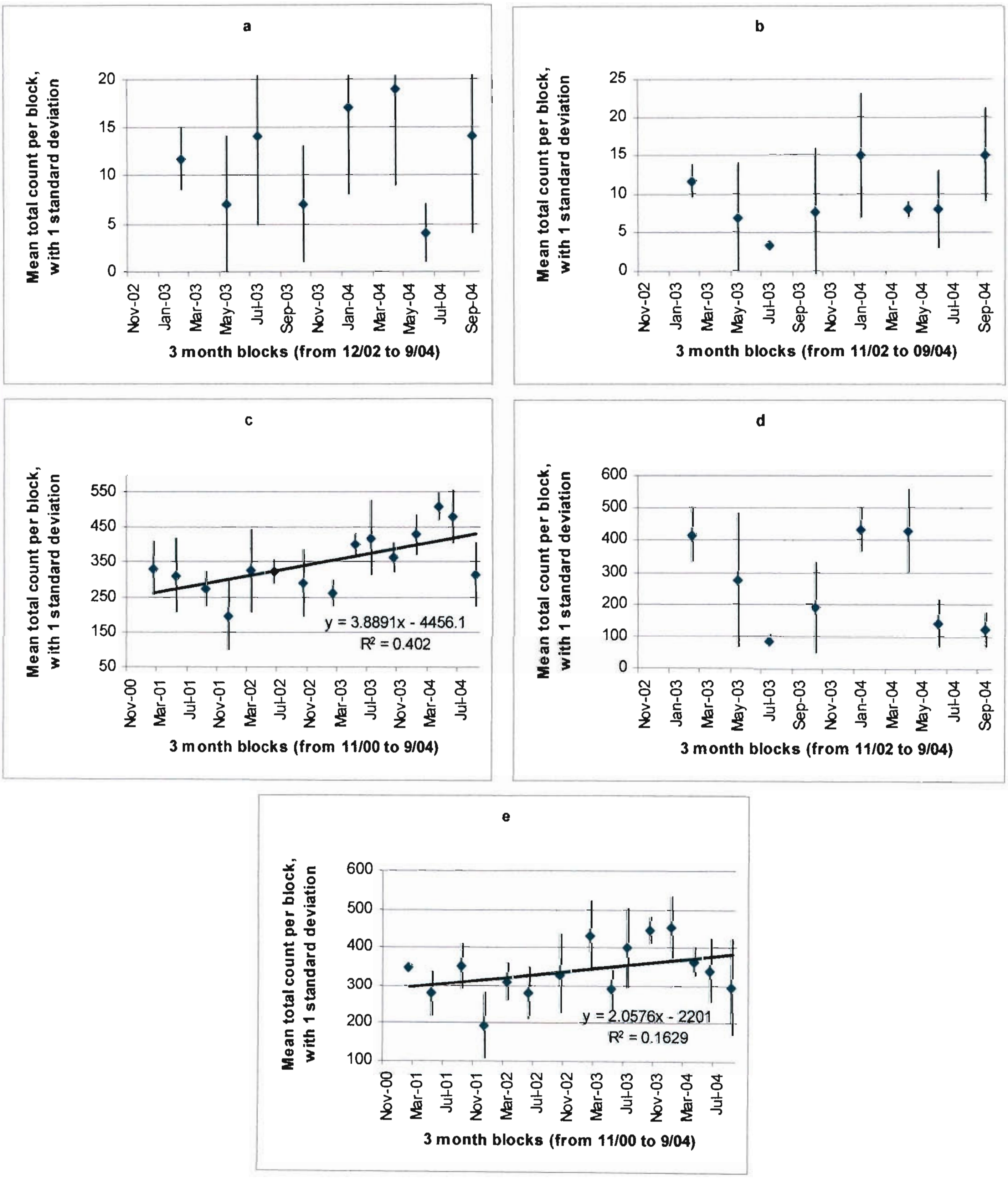


Fig 3.2: Changes in numbers counted, shown as the mean total count per three month block, with +_ one standard deviation. a = waterbuck, b = white rhino, c = wildebeest, d = zebra and e = impala. Increases over the study period are seen for numbers of wildebeest and impala, with waterbuck counts showing marked variance.

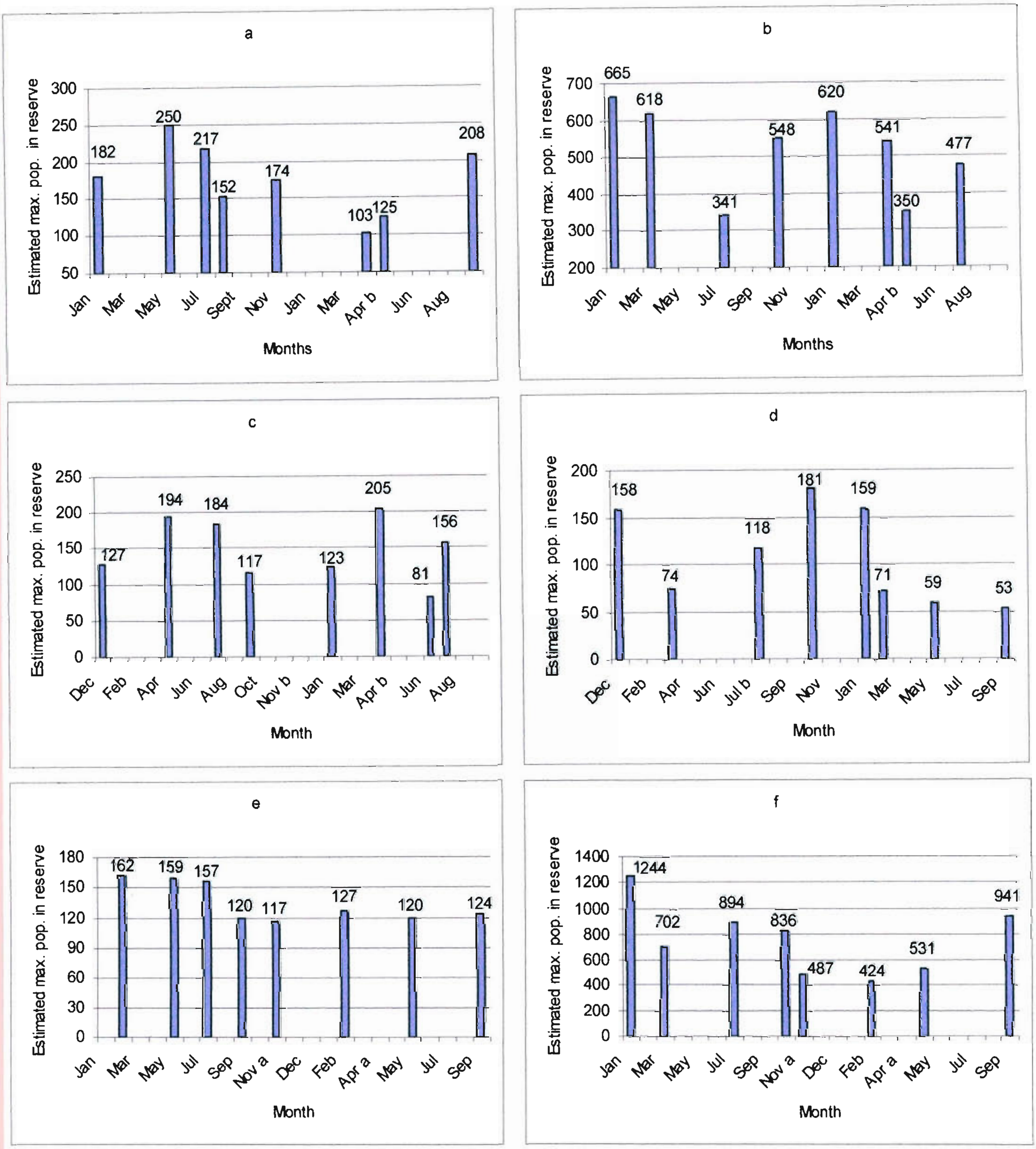


Fig 3.3: Estimated maximum numbers of herbivores in the reserve, based on the maximum count in each of the three month sampling blocks. a = giraffe, b = kudu, c = hartebeest, d = reedbuck, e = tsessebe and f = warthog. Giraffe, kudu, reedbuck, tsessebe and warthog estimated numbers show, to varying degrees, a decline over the study period. Variance in the estimates varies between species, with reedbuck showing high variance and tsessebe low variance.

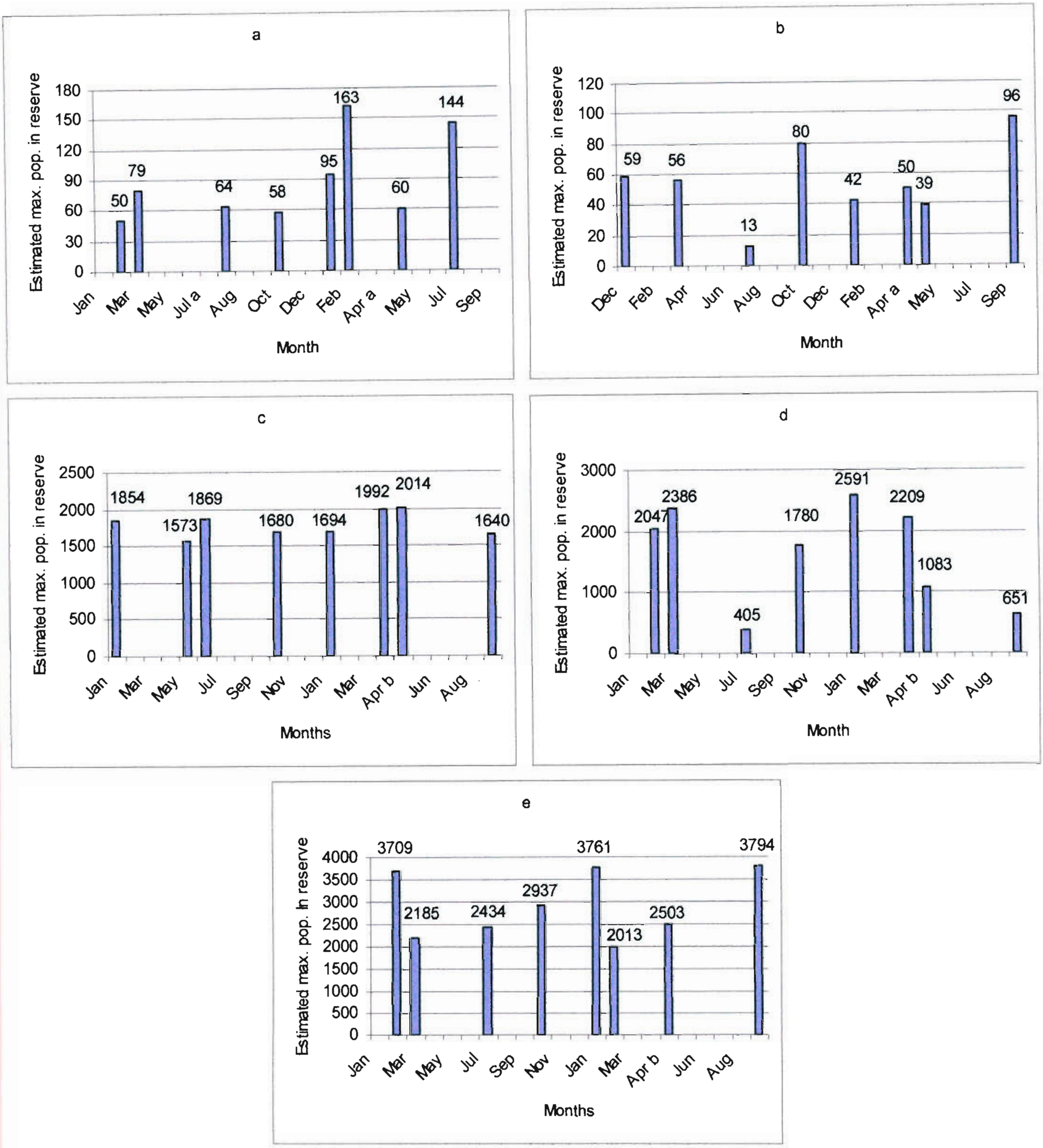


Fig 3.4: Estimated maximum numbers of herbivores in the reserve, based on the maximum count in each of the three month sampling blocks. a = waterbuck, b = white rhino, c = wildebeest, d = zebra and e = impala. Wildebeest and impala numbers show an increase over the period, with zebra showing markedly lower numbers in the dry season. Waterbuck counts show marked variance.

Table 3.1: Annual average of the four three monthly estimated maximum populations, by species, in the reserve. Amongst the more numerous species, wildebeest and impala show an increase in numbers, whilst zebra numbers are stable. Giraffe, kudu, reedbuck, tsessebe and warthog show a decline, whilst hartebeest and white rhino numbers are stable. Waterbuck appear to show an increase. Also shown, maximum counts in summer and winter and densities per square kilometre.

Species	Year	Maximum count in summer	Maximum count in winter	Annual average of max. pops. in reserve	Density (per sq. km.)
Giraffe	2003	40	27	200	0.69
	2004	25	28	152	0.52
Kudu	2003	62	69	543	1.87
	2004	74	51	497	1.71
Hartebeest	2003	55	52	156	0.54
	2004	58	44	141	0.48
Reedbuck	2003	28	16	132	0.45
	2004	39	15	85	0.29
Tsessebe	2003	34	47	150	0.52
	2004	36	35	122	0.42
Warthog	2003	130	187	919	3.16
	2004	128	226	596	2.0
Waterbuck	2003	14	18	62	0.21
	2004	28	26	116	0.4
White rhino	2003	15	2	52	0.18
	2004	17	8	57	0.2
Wildebeest	2003	302	524	1744	6.0
	2004	468	560	1835	6.3
Zebra	2003	511	71	1655	5.69
	2004	490	216	1633	5.61
Impala	2003	504	445	2816	9.68
	2004	527	431	3018	10.37

Sampling adjusted for live/dead removals:

Giraffe

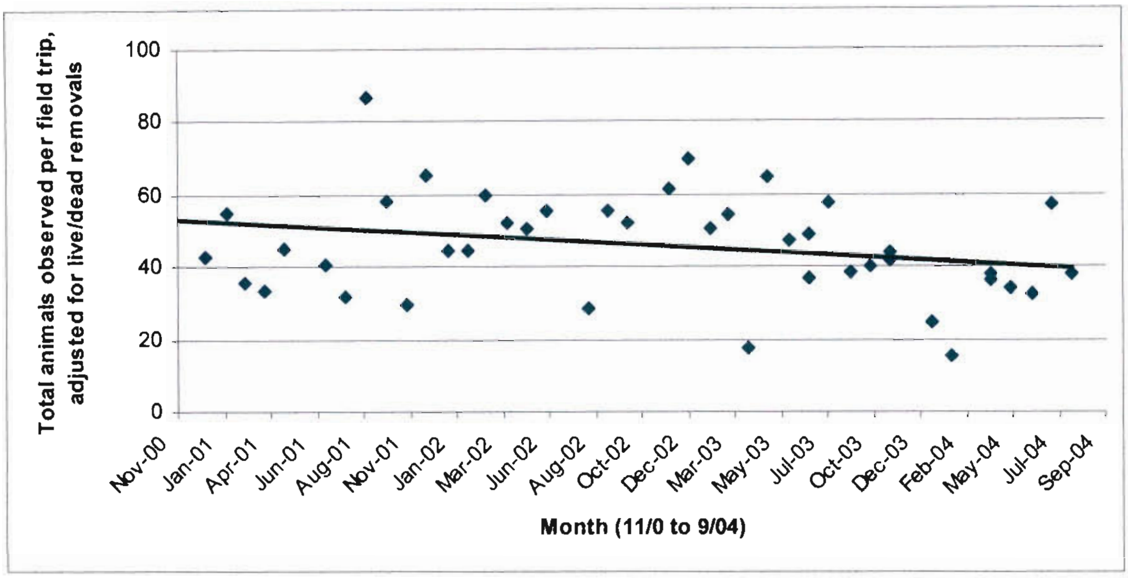


Fig 3.5: Giraffe, raw totals per field trip, adjusted for live/dead removals. Cumulative percentages removed, minus 10% per annum, are added to the monthly raw totals.

Kudu

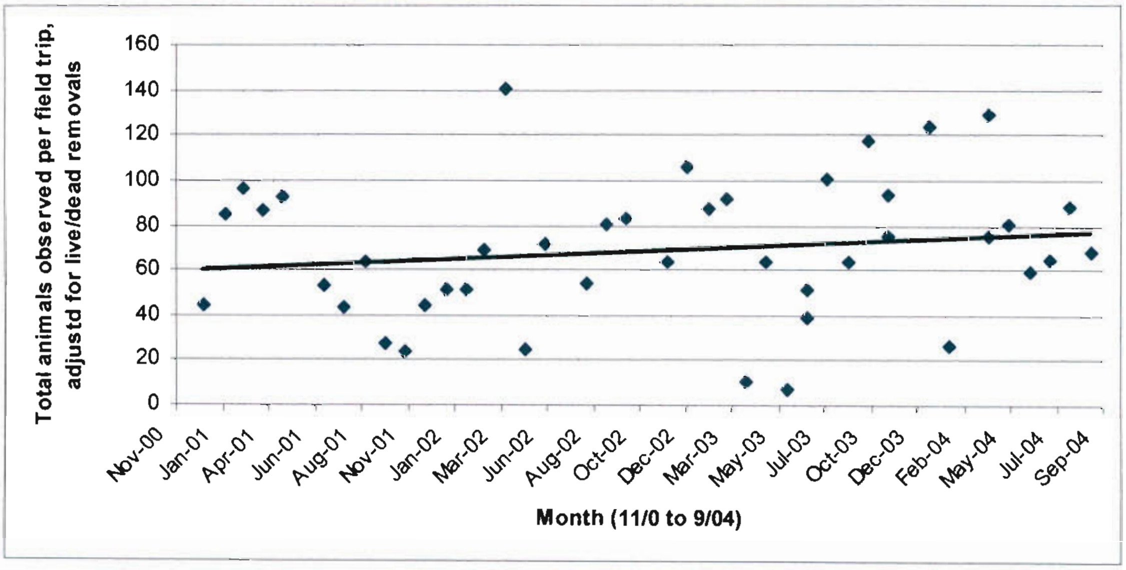


Fig 3.6: Kudu, raw totals per field trip, adjusted for live/dead removals. Cumulative percentages removed, minus 10% per annum, are added to the monthly raw totals.

Insufficient data:
For buffalo, bushbuck, duiker, eland, elephant, and nyala insufficient data was collected to analyse numbers.

Discussion

Assessment of technique:

Estimates of the average maximum absolute populations obtained in this study are compared below with estimates currently held by management (Table 3.2). Management's annual estimates are an attempt to correct for inevitable under counting, due to restricted visibility, by aerial observers when flying over a reserve such as Ithala Game Reserve, with high aerial cover of trees and shrubs and extreme relief. These estimates are obtained by subjective extrapolation, based on casual field observations and experience, from the aerial count (Pillay pers. comm.).

Table 3.2: Maximum population estimates aerial/ground. Aerial count = number of animals actually counted during annual aerial survey (fixed wing), management's estimate = management's estimates of reserves maximum absolute populations (see text), this study= annual averages of estimated maximum populations figures obtained in this study. Aerial counts are seen to be markedly lower than management's estimates and estimates obtained in this study.

		2003			2004	
Species	Aerial count	Management's estimates	This study	Aerial count	Management's estimates	This study
Giraffe	84	150	200	109	120	152
Kudu	231	800	543	n/c	700	497
Hartebeest	79	120	156	84	130	141
Reedbuck	n/c	n/e	132	n/c	n/e	85
Tsessebe	48	100	150	69	120	122
Warthog	290	1200	919	n/c	1200	596
Waterbuck	36	150	62	45	180	116
White Rhino	44	50	52	51	53	57
Wildebeest	1312	1500	1744	1226	1600	1835
Zebra	955	1400	1655	1346	1450	1633
Impala	n/c	4000	2816	n/c	3500	3018

Although estimates obtained in this study are seen to be broadly in agreement with existing management figures, both in scale and in direction of change, there are a number of obvious exceptions. These estimates, and how they relate to management's estimates and removals, are discussed below in the context of the acceptability of the ground count method presented here. Broader discussion of animals' seasonal and annual variations in numbers and of their densities then follows. Recruitment related demographics, which are presented in more detail in Chapter 4, are briefly mentioned where appropriate and, in general, are seen to support both the above estimates and conclusions drawn below.

Both browser species counted, giraffe and kudu, have been removed by management in large numbers relative to their population over the period of study (Table 3.3). This has shown up in the ground count figures but not in the aerial count where there was an increase in giraffe numbers counted in 2004, whilst kudu were only counted in 2003 (in most years kudu were not counted from the air due to poor visibility in their preferred habitat, woodland/thornveld/riverine). Whether the ground count or management's estimate is likely to be the more accurate in the case of giraffe is difficult to determine with the amount of data available, since in both cases the change in estimated numbers is compatible with numbers removed. For kudu, management's estimates are more compatible with the large numbers removed; the ground count may be slightly under estimating numbers, probably due to the furtive nature of kudu (Estes 1997).

Table 3.3: Game removals. Removals= numbers removed based on management's records of game removals, % of population *= % of total population removed, based on population as estimated by this study (2003/04) or management (2001/02). Hartebeest, reedbuck, tsessebe, warthog, waterbuck, white rhino and zebra were not counted in this study in 2001/02; data is given here (in italics) for completeness.*

	2001		**2002**		**2003**		**2004**	
Species	Removals	% of population	Removals	% of population	Removals	% of population	Removals	% of population
Giraffe	37	19	53	41	49	25	23	15
Kudu	170	20	181	20	201	37	52	10
Hartebeest	*2*	*2*	*2*	*2*	1	1	0	0
Reedbuck	*0*	*0*	*0*	*0*	0	0	0	0
Tsessebe	*0*	*0*	*24*	*19*	2	0	0	0
Warthog	*111*	*10*	*107*	*9*	94	10	76	13
Waterbuck	*0*	*0*	*0*	*0*	0	0	0	0
W. Rhino	*0*	*0*	*13*	*27*	0	0	0	0
Wildebeest	226	16	49	4	40	2	13	1
Zebra	*14*	*1*	*28*	*2*	12	1	29	2
Impala	442	22	223	11	203	7	212	7

In the case of the larger and more numerous plains dwelling grazers, wildebeest and zebra, one would expect aerial counts to provide a greater degree of accuracy. White rhino are the subject of an intensive ongoing monitoring programme in the reserve and consequently their numbers are known precisely. Should population estimates of these species by the ground count method tally, it is reasonable to conclude the technique is producing acceptable estimates for both large and numerous and rare (as long as the latter are as visible as rhino) plains dwellers. Encouragingly, there is close agreement; surprisingly so in the case of white rhino. Consequently, ground count estimates for hartebeest, tsessebe, white rhino, wildebeest and zebra appear to be acceptable.

There is less agreement between the estimates of management and this study for reedbuck, warthog and waterbuck. As these species are more cryptic, by virtue of behaviour (reedbuck), size (warthog) or habitat selection (waterbuck), this is not altogether surprising (Estes 1997).

Reedbuck are not counted from the air nor are they estimated by management, consequently there is no 'internal audit' to asses the ground count figures by. However, the counts show large variance (Fig 3.1) and widely ranging estimates of maximum population (Fig 3.3). Although this variance may be partially explained by the trend of higher counts in the summer months versus lower counts in the winter, the final estimates showing a marked reduction from 2003 to 2004 (Table 3.1) should be regarded as preliminary pending further data.

Warthog counts, in contrast, show small variance (Fig 3.1) and the trends correspond slightly with season, with mid to late winter counts being slightly higher than summer counts. Grass height, and consequent visibility, may be the factor influencing counts such that when the grass is at its highest and most dense (typically from mid-summer to before winter burning occurs) counts are small; when at its lowest and most sparse (mid-winter to early summer) counts are larger. Caro (1999), estimating densities of a wide range of mammals, recorded significant effects of grass height on numbers of animals sighted only in the case of warthog. It seems probable, therefore, that the apparent reduction in the warthog population from 2003 to 2004, as indicated by the ground count results, is a Type 1 error consequent on the census not being continued into the spring/early summer of 2004; thus explaining the contradiction with managements estimation of a stable population in the face of significant removals (Table 3.2). Additional data are required to support or refute managements view; data is not available from aerial counts as warthog are not censused by this method due to their size (a one off attempt to do so in 2003 produced ludicrously low figures confirming the unsuitability of the technique with this species). Absolute numbers estimated are also generally lower in the ground count method than management's estimation; this again may be due to the reduced visibility associated with high/dense grass. More accurate results might therefore be obtained with warthog if data is only collected mid-winter to early summer when visibility is generally higher, especially as warthog were seen to show little difference in their habitat selection between wet and dry seasons (Chapter 2), thus reducing the need to sample in both seasons to compensate for such habitat changes and the consequent variation in counts.

Waterbuck are probably the most highly water dependent antelope (Taylor et al. 1969) and have a preference for a combination of near by water, open grassland and cover, resulting in a patchy ecotone distribution within valleys and along drainage lines (Tomlinson 1981, Estes 1997). The ground count method, partially due to the routes traversed including little of this type of habitat relative to its occurrence in the reserve and partially due to that specialised habitat type not being separately identified in the GIS vegetation theme, would be expected to under estimate the waterbuck population – as is the case. Additionally there is a large variation in the census count (Fig 3.2) which is not related to any obviously explicable biological process such as seasonal change; it would therefore appear to be random – as would be expected when sampling a small proportion of a population. The ground count method therefore appears inappropriate for censusing waterbuck.

The only mixed feeder studied, the impala, is not censused by air as some of their favoured habitat (thornveld/bushveld/woodland) is poorly visualised by this method due to dense, high canopy cover (Balfour 2003). Management thus has nothing apart from educated guess work to guide its estimates. Since only 5% of animals were removed in 2003, it is not clear why management have estimated a reduction in the impala population 2003 to 2004 of >12%. The ground count technique indicates an increasing population but with an absolute population estimate lower (by ~20%) than management's. Since the ground technique appears to be reasonably accurate at estimating numerous, easily visible animals on the plains (one of impalas preferred habitats) and impala are relatively easily counted in closer vegetation types (thornveld/bushveld/woodland) as, being habituated to vehicles in the reserve, they rarely flee, it would seem reasonable to regard the ground count estimates as the more accurate.

The ground count method appears, therefore, to produce acceptable estimates for the reserves populations of giraffe, kudu, hartebeest, tsessebe, white rhino, wildebeest, zebra and impala. More data are needed to determine its suitability for reedbuck, it may be suitable in a modified format for warthog, but it seems inapplicable to waterbuck where walked transects should replace road strip counts as the road network does not traverse their habitat adequately.

The required sampling frequency is of relevance to the applicability of the technique as a standard censusing tool within the reserve. Here, censusing carried out once a month equated to 197 man hours and 1,600kms driven in the year; the man hours required to census only numbers (here age and sex were also determined) would obviously be considerably lower. Since all that is required of the researcher is to drive at a steady pace over the designated routes and record the number of different animals in each vegetation type seen, little experience or in-depth zoological knowledge is required. Although, therefore, the technique appears to be cost effective, such is the paucity of funds available it is worth considering the effect of reducing the sampling intensity (and hence cost). Variance in the total counts per trip is such that considering estimated totals based on sampling blocks of less than three consecutive field trips is ill advised. Here, four 'three trip' sampling blocks per year were analysed; the theoretical minimum would appear to be one block from the wet and one block form the dry (to compensate for likely over and under estimation of numbers due to animals seasonal movements and for seasonal mortality). If this is done (taking the wettest and driest months) the estimates for impala and tsessebe alone are of the same magnitude *and* show the same direction of change 2003 to 2004, whilst for giraffe, kudu, hartebeest and wildebeest although estimates are of the same magnitude the *direction* of change is the opposite of that found in this study. For zebra, due to their exceptional wet/dry season variation (Fig 3.2), taking only one block per season carries the risk, depending on rainfall, that the lowest count is missed – seriously skewing results. For white rhino, not surprisingly in view of the very small numbers involved, such a reduction in the sampling intensity produces erroneous results. Four 'three trip' sampling blocks would appear, therefore, to be the lowest, in terms of man hours, cost effective application of this GIS based ground count technique in Ithala Game Reserve.

It is reasonable to expect that the technique could be successfully applied in other reserves with similarly diverse topography/vegetation where the relevant GIS themes are available (e.g. Hluhluwe – Umfolozi).

Trends in numbers; the influence of rainfall:

Seasonal variation

Although there is sample variation, numbers seen are generally lower in the winter months versus the summer months. Although winter mortality, especially juvenile (Chapter 4), may partially account for this, the magnitude of the difference between seasons in some species suggests other factors are involved. The sampling routes inevitably make use of tourist routes which have been, in part, designed to afford the visitor maximum viewing opportunities and consequently tend to follow the higher ground and avoid too many valley bottoms. Herbivores tend to move to lower, more water/mineral retentive soils in the drier winter months (Bell 1970); this has been shown in this study (Chapter 2) to be the case for many of Ithala's herbivores– hence the reduction in sighting intensity. This spatial exploitation of seasonal variation is the small scale equivalent of the large scale seasonal migrations that occur in savanna ecosystems such as the Serengeti and central Kalahari (Scholes and Walker 1982). Zebra showed particularly large summer/winter variation (Fig 3.2) suggesting they are moving in comparatively large numbers to other parts of the reserve. The routes covered include a high proportion of habitat suitable to wildebeest (grassy plains) and competition with wildebeest who, being ruminants, are comparatively limited in how low a quality forage they can survive on and thus need to remain on the plains (albeit further down the catena), may, in times of forage shortage (i.e. winter), result in zebra moving to more marginal habitat characterised by the rank swards they, being hindgut fermenters, can survive on (Bell 1971, Page and Walker 1978, Owen-Smith 1988a, Bodenstein et al. 2000). Warthog showed less clear summer/winter variation and this most probably relates to the effect of grass height on their visibility. Waterbuck show no seasonal variation; the inappropriateness of the ground count method to this species has been discussed.

Annual variation

Standing crop biomass and production by large mammalian herbivores in the African savannas show a high degree of correlation with mean annual precipitation, particularly where mean annual precipitation is less than 700mm (Coe et al. 1976, East 1984). For the period 2000 to 2004 inclusive mean annual precipitation in Ithala Game Reserve was 632mm (Fig 3.7); therefore, and especially in the absence of any significant predation, one would expect herbivore numbers to broadly correlate with rainfall (East 1984)– provided their density is not so high as to effect the population through food limitation (Lack 1954, Sinclair 1974, 1985b, Mduma et al. 1999).

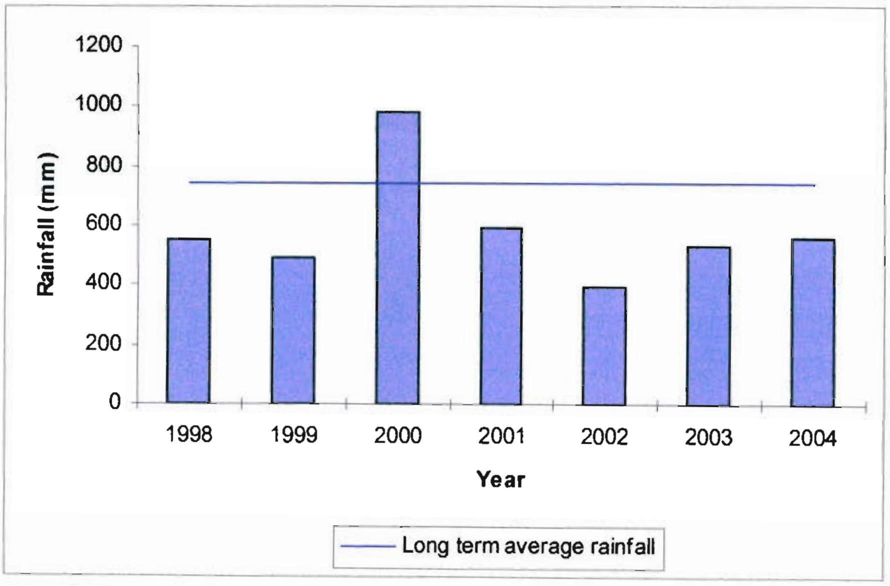


Fig 3.7: Annual rainfall Ithala Game Reserve. Long term average (30 yrs) =743 mm

Both browsers, giraffe and kudu, showed a reduction in both counts (2001 to 2004, Fig 3.1) and absolute population estimates (2003 and 2004, Table 3.1). Large percentages of both animals have been removed over the period from the reserve by management (Table 3.3); giraffe as they are believed to be causing detrimental changes to the reserve's vegetation and kudu as they are believed to compete for resources with black rhino. If numbers are corrected for the removals, giraffe still show a reduction (Fig 3.5) whilst kudu show an increase (Fig 3.6). Bond and Loffell (2001) described the manner in which Ithala giraffes are apparently killing off certain *Acacia* species, typically those not found in giraffes' usual range and therefore, presumably, ones with little resilience to high level browsing. As well as leading to a change in acacia distribution in the reserve, this has inevitably led to greater pressure on the remaining more browse resistant species leading to the poor state of the upper browse seen in Ithala today (Appendix 5, Plate 2) and the not infrequent sight, especially in winter months, of giraffe, legs splayed, browsing on small, discreet bushes in the middle of open plains (Appendix 5, Plate 3) Thus it would appear giraffe are currently resource limited in

Ithala; the marked reduction in their range in winter (Chapter 2) and their abnormally low recruitment demographics compared to other reserves (Chapter 4), support this scenario. Kudu, contrastingly, in the absence of management removals would appear to be able to increase their numbers; the healthier state of the intermediate/lower browse in the reserve (pers. obs.) supports this supposition, as do their recruitment demographica which are comparable to other locations (Chapter 4).

The grazer and mixed feeder for whom four years of data were collected, wildebeest and impala, show an increase in both counts (2001 to 2004, Fig 3.2) and absolute population estimates (2003 and 2004, Table 3.1). Apart from in 2001, small percentages of these animal's populations have been removed over the period. Their ability to increase their numbers during a period of below average rainfall indicates that they are not currently resource limited; recruitment demographica (Chapter 4) are comparable to other reserves. During the period one year, 2002, had well below average rainfall (Fig 3.7); the expected reduction in population growth, especially in wildebeest (a pure grazer), is not apparent in either of these two species from the raw numbers (Appendix 7). Since absolute estimates were produced only for 2003/04, it is not possible to determine whether there was reduction in year on year growth in absolute population 2002 going into 2003. Analysis of juvenile : adult female ratio (Chapter 4) does show a reduction in wildebeest fecundity over the period of low rainfall, indicating the expected effect of low rainfall on herbivore production. The failure of the raw figures to detect this effect may be due to the relative subtleness of it (it was not a drought) combined with the sizeable sample variation. Impala, being mixed feeders who optimize the quality of diet selected (Meissner et al. 1996), would be expected to be less effected than pure grazers by one year of below average rainfall; indeed, no similar reduction in fecundity was recorded.

For the other grazers on whom the ground count technique appears to be applicable (hartebeest, tsessebe, white rhino and zebra), only two years of data is available. With such limited data, results should be interpreted with caution. Hartebeest, white rhino and zebra numbers appear broadly stable (Table 3.1); none of these animals were removed in significant numbers during the period of study (Table 3.3). The apparent failure of the zebra population to increase over a period wildebeest increased (by 5%) may be of interest. In the Serengeti similar results (Sinclair and Norton-Griffiths 1982, Senzota 1988) were explained by the zebra population being prevented from growing by the social organization of the species and/or disease and/or predation; as the Ithala population is manifestly healthy, shown both by its normal recruitment demographica (Chapter 4) and visual appearance (pers. obs.), and not subject to predation, if this finding was to be repeated over subsequent years it would support the social organization hypothesis.

Tsessebe, however, show an estimated reduction of 20% 2003 to 2004 (Table 3.1); if this is the case, in such a rare species it is cause for concern. As discussed above, the numbers and visibility of white rhino and tsessebe in Ithala are compatible and this, together with the observation that tsessebe in Ithala tend to occupy the same undulating plains area, which is highly visible from a car, throughout the year, suggests the ground count estimates, and associated fall in numbers, for tsessebe are accurate. Tsessebe prefer short grassland (Child et al. 1972, Joubert and Bronkhorst 1977). Declines in numbers of tsessebe were found to be related to reductions in both annual and dry season rainfall in the Kruger National Park and on a wildlife ranch in Zimbabwe (Dunham and Robertson 2001, Dunham 2003). Annual rainfall at Ithala (Fig 3.7) has been below the long term average for six of the past seven years. Dry season rainfall over the same period is in keeping with the long term picture, but daily records kept at a nearby site (unfortunately daily records are not kept at Ithala) show winter rainfall occurring in sporadic large amounts (Kilian pers. comm.) – most of this is likely to 'run off' and not be available for growth. Reduced rainfall as well as directly reducing the availability, especially in the dry season, of green grass leaf, the preferred food of tsessebe (Kingdon 1982), may lead to sward composition shifting away from leafy grasses towards small, wiry leaved grasses and allow increased shrub encroachment (Dunham 2003). Additionally, a low fuel load available for winter burning limits fire intensity and this tends to disproportionately spare shrubs (Norton-Griffiths 1979); burns in Ithala appeared to be patchy in a manner consisted with 'cool' fires, presumably consequent on the high density (see below) of grazers. Indeed, a subjective increase in small bush density was observed over the period (pers. obs.). As global climate models mostly predict drier and warmer conditions in the decades ahead with an associated increase in the woody biomass (Rutherford et al. 2000), this problem is likely to increase. Interspecific competition, especially in the resource depleted winter months, might also be expected to be instrumental in the tsessebe population performing poorly. Smuts (1972) commented that large numbers of zebra compete with rare antelope species, such as tsessebe, in the Kruger National Park and management there, subsequently, reduced zebra density in the tsessebe habitat believing it to be pivotal in the precipitous drop in tsessebe numbers; tsessebe numbers did not, however, respond (Grant and Van der Walt 2000, Grant 2002). At Ithala zebra, especially during the winter months, were seldom seen in the same part of the reserve favoured by tsessebe. Food intake studies on wildebeest and topi (Murray and Illius 2000), an animal closely related to tsessebe, suggested that wildebeest, which have relatively wide mouths, graze down swards to a height below that which can be tolerated by topi, whilst the narrow mouthed topi reduces the leafy components of swards through selective feeding to a level below that which wildebeest can tolerate. In this way species effectively modify the vegetation in a way that makes it less profitable to competing species and, in effect, they 'capture' the vegetation as a resource. This may explain why, despite the vegetation and topography superficially appearing similar, wildebeest and tsessebe are generally not seen in the same parts of the reserve (Fig 3.8) – and also why white rhino, another wide mouthed grazer and one which, due to its poor digestive capabilities (Owen-Smith 1973), requires quality forage despite being a non-ruminant, is also not seen in the vicinity of tsessebe. If this process is occurring, presumably the relative size of habitat 'captured' will be influenced by the relative densities of these two species – indeed, the area favoured by tsessebe is very small – and the high density (see below) of wildebeest may thus be a factor in the tsessebe's problems. Recruitment demographics (Chapter 4), which were abnormally low, support this finding of a declining tsessebe population. The broadly stable numbers for hartebeest compared to tsessebe, both alcelaphines of similar size and jaw breadth, may be due to its apparent ability to survive on lower quality forage commensurate with its relatively low energy intake and slow growth rate (Arman and Hopcraft 1975, Murray 1993). Recruitment demographics for hartebeest were not found in the literature for comparison.

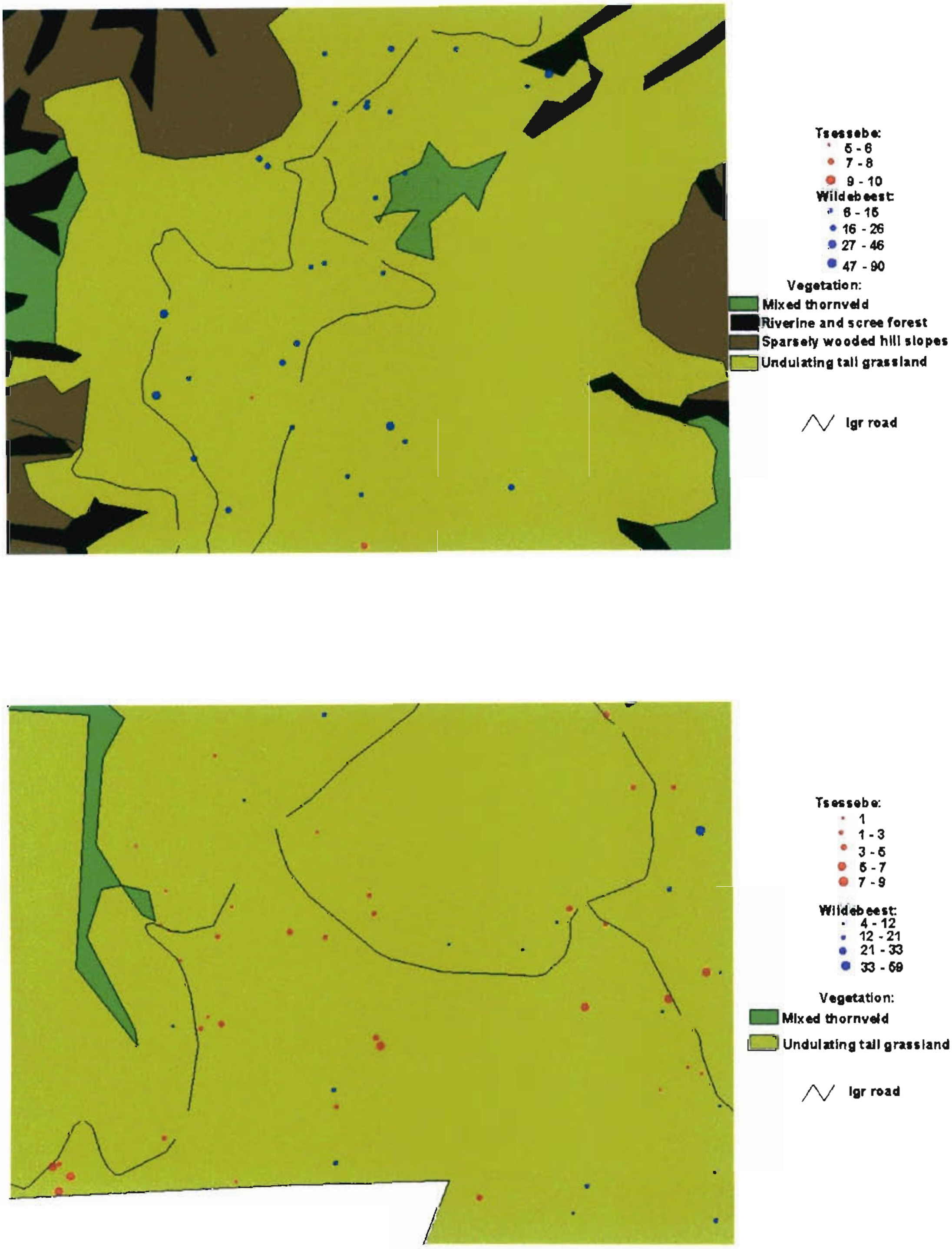


Fig 3.8: Wildebeest and tsessebe habitat selection. Wildebeest favoured locations (above) and tsessebe favoured locations (below) do not coincide, although they are on the same vegetation type.

Densities:

The concept of carrying capacity is useful in slightly variable environments but misleading in markedly variable environments (McLeod 1997); in environments where plant-herbivore dynamics do not reach or closely approach equilibrium levels, carrying capacity is more a mathematical abstraction than a measurement of sustainable population size (Macnab 1985). In a variable environment such as Ithala where plant-herbivore dynamics are clearly not at equilibrium, in reality only long term experience, supported by reliable censusing, will enable management to determine what are appropriated population ranges, the laxity of which will reflect the stochastic nature of the environment, for the reserve's herbivores. In the interim, comparison with other reserves' densities clearly assists management in their decisions. Hluhluwe-Umfolozi Game Reserve, which lies further to the south-east in Zululand, closely resembles Ithala (although its topography is not as variable and consequently less of it is inaccessible to large herbivores) and is the most appropriate reserve for such comparison; densities given here refer to managements estimates (based, as at Ithala, on aerial counts and management's opinion) for 2003 (Balfour pers. comm.).

Much of the reserve is too steep or otherwise inaccessible to giraffe and the area they actually use is estimated to be only a third of the reserve (Bond and Loffell 2001); this gives an effective density of ~ 1.8 km^{-2} (from Table 3.1). Hluhluwe –Umfolozi's density is 0.8 km^{-2}. Foster (1966), Foster and Dagg (1972), Van der Jeugd and Prins (2000) and Pellew (1983b) summarise densities of giraffe populations across a wide range of habitats; the effective density at Ithala is well in excess of virtually all these. A density of 1.2 km^{-2} was found at a similar reserve in South Africa, Fleur de Lys, where the researcher noted that preferred trees were completely defoliated and that numbers were probably exceeding carrying capacity (Innis 1958); a density of 1.9 km in a Kenyan reserve was shown to be detrimental to the existing browse and tree replacement (Birkett 2002).There is little doubt, therefore, that giraffe density is too high at Ithala – and this in an area where they are alien species and consequently vegetation shows little resistance to their browsing. Although kudu are more agile than giraffe, by no means all the reserve would be topographically accessible to them and therefore the estimated density of ~ 1.8 km^{-2} (Table 3.1) most probably represents an under estimation. Hluhluwe -Umfolozi's density is 1.4 km^{-2}. Densities ranging from 2.3 km^{-2} to 3.4 km^{-2} were reported in the Kruger National Park (Owen-Smith 1984a) over a period of four years in a healthy population; Ithala's population would appear therefore to be within the likely carrying capacity. Since a large percentage of kudus are removed annually by management (Table 3.3), had this not been the case and their density had risen (Fig 3.6), their currently relatively minor effect on the browse in Ithala (Wiseman et al. 2004) might have increased to the detriment of other low/mid level browsers (du Toit 1990), including black rhino. Indeed, browsers other than elephant and giraffe have had a marked effect on vegetation structure and composition elsewhere in Africa (Belsky 1984, Prins and Van der Jeugd 1993).

Amongst the grazers, hartebeest and tsessebe populations are too small for there to be any concerns over their density (~0.5 km^{-2}, Table 3.1) being excessive. White rhino densities of 0.2 km^{-2} (Table 3.1) are considerably less than the 1.9 km^{-2} found in Hluhluwe-Umfolozi. Although Hluhluwe -Umfolozi is particularly suited to white rhino (it is their main sanctuary in South Africa), previous assessments (Le Roux 1987) have concluded that Ithala could support a markedly higher density of white rhino – these, however, were undertaken before wildebeest and zebra had reached their current densities. The absence (pers. obs.) of 'satellite' bulls (Owen-Smith 1973) in Ithala suggests that not all available territory is being utilised by the adult males. The density of wildebeest (~6.0 km^{-2}, Table 3.1) is higher than the 3 km^{-2} reported in Hluhluwe - Umfolozi previously (Attwell 1977, Attwell and Hanks 1980) or the 3.4 km^{-2} now estimated in that reserve. The peak density reported in the Central Region, where wildebeest are most numerous, of the Kruger National Park was 0.6 km^{-2} in 1987 (Mason 1990a). Although considerably higher densities are recorded elsewhere in non-migratory populations of wildebeest, such as 40 km^{-2} in Ngorongoro (Runyoro et al. 1995), comparison with similar populations is more appropriate. The zebra density of ~ 5.6 km^{-2} (Table 3.1) is also higher than the 3.8 km^{-2} estimated at Hluhluwe -Umfolozi, or the range of ~2.1 km^{-2} to ~1.2 km^{-2} recorded in the Central District of the Kruger National Park between 1969 and 1975 (Smuts 1974, 1976). Both the wildebeest and zebra populations at Ithala therefore represent a high density for the region and this is before any allowance is made for inaccessible terrain.

Impala density, at ~10 km^{-2} (Table 3.1), is low compared to the 27 km^{-2} currently estimated in Hluhluwe –Umfolozi. A review of impala densities at a number of locales across southern Africa (Brooks 1975) also showed higher values, ranging from 16 to 80 km^{-2}.

For food limited populations of herbivores in semi-arid environments, survival and reproduction should be functions of the ratio R/B, where R is rainfall and B is herbivore biomass (Owen-Smith 1990). Fowler (1981) suggested that for large mammals most density dependent change will occur at population levels close to the carrying capacity. In the absence of predation, large herbivores may attain atypically high densities (Owen-Smith, op. cit.); this appears to be the case with wildebeest and zebra in Ithala which have not been removed by management to any significant extend. As these two species represent a substantial proportion of the reserve's herbivore biomass, it would appear there is a high likelihood of a significant drop in survival and reproduction amongst the reserve's herbivores should drier conditions prevail – as seems likely. The inability of animals to migrate in response to forage scarcity (due to the reserve being enclosed), the extensive network of surface water (supporting high densities), the changing nature of the browse towards less palatable species and the sensitivity of burnt pastures to overgrazing (Pratt 1967), are all likely to exacerbate the situation.

Summary

Replicated, stratified, variable width road strip counts described in this study produced cost effective, reasonably accurate estimates of population numbers for most of the larger herbivores in Ithala Game Reserve. For most species these were apparently more accurate than those provided by aerial counts. The level of stratification, as defined by the routes covered and the range of habitats defined, seems therefore to be appropriate. Six counts in both the wet and dry season represents the minimum level of replication required, for most species, to obtain accurate population estimates and reveal trends. Estimates for reedbuck, warthog and waterbuck were less satisfactory. Reedbuck and waterbuck counts were associated with high variability, probably because the level of stratification was inappropriate for these species. Warthog counts are complicated by wide seasonal variation in visibility relating to grass height. Two of the reserve's larger herbivores, buffalo and elephant, were seen too infrequently to allow population estimates. Avoidance of vehicles and man are probably the explanations in the case of elephant.

Most species populations are stable or increasing, with the exception of giraffe (even after correcting for management's extensive removals) and tsessebe which appear to be in decline. The high effective density of giraffe and their alien nature to the reserve's vegetation, resulting in deterioration of the upper browse, appear to be putting them under marked resource limitation. Tsessebe's decline may relate to the high density of wildebeest in the reserve, possibly depriving tsessebe of forage both generally and in terms of 'sward capture', and/or to recent drier conditions. In addition to giraffe and wildebeest, zebra densities were found to be high compared to other comparable conservation localities.

Findings may thus be summarised:

1) The G.I.S. based ground count method described here produces acceptable estimates for the reserves populations of giraffe, kudu, hartebeest, tsessebe, white rhino, wildebeest, zebra and impala. Reedbuck results are equivocal, warthog censusing needs modification and waterbuck results are unrealistic.
2) Sampling frequency required equates to ~ 150 man hours and 1,600Kms driven per year.
3) Fewer animals are seen in the dry season, partially due to movement down slope.
4) Even correcting for management removals, giraffe numbers are in decline. This is likely to be due to their detrimental effect on the upper browse and their high density, leading to resource limitation.
5) Tsessebe numbers also appear to be in decline; this may relate to drier conditions and/or the high density of wildebeest in the reserve.
6) Giraffe (~1.8 km^{-2}), wildebeest (~6.0 km^{-2}) and zebra (~5.6 km^{-2}) densities are high compared to other reserves.

Implications for conservation management are as follows:

1) An accurate, and cost effective, ground based method for estimating maximum total populations, and determining trends in numbers, for most of the reserve's large herbivores has been developed and implemented.
2) The technique may usefully be applied to other reserves with similarly diverse topography/vegetation.
3) Giraffe, wildebeest and zebra densities in the reserve are abnormally high.
4) Giraffe and tsessebe numbers are in decline.

CHAPTER FOUR

DEMOGRAPHICS OF LARGE MAMMALIAN HERBIVORES IN ITHALA GAME RESERVE

Introduction

Abnormal demographics may lead to negative social interactions, have implications for population growth (Jarman and Jarman 1973, Fitzgibbon and Lazarus 1995) and, in the longer term, may affect natural selection. Such factors may negatively impact biodiversity, tourist revenues, game sales and initiatives to develop conservation partnerships with neighbouring communities based primarily on the harvesting of game. The demographics of black rhino, white rhino and tsessebe have been studied in Ithala, and it has been shown that in these species the population growth has been significantly lower than the potential of the species (Wolf 1997, Adcock 2000, Openshaw 2000). KZN Wildlife, who administers the reserve, had expressed concern that abnormal sex ratios might exist amongst the herbivores in the reserve (Rushworth pers. comm.). Additionally, although changes in number can be determined from repeated annual censuses, unless these are carried out over many years separating annual differences due to demographics from counting error is not possible. If recruitment and mortality are recorded annually however, a means of separating counting error from demographic changes is provided. For these reasons management of the reserve require data on the demographics of the reserve's herbivores. Aging and sexing animals is, inherently, difficult from aerial surveys; a representative ground sample of the population is required.

A snap shot in time of demographics is of limited use; reliable information on trends is central to the conservation and management of game populations (Mason 1990b). Consequently, they need to be repeatedly determined over a time frame likely to pick up any such trends.

Caughley (1974b) observed that age ratios *per se* contain little relevant information and large variations in numbers may go undetected by changes in age ratios. Attwell (1977) described more relevant parameters of population structure, namely the sex ratios of adults, the percentage of juveniles and the juvenile to adult female ratio. Analyses chosen in this study were those that would reveal the different species populations' growth potential (e.g. juvenile: adult female ratio, cohort survival), their structure (e.g. adult sex ratios) and aspects of their behaviour (e.g. group size, breeding herd composition).

Standing crop biomass and production by large mammalian herbivores in the African savannas show a high degree of correlation with mean annual precipitation, particularly where mean annual precipitation is less than 700mm (Coe et al. 1976, East 1984). For the period 2000 to 2004 inclusive mean annual precipitation in Ithala Game Reserve was 632mm (Fig 3.7); therefore, and especially in the absence of any significant predation, one would expect herbivore numbers to broadly correlate with rainfall (East 1984)- provided their density is not so high as to effect the population through food limitation (Lack 1954, Sinclair 1974, 1985b, Mduma et al. 1999).

The aim of this part of the study was to determine, and establish what environmental factors influence, the demographics of the large mammalian herbivores in Ithala Game Reserve over a number of years.

The specific objectives were (1) to determine the demographics of the larger herbivores in the reserve, and to show and explain any changes in these findings over time (2001 to 2004 for giraffe, kudu, wildebeest and impala; 2003 and 2004 for the remainder), and (2) to compare and explain similarities/differences between the above findings and results from other conservation localities.

Methods

Data analysis:

As described earlier (Chapter 1), different aspects of different species were recorded in the field; obviously this leads to inter-species differences in what was available to be analysed (Table 4.1). Where sufficient data were available, in addition to annual changes in these demographic parameters, monthly changes were also analysed and rainfall regressions performed. For uniformity, the year was taken as per the breeding year for the strictly seasonal breeders, namely 1st November to 31st October.

*Table 4.1: Summary of annual demographic analyses undertaken, by species. *Indicates analysis performed, # indicates additional monthly analysis and ^ indicates regression with rainfall.*

Species	Adult sex ratio	Age/sex structure	% juvenile	Juvenile: adult female ratio	Cohort survivorship	Group size by season	Miscellaneous
Giraffe	* ^	*	*	* ^		*	
Kudu	* ^	*	*	* ^		*	Bull association with female
Hartebeest			*			*	
Reedbuck	*		*	*		*	
Tsessebe			*			*	
Waterbuck	*		*	*		*	
Warthog	*	*	* #	*		*	Boar association with female
White Rhino	*	* (just age)	*	*		*	
Wildebeest	* # ^	*	* #	* # ^	*	*	Territorial bulls/yearlings' associations
Zebra	*	* (just age)	*			*	
Eland			*			*	
Impala	* # ^	*	* #	* # ^	*	*	Breeding and bachelor herd composition
Ostrich	*		*			*	

The analyses were performed by querying the data base. Where large percentages of observations contained unclassified (by age and/or sex) data, only observations in which all animals were fully classified were used. Such data are referred to as 'filtered'. Thus, for example, large numbers of warthog (due to their size and, at distance, consequent difficulty in accurately visualizing) were not sexed; sex ratio data presented therefore includes only observations in which all animals were sexed. The null hypothesis of parity of sex ratios (i.e. 1:1) was tested using a Chi-square goodness of fit test with 1 degree of freedom (Rayner 1967). The null hypothesis was rejected if $P > 0.05$. Where significant numbers of animals had been removed by management over the period of study (Appendix 8), adjusted annual sex ratios are also presented. These were calculated by cumulatively incorporating 90% (thus allowing for 10% mortality per annum (Balfour pers. comm.)) of male/females removed at the end of the previous year (removals are done over October/November) into the subsequent year's male/female totals.

To assess any change in percentage juveniles and juveniles: adult females, a null hypothesis of no change between the two years being compared was postulated and tested using a Chi-square goodness of fit test with 1 D.F.. The null hypothesis was rejected if $P > 0.05$.

Group sizes were averaged (with 1 standard deviation) over the wet seasons and over the dry seasons, to ascertain if there was any difference between the two seasons. High standard deviations necessitated the construction of histograms for each species, showing group sizes for these seasons.

The wet and dry seasons were taken as 1st October to 31st March and 1st April to 30th September respectively.

Results and Discussion

Influences of rainfall and habitat quality

-Fecundity-

As discussed earlier, the high correlation between standing crop biomass, production by large mammalian herbivores and mean annual precipitation in the African savanna is well established. Fecundity is a major component of herbivore production and thus might likewise be expected to correlate with rainfall. Strictly speaking, fecundity relates to the ratio of juveniles to adult (and, in appropriate species, yearling) females immediately after parturition but this is difficult to determine in the field and greatly limits the data sample (Attwell 1977). Therefore the term is used here to describe the number of juveniles per 100 adult females averaged over the entire breeding year. As such it encompasses fecundity and juvenile deaths during their first year of life. However, the availability of monthly percentage juvenile figures (Table 4.1) allows juvenile deaths to be disentwined from fecundity in some species.

-Fecundity regressed with rainfall-

Being browsers (the browse responds in a delayed, less defined manner to rainfall compared to grass (Hughes pers. comm.)), having an ill defined breeding period and a gestation period of longer than a year (14 months (Leuthold 1979)) makes it difficult to attempt meaningful regressions between giraffe fecundity data and rainfall; those presented below would seem likely to encompass any possible link between the two. Too little data was available to attempt monthly regressions (e.g. newborn/infants in each month against total rainfall over previous 12 or 24 months). Although kudu are fairly seasonal breeders in Ithala and have a gestation period of less than a year (nine months (Kingdon 1982)), being browsers again presents problems in attempts to link rainfall and fecundity.

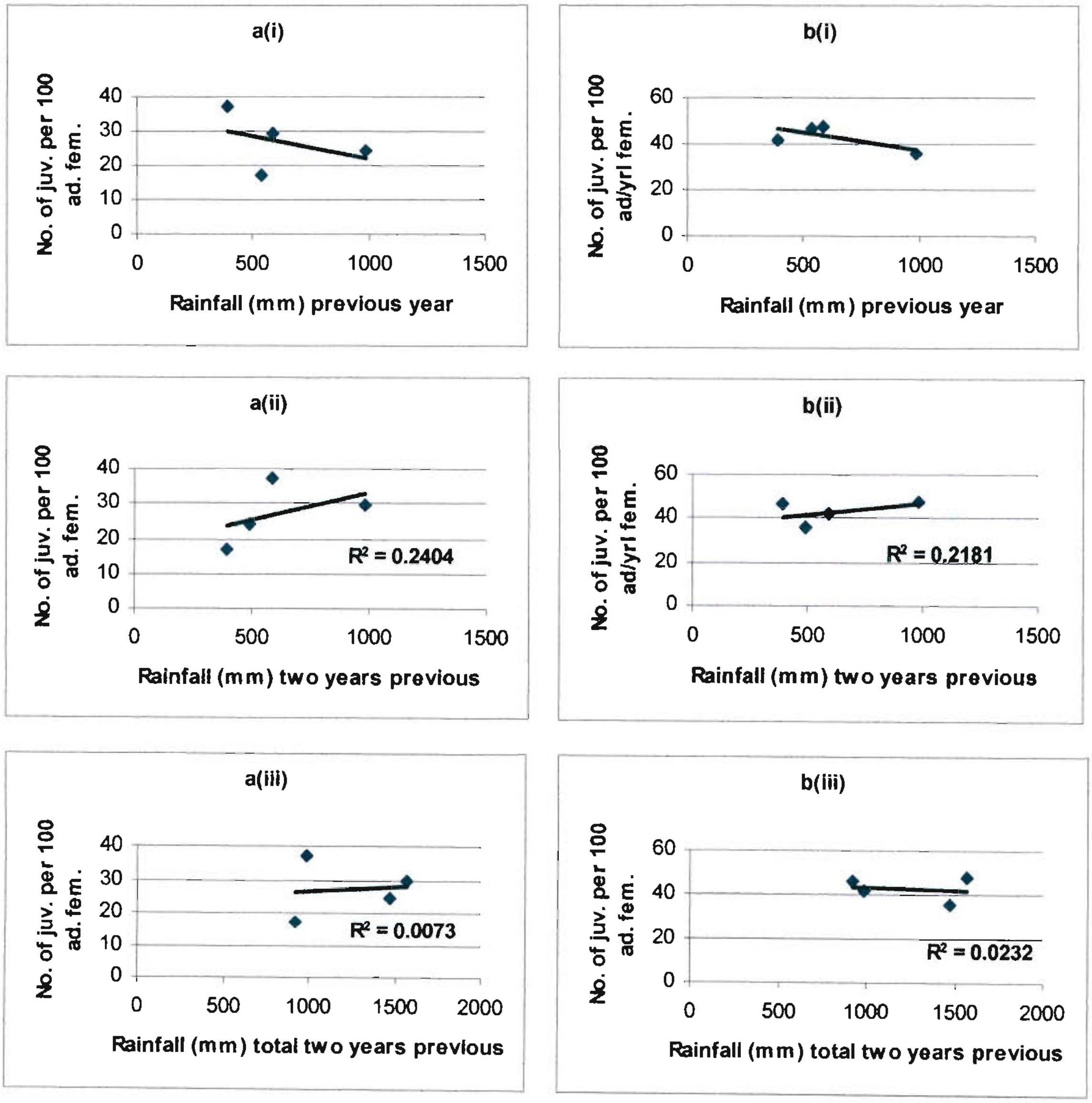


Fig 4.1: Rainfall versus fecundity regressions. a = giraffe, b = kudu. (i) = average annual fecundity, for each of the four years of study, regressed against corresponding previous year's total annual rainfall, (ii) = average annual fecundity, for each of the four years of study, regressed against total annual rainfall from two years previous, and (iii) = average annual fecundity, for each of the four years of study, regressed against sum of total rainfall of two previous years (e.g. fecundity in 2003 is regressed with total of rainfall from 2001 plus 2002). In all charts figures are 'filtered'. For giraffe: 2001 n = 140, 2002 n =143, 2003 n =165, 2004 n =112. For kudu: 2001 n = 435, 2002 n =378, 2003 n =367, 2004 n =384.

Being grazers, with a strictly seasonal breeding cycle and a gestation period of less than a year (~ 8 months (Attwell 1977)), wildebeest would be expected to show a link between previous year's total rainfall and fecundity.

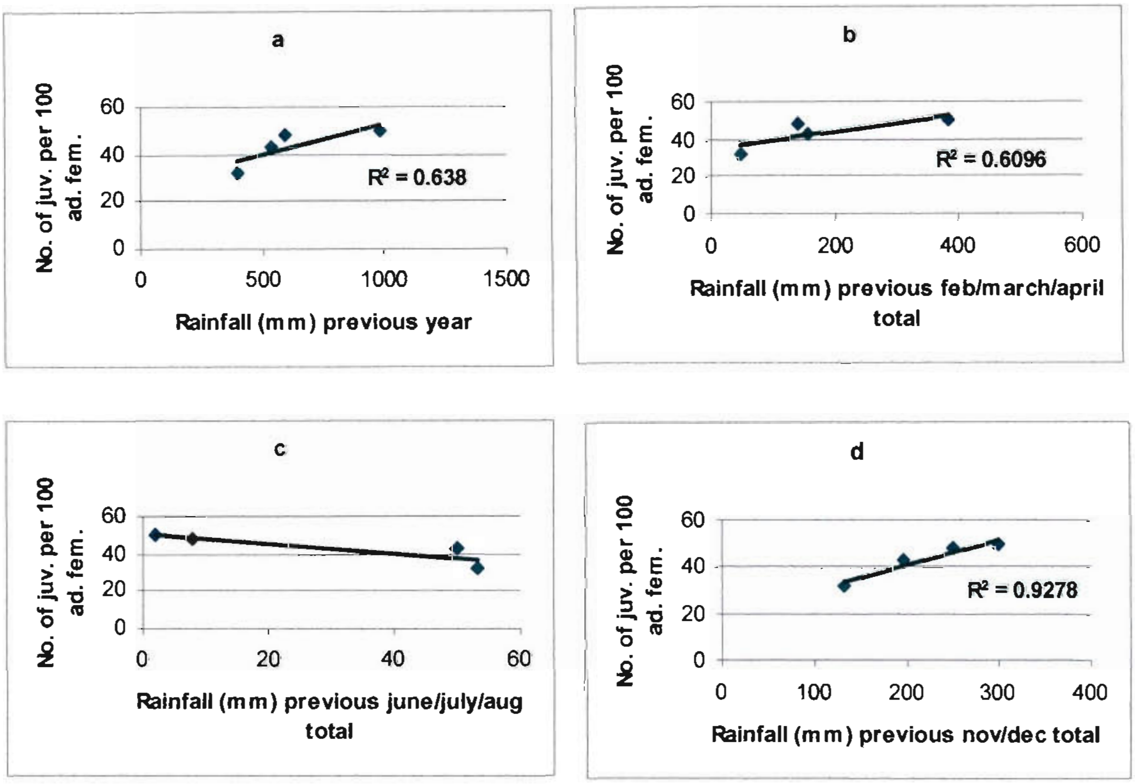


Fig 4.2: Wildebeest, rainfall versus fecundity regressions. Fecundity regressed against previous year's a = annual rainfall, b = rainfall over time of conception, c =rainfall over driest months and d = rainfall over peri-natal period (2 months). 2001 n = 1574, 2002 n =1938, 2003 n =2107, 2004 n =2781.

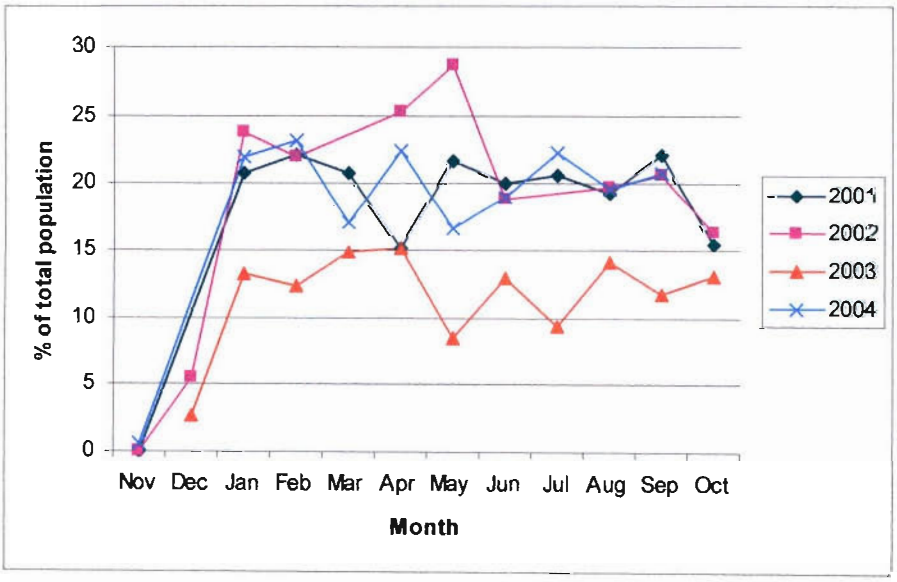


Fig 4.3: Wildebeest, juveniles as a % of the total wildebeest population by month, 2001 to 2004.

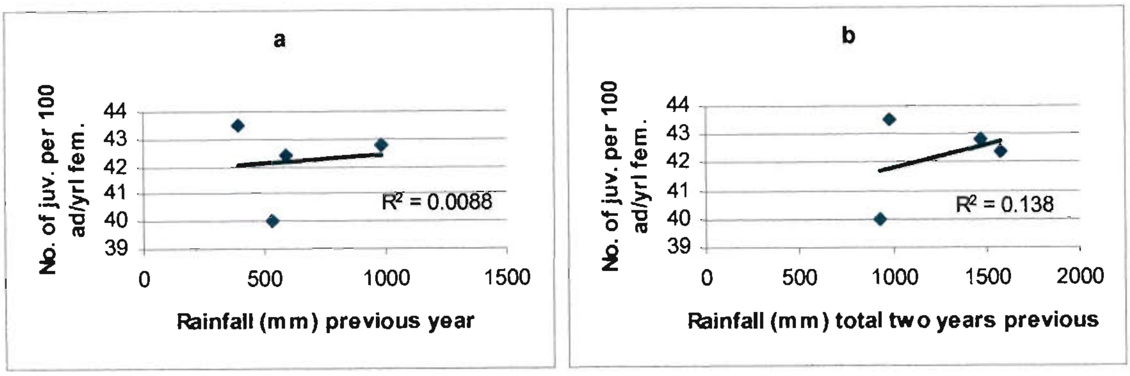


Fig 4.4: Impala, rainfall/fecundity regressions. a = Average annual fecundity, for each of the four years of study, regressed against corresponding previous year's total annual rainfall and b = average annual fecundity, for each of the four years of study, regressed against sum of total rainfall of two previous years (e.g. fecundity in 2003 is regressed with total of rainfall from 2001 plus 2002). 2001 n = 2133, 2002 n =2308, 2003 n =3012, 2004 n =2618.

For both giraffe and kudu, the only (weak) link between rainfall and fecundity suggested is in connection with the rainfall of two years prior (Fig 4.1ii); this may be related to their extended gestation period and/or to the more complex interaction of browse, compared to grass, with rainfall.

For wildebeest, a pure grazer, stronger links are seen between fecundity and the previous year's rainfall (Fig 4.2); examination of monthly percentage juveniles (Fig 4.3) shows this finding does relate to cows actual fecundity, rather than being a possible distortion due to juvenile survival rates. Considering monthly rainfall (Fig 1.1, page 4) and different parts of the breeding year suggests that whilst overall annual rainfall (Fig 4.3a) and that at the time of conception (Fig 4.3b) are of equal importance, rainfall over the peri-natal period is of greatest importance (Fig 4.3d). Specifically, rainfall over the two months of and immediately after birth (which occurs over November in Ithala) seems to have the greatest influence; this finding is in agreement with results from the Central Region of the Kruger National Park (Whyte 1985, Mason 1990a). Since juveniles are dependent on their mother's milk during this period (Attwell 1977), it appears the quantity/quality of grass available to lactating wildebeest immediately post-partum is of central importance to their calf's survival. Kreulen (1975), studying Serengeti wildebeest, concluded older, longer grass provides insufficient calcium for lactating wildebeest and that their move to the eastern plains related to the acquisition of sufficient calcium. Presumably relative failure of the spring rains depriving, as it would, wildebeest in Ithala of sufficient quantities of new grass growth, might therefore be having a detrimental effect on fecundity, at least in part, via insufficient calcium. Rainfall during the driest period of pregnancy (Fig 4.3c) appears to be of little relevance. A previous study of overall population trends, as opposed to specifically fecundity, in wildebeest over a twenty year period (Ottichilo et al. 2001), revealed significant relationships with annual total and wet season rainfall but not with dry season rainfall.

For impala, a mixed feeder (Hofmann 1973), there appears to be no or little connection between fecundity and the preceding year's rainfall (Fig 4.4a) or that of the previous two years (Fig 4.4b). Although impala prefer grass, they are adapt at switching between browse and grass (Smithers 1983) to an optimal extent (Meissner et al. 1996).

Since the effect of one year's lower rainfall on the browse would be limited compared to its effect on grass growth, it is perhaps not surprising that, of the animals considered above on whom four years data allowed rainfall/fecundity regressions, the only animal's fecundity clearly affected, wildebeest, is the only pure grazer.

The remaining herbivores on who sufficient data was collected (hartebeest, tsessebe, reedbuck, warthog, waterbuck and zebra) are grazers. As only two years of data are available formal regressions of annual fecundity against rainfall are of little meaning. However, since data obtained in the first of those two years (2003) followed one year of lower rainfall, simple comparison of fecundity related demographics between 2003 and 2004 might be expected to show a difference – namely lower juvenile: adult female ratios and lower percentage juveniles in 2003 compared to 2004. Although differences were found, these were only significant ($P < 0.01$) for reedbuck, were there was a *fall* in these values from 2003 to 2004. Thus whilst wildebeest, a pure grazer, showed a highly significant ($P< 0.001$) rise in these fecundity related demographics 2003 to 2004, the other grazers studied did not, implying that the lower rainfall of 2002 did not affect these demographics in these species. As previously discussed, for food limited populations of herbivores in semi-arid environments, survival and reproduction should be functions of the ratio R/B, where R is rainfall and B is herbivore biomass (Owen-Smith 1990). Fowler (Fowler 1981) suggested that for large mammals most density dependent change will occur at population levels close to the carrying capacity. Densities of hartebeest, tsessebe, warthog and waterbuck in Ithala are low whilst those of wildebeest (~ 6.0 km^{-2}) are high (Chapter 3), possibly explaining this contrast. Additionally, the ability of warthogs to adapt their diet during the dry season to include material shovelled from beneath the soil surface with the snout, would reduce their dependence on grass. Although zebra densities are also high (~ 5.6 km^{-2}), this species ability to process a wider range of quality of forage (Bell 1971, Page and Walker 1978, Owen-Smith 1988a, Bodenstein et al. 2000) compared to wildebeest may mean it does not, even at these high densities, currently suffer resource limitation, in terms of these fecundity related parameters, in Ithala during one slightly drier year.

Reedbuck also showed an apparent drop in absolute numbers in the reserve 2003 to 2004; sampling for population estimates showed, however, excessive variance for this species (postulated as being due to its flighty nature amongst the taller grasses it prefers) calling into question, without further data, the fall in numbers (Chapter 3). Since the adult sex ratios observed in reedbuck (Table 4.5, page 99) have been pretty constant, it is reasonable to conclude that whatever inaccuracies there may or may not have been in censusing numbers, representative sampling of adults has occurred over the two years. As juvenile reedbuck stay close to their mothers (Estes 1997), it follows that estimates of juvenile: adult female ratio and percentage juveniles should be fairly accurate. Since both numbers and fecundity related data are pointing in the same direction, it seems probable that there was a marked reduction in both these variables for reedbuck between 2003 and 2004; the cause of this is not apparent.

-Fecundity values-

When considering actual values of various demographica, rather than their fluctuations and association with rainfall, comparisons with other (where possible, similar) localities are frequently complicated by data being presented from widely varying periods of the year; only the broadest conclusions should therefore be drawn from such comparisons.

For giraffe, the number of juveniles per 100 adult females (22, 30, 36, 17 per 100 for 2001, 2002, 2003 and 2004 respectively) was lower than the 45 per 100 found by Dagg and Foster (1976). Juveniles as a percentage of the population are additional demographics influenced by fecundity. The percentage of juveniles recorded (6%, 9%, 13%, and 7% for 2001, 2002, 2003 and 2004 respectively), was lower than in previous studies (Backhaus 1961, Dasmann and Mossman 1962b, Dagg and Foster op. cit.) which show a range of 14% to 20% (juveniles as a percentage of the population, averaged over the year).

Although the comparatively low percentage juveniles recorded for giraffe are possibly partially accounted for by the comparatively high ratio of males to females (Table 4.4, page 93), taken with the low ratio of juveniles: adult females it suggests that giraffe fecundity is abnormally low in Ithala. The lack of reliable monthly percentage juvenile figures for giraffe (the samples were too small), prevents one from stating that these results are definitely due to low fecundity, but the virtual absence of predators and the lack of any obvious, serious disease amongst the giraffe population (pers. obs.) means they are unlikely to be accounted for by excessive juvenile mortality. The high density of giraffe in the reserve and their detrimental effect on the browse have been discussed in previous chapters; it seems likely, therefore, that the low fecundity is caused by a paucity of suitable forage. It is perhaps worth adding that although the poor state of the browse would logically be expected to increase juvenile mortality to an extent (both through its effect on maternal lactation and quality/quantity of herbivory directly available to juveniles), it seems highly improbable that it would do so without significantly affecting fecundity. Interestingly, giraffe were frequently observed (pers. obs.) chewing bones (osteophagia), possibly implying a shortage of calcium in their diet; this might in itself be expected to negatively affect fecundity, as has been suggested in wildebeest (Kreulen 1975).

Note: Some animals, especially giraffe and kudu, have been removed during the period of this study in large numbers relative to their total population in the reserve (Appendix 8). Since only adults are removed (live or dead) and the fertility of the removed females is an unknown quantity, correction of fecundity, percentage juvenile and age structure data to allow for management's removals is difficult. However, since the adults (with the possible exception of giraffe) have been removed broadly in line with their prevalent sex ratios, it is reasonable to conclude these removals will have had little effect on these aspects of demographics. The situation with giraffe is confounded by the lack of any clear evidence for the prevalent adult sex ratios (the results are not significant). However if more males than females do exist in the reserve, removals have been in line with this or, if this is an artefact, the removal of excessive males would have artificially increased the fecundity and percentage juvenile. In either case, therefore, the observations on the low reproduction rate of the Ithala giraffe appear sound.

Kudu ratios of juvenile: adult/yearling female (35, 47, 42, and 46: 100 for 2001, 2002, 2003 and 2004 respectively) are comparable with an average ratio of 45: 100 found over a ten year study of a population in the Kruger National Park (Owen-Smith 2002b); juvenile percentages (19%, 23%, 23%, and 24% for 2001, 2002, 2003 and 2004 respectively) are also comparable with the same study, where they varied from a low of 10% in drought years to average 20% to 30% in average to good years (Owen-Smith 1990).

Excepting the lower values for 2003, ratios of wildebeest juvenile: adult female (50, 48, 32, and 43: 100 for 2001, 2002, 2003 and 2004 respectively) are comparable to other studies (Talbot and Talbot 1963, Attwell 1977, Attwell and Hanks 1980, Mason 1990b); juvenile percentages (18%, 20%, 12%, and 17% for 2001, 2002, 2003 and 2004 respectively) are likewise similar to those found in comparable reserves (Vincent and Hitchins 1967, Braak 1973, Attwell op. cit., Attwell and Hanks op. cit., Berry 1980, Mason op. cit.) but higher than those found in East Africa (Kruuk 1972, Kingdon 1982).

Impala ratios of juvenile: adult/yearling female (42, 42, 43, and 40: 100 for 2001, 2002, 2003 and 2004 respectively) are comparable to Cowley's (1975) findings in Sengwa and Vincent's (1972, 1979) in near by Mkuzi; Stewart and Stewart (1965), working fifteen years earlier in Mkuzi, recorded a lower ratio of 39: 100. Juvenile percentages (19%, 21%, 19%, and 17% for 2001, 2002, 2003 and 2004 respectively) are similar to those found in Mkuzi (Stewart and Stewart op. cit., Vincent op. cit.).

Tsessebe percentage juveniles (13% and 11% in 2003 and 2004 respectively) are considerably lower than those found over three years in the Kruger National Park (Joubert and Bronkhorst 1977). Adults are difficult to sex (Anthony and Lightfoot 1984) and consequently number of juveniles per 100 adult females was not determined; if it is estimated from the percentage juvenile figures using other workers adult sex ratios, values of ~ 15: 100 are obtained – well below that found in a wide range of other reserves (Dunham 2003). Warthog percentage juveniles (26% and 24% in 2003 and 2004 respectively) and number of juveniles per 100 adult females (121 and 109: 100 in 2003 and 2004 respectively) are comparable with those found in the Central Region of the Kruger National Park during non-drought years (Mason 1990a). Zebra percentage juveniles (11% and 10% in 2003 and 2004 respectively) are similar to the 12% recorded both for a sample of 4,078 zebra counted in the Central District of the Kruger National Park (Smuts 1976) and a sample of 1,125 zebra counted in the Hluhluwe – Umfolozi Park (Robertson 1993a). Number of juveniles per 100 adult females (32 and 31: 100 in 2003 and 2004 respectively) compare with those found in the Kruger National Park (Klingel 1969, Smuts 1976) and, interestingly, fit into the range of values from reserves over Africa and their direct relationship with regional rainfall discussed by Klingel (op. cit.).

The low values in these fecundity related demographica for tsessebe complement the finding of a decline in its numbers over the two year period; some possible reasons for this poor performance of the population have been discussed (Chapter 3). Additionally, the small size of the population may incur adverse genetic consequences. Although it is not possible to predict how a population will respond genetically to reduced population size, and there is no universal minimum sustainable population size, genetic threats to small populations include the loss of genetic variation and inbreeding which may lead to inbreeding depression and reduced fitness (Grant and Van der Walt 2000). The latter may be manifested as reduced fertility or fecundity. Garstang (1982) observed that young tsessebe are susceptible to bad weather; the severe cold in May and again in October of 2003 (page 85) may therefore have affected juvenile survival.

Hartebeest percentage juveniles (11% and 14% in 2003 and 2004 respectively), reedbuck percentage juveniles (8% and 3% in 2003 and 2004 respectively) and number of juveniles per 100 adult females (16 and 5 : 100 in 2003 and 2004 respectively), and waterbuck percentage juveniles (25% and 21% in 2003 and 2004 respectively) and number of juveniles per 100 adult/yrl females (59 and 44 : 100 in 2003 and 2004 respectively), could not be compared with other localities as values for these demographics were not found in the literature.

Eland, a mixed feeder, did show a significant ($P < 0.01$) rise in percentage juveniles 2003 to 2004 (from 5% to 14%), but sample size for eland was however very small (total number of animals observed over 2003 = 63, 2004 = 105) making this finding questionable.

Summary

These results highlight variations in the inter-play between rainfall, habitat quality, the species diet, density dependence and fecundity. Giraffe, due to their excessive density in a largely inappropriate habitat, have degraded their food source to an extent whereby they are showing abnormally low fecundity related demographics virtually irrespective of annual rainfall variation. Wildebeest, at 'carrying capacity' in an appropriate habitat, show low values in the same demographics only in response to a drier year. Browsers and mixed feeders are barely affected by one slightly drier year, as is the case with grazers at low densities and/or those which are not totally dependant on short grass (e.g. warthog, zebra) - a resource particularly sensitive to annual fluctuations in rainfall.

-Juvenile mortality-

For strictly seasonal breeders, provided sufficient data can be collected, monthly percentage juvenile figures reveal juvenile mortality as the breeding year progresses. Such data was collected on warthog, wildebeest and impala.

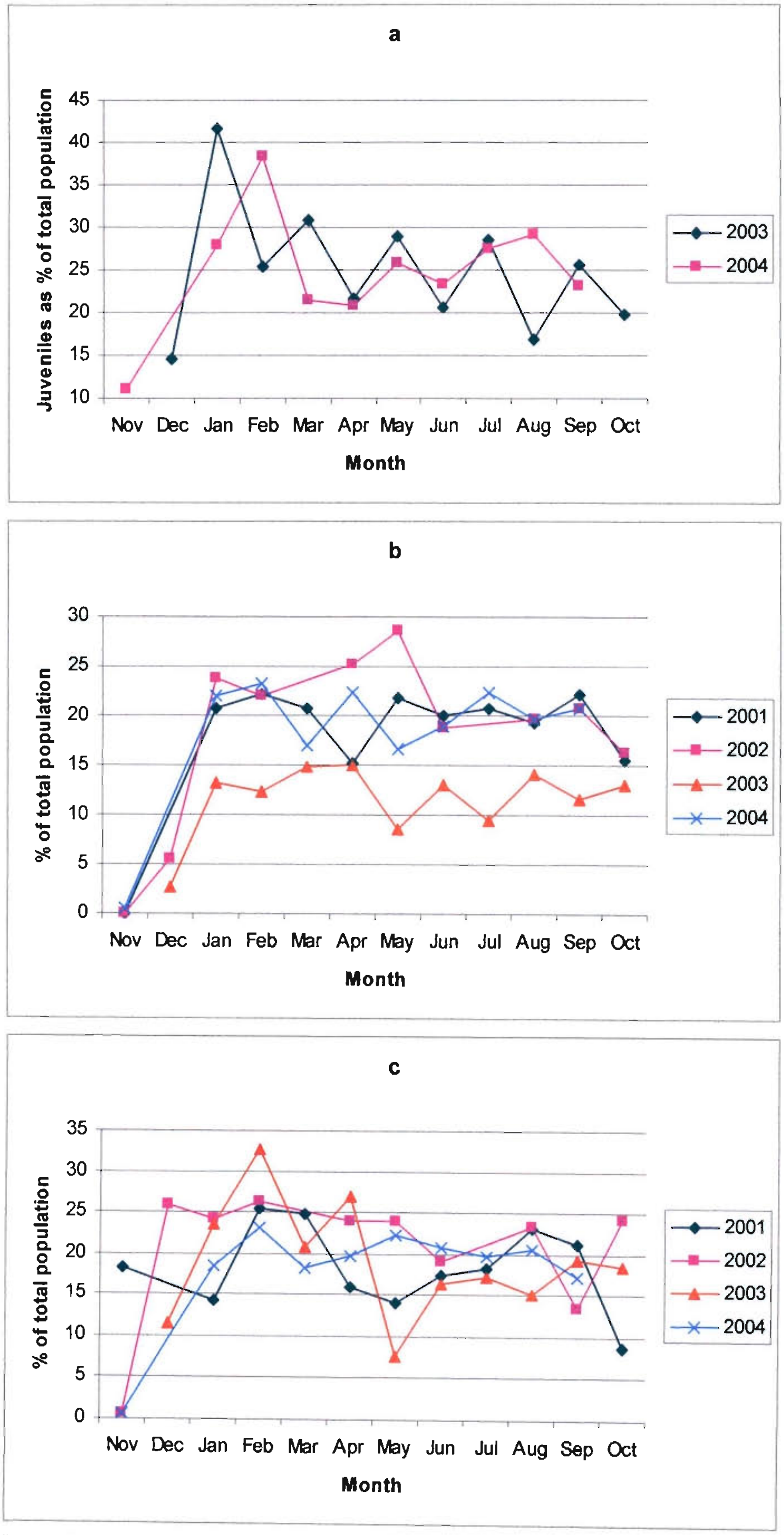


Fig 4.5: Juveniles as a % of the total population by month. a = warthog, b = wildebeest and c = impala.

Table 4.2 Average daily minimum temperatures: Vryheid

Year	May	June	July
1999	8.7	4.9	5.6
2000	6.1	5.4	4.7
2001	8.4	5.9	4.8
2002	6.3	2.4	2.0

As data was collected on warthog over two years of similar and reasonable rainfall, numbers of juveniles would be expected to decline at a similar rate in each year. Although this was broadly, allowing for sample variability, the case (Fig 4.5a), a larger dip was seen in percentage of juveniles over winter 2004 compared to winter 2003. A major cause of sample variability in warthog, especially when recording numbers of piglets, is the tall grass that is prevalent towards the end of summer and in early winter. The resultant restriction on visibility lasts until either the grass collapses naturally, at the very end of winter, or is removed by management placed fires. Fires were introduced much later in 2004 compared to 2003 (30th July as opposed to 8th May) and this may account for this difference.

Wildebeest percentage juveniles (Fig 4.5b) show a noticeable, and lasting, mid-winter reduction during the drier year of 2002, suggesting that juveniles succumbed at a higher rate than yearlings or adults – as might be expected. This mid-winter fall is also seen in the cohort survivorship chart covering that year (Appendix 9). Unfortunately daily temperature records are not kept at Ithala and even those recorded at the nearby town of Vryheid, by the national authority, were incomplete during 2003 and ceased all together in 2004. However, records for Vryheid (Table 4.2) show that mid-winter average daily minimum temperatures were unusually low in 2002; it seems likely this will have had a compounding effect on the poor nutritional status (consequent on the low rainfall) and resultant juvenile mortality of wildebeest.

Uniquely with wildebeest, markedly lower 'starting points' for percentage juveniles are seen in 2003 corresponding to the reduced fecundity, consequent on the previous year's low rainfall, discussed earlier.

Impala juveniles show a less marked reduction in 2002 (Figs 4.5c), suggesting they were not as susceptible as wildebeest juveniles to the lower rainfall and/or lower temperatures. A decreased susceptibility to the lower rainfall would be explained by their ability to utilise the browse, unlike wildebeest, thus mitigating the effects of reduced availability of grass. Impala, unlike wildebeest, show an additional, and more marked, reduction in juveniles early in the winter of 2003. Rainfall was about average during the year and over the winter but daily temperatures, when they were recorded in Vryheid around the time of this reduction (May), were unusually low (-3.8° on 28th and -3.0° on 29th May); reserve staff also noticed, subjectively, this unseasonable weather. This reduction in impala juveniles might thus be due to the effects of a very cold spell earlier in the winter than usual; the lack of a similar effect on wildebeest juveniles might be a reflection of the latter's greater size and hence, through the body surface area/volume relationship (Owen-Smith 1988b), reduced proportional heat loss and susceptibility to cold.

During October of 2003 a severe cold spell gripped the whole region. Records at a dam some thirty kilometres from Ithala were the coldest for fifteen years and local farmers suffered unusually high losses amongst their young livestock (Kilian 2004, pers. comm.); scorched vegetation was seen in the reserve along valley bottoms (pers. obs.). Interestingly, no marked reduction was seen in wildebeest or impala juveniles (or adults) during the field trip (October 2003) immediately following this very cold period – suggesting that, whether or not unusually cold weather contributes to juvenile mortality earlier in the winter, unusually cold weather at this stage of the breeding year (when juveniles would be eleven months old) does not noticeably affect juvenile mortality.

Heavy precipitation coinciding with exceptionally cold weather would be expected to increase heat loss (via a reduction in the insulating effect of fur) and consequent juvenile mortality. The absence of daily rainfall/temperature data within the reserve prevented any analysis along these lines.

-Territoriality-

Of the species where adults were sexed (Table 4.1), territories are held by mature males for most of the year in the case of reedbuck (Jungius 1971a), waterbuck (Spinage 1982), white rhino (Owen-Smith 1973) and wildebeest (Estes 1969, Attwell 1977, Attwell and Hanks 1980). Only with wildebeest was sufficient data collected to analyse changes in territoriality through the year(s).

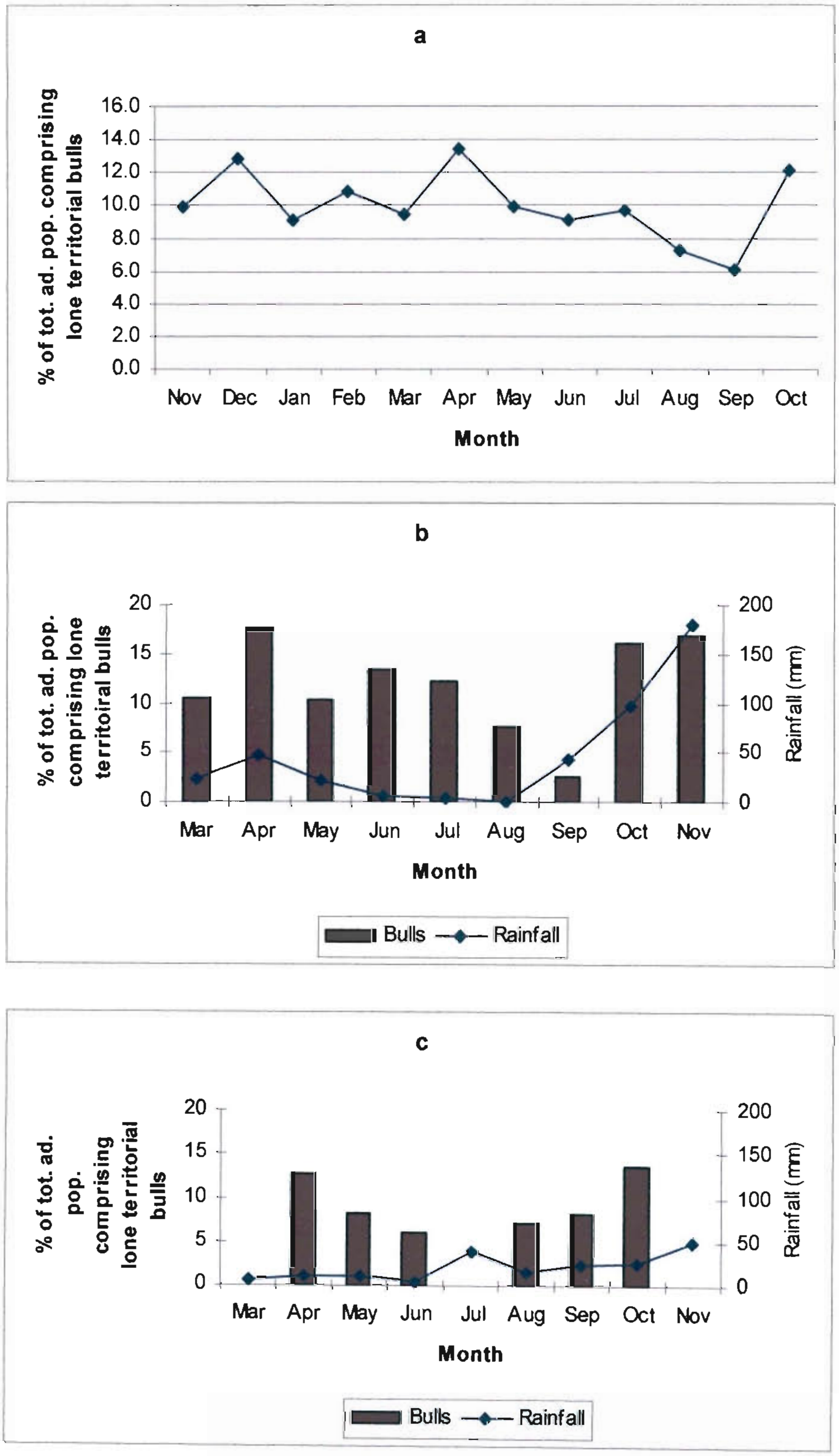


Fig 4.6: Wildebeest, lone territorial bulls as a % of the total adult population. a = as a % of total adult population by month (averaged) 2001 to 2004, b = as a % of total adult population by month 2001 with rainfall, c = as a % of total adult population by month 2002 with rainfall.

The percentage of the total adult population of wildebeest that were territorial bulls decreased in all four years of study during the depths of winter (Fig 4.6a).Territories were abandoned in greater numbers during drier winters and re-occupation of territories occurred soon after the return of the rains (Fig 4.6b/c). Wildebeest territorial behaviour is seen therefore to be linked to rainfall and resultant habitat quality, with bulls retaining their territories until forced by insufficient resources in the depths of winter to give them up but returning once conditions have improved after the rains return. Even in winter, animals are never far from water in Ithala and therefore it seems likely that the resource lacking is grass of acceptable quality; this would also fit in with the lag observed between reoccupation of territories and rainfall. That only a proportion of territories are abandoned is presumably explained by variations in the quality of different territories and/or their response to winter conditions; some areas were particularly affected with almost complete abandonment of territories (Fig 4.7).

The additional influence of the breeding cycle is shown by numbers of territorial bulls peaking at the time of the rut (~ April).

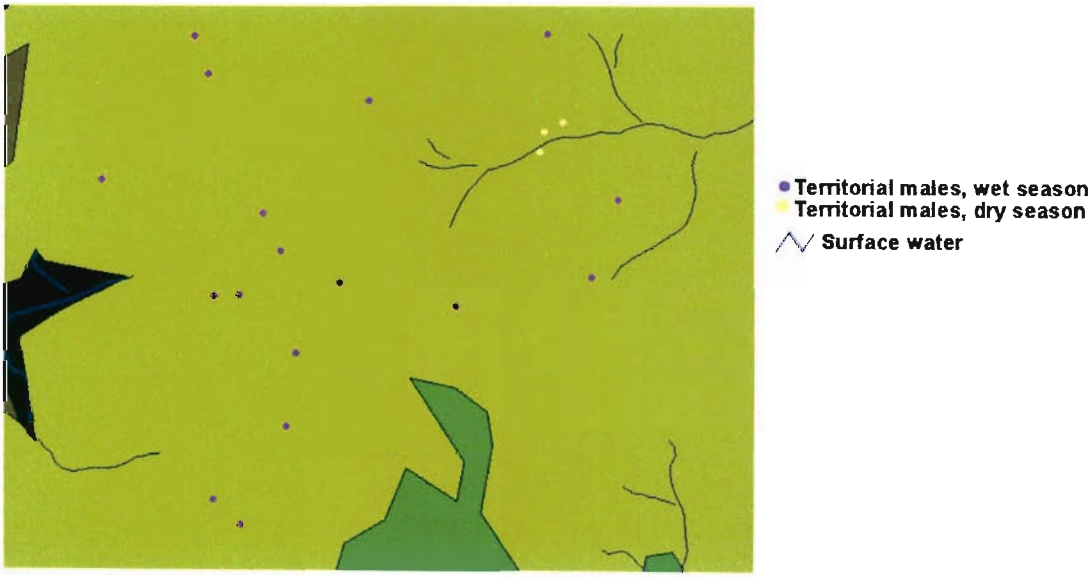


Fig 4.7: Wildebeest, lone territorial male sightings (Bergvliet Loop) wet and dry seasons of 2003 and 2004 combined. Vegetation legends as per Fig 1.5; maps orientated north.

-Group size-

Jarman (1974) argued that ungulate group size is influenced by the dispersion and availability of food and anti-predator behaviour. Aggregation reduces the individual's chances of being selected by a predator and increases the probability of a predator being detected. Decreased availability of food results in greater spacing between individuals when feeding (to avoid competition) and faster movement of the group through the resource to compensate for reduced energy intake per bite; hence group size will reduce to maintain communication within the group and hence group cohesion. Thus, Jarman argued, groups will be as large as possible without losing group cohesion. Jarman ignored, however, the direct effect density of vegetation will have on visual communication; decreased visibility in browse may also contribute to smaller group sizes (Leuthold 1970, Leuthold and Leuthold 1975, LaGory 1986, Perrin 1999).

The dry season, associated with comparatively reduced availability of food, has indeed been shown to be linked to decreases in group size (Jarman and Jarman 1974, Leuthold 1976, Rodgers 1977), but also to increases specifically when aggregation occurs in favourable areas (Hanks et al. 1969, Marchinton and Hirth 1984). Average group sizes by season on the range of ungulates studied in Ithala (Table 4.3) showed high standard deviations and, consequently, histograms were produced for each species (Appendix 10). As the direction of change was similar in each year, histograms were based on combined data from the years available. Subjective study of the histograms confirms the trends revealed by simple averaging of group size and, in most cases, shows that an increase in average group size occurs both as a result of an increase in incidence of very large groups and of a general shift across the whole range of group sizes to the right (i.e. larger groups); the reverse scenario applies where there is a decrease in group size.

Table 4.3: Average group size of herbivore species in the wet and in the dry season. Figures in brackets indicate results excluding juveniles. For giraffe, kudu, wildebeest and impala results are averaged across 2000 to 2004; for the remainder 2003 and 2004. Additionally, if the data from the winter month with the most marked 'green flush' (July 2003, Sept 2004) are excluded, the changes in group size are exaggerated e.g. wildebeest dry season average increases to 120% (113%) of wet season averages for those two years, impala same period dry season averages decrease to 79% (85%) of wet season averages.

			Average group size by season					
			Wet season: 1/10 to 31/3		**Dry season: 1/4 to 30/9**			
	Species		**av. (excl. juvs)**	**St. dev.**	**av. (excl. juvs)**	**St. dev.**	**Dry as % of wet (=excl. juvs.)**	**Family structure**
Browsers	Giraffe	Breeding	3.4 (3)	1.9	2.8 (2.3)	1.6	80% (75%)	open
	Kudu	Breeding	4.9 (3.8)	3.1	4.7 (3.4)	2.7	95% (90%)	closed
Short grass grazers	Hartebeest	Overall	6.15 (5.2)	4.1	8 (7.1)	4.6	130% (135%)	variable
	Tsessebe	Overall	4.6 (3.95)	2.1	4.55 (4)	2.3	~ 100% (~100%)	closed
	W. Rhino	Overall	2.2 (2)	0.5	2.2 (1.8)	0.5	~ 100% (~100%)	closed
	Wildbst.	Breeding	17 (13.7)	10.3	19 (14.4)	11.4	112% (105%)	open
	Reedbuck	Overall	3	1.3	2.8	1.1	93%	variable
generalist grazers	Warthog	Breeding	3.35 (2.1)	1.6	3.4 (2.1)	1.6	~ 100% (~100%)	closed
	Waterbuck	Breeding	4.9 (3.6)	2.8	4.2 (3)	2.3	85% (83%)	open
	Zebra	Breeding	5.4 (4.45)	4.5	4.55 (3.8)	2.2	85% (85%)	closed
Mixed	Impala	Breeding	13.6 (9.7)	12.3	11.2 (8.5)	8.2	83% (87%)	open

Although many of the species show the reduction in group size going from summer into winter as predicted by Jarman (op. cit.), two, wildebeest and hartebeest, show the reverse trend i.e. an increase in group size in winter compared to summer. Interestingly, if the grazers are broken down into the general categories of short grass specialist grazer or generalist grazer, it is amongst the short grass grazers where there is an increase in winter. The strong attraction of certain species to flushes of new grass growth, following management burning in winter, has been previously discussed (Chapter 2). Group size might be expected to increase on such flushes both due to the increased availability of food and to the increased visibility (the fire clears the tall, rank grass growth of the previous growing season) – thus suggesting a possible explanation for group size increase in the winter. However, if the data from the winter months with the most marked green flush is excluded, the changes in group size are in fact exaggerated (Table 4.3). These short grass grazers' increase in group size in winter appears, therefore, to be a genuine response to winter conditions.

This increase in the average group size in winter of wildebeest is in contrast to the findings of previous workers, both in similar and different locales (Talbot and Talbot 1963, Attwell 1977, Rodgers op. cit.). Although analysis of groups' composition shows that in winter >1 adult male is frequently associated with breeding herds (as might be expected with the break down of bull territoriality), the majority of the increase is due to greater numbers of cows (with juveniles). Previously in has been shown that area used by wildebeest in winter is considerably more restricted than in summer (Chapter 2), and that wildebeest density is unusually high in Ithala (Chapter 3). High densities combined with the winter move into more restricted locations might result in larger group sizes and, additionally, may in themselves cause degradation of the pastures, further reducing suitable areas available during times of resource limitation, i.e. winter, and putting upward pressure on group size both for that and other species which utilise the same resource (e.g. hartebeest). Additionally, group cohesion considerations are presumably less relevant in the absence of significant predation and therefore will have a reduced effect in limiting group size. In these circumstances it is therefore proposed that Jarman's suggested determinants of seasonal group size are overridden.

Jarman proposed his determinants of seasonal group size with regard to impala and ungulates with an open structure in general; species with a closed family unit structure would be expected to exhibit a constant group size irrespective of season (Rodgers 1977). Of the species studied a closed family or harem structure is shown by kudu (Perrin 1999), in Ithala's type of habitat by tsessebe (Garstang 1982), by white rhino (Owen-Smith 1973), by zebra (Smuts 1974, 1976) and by warthog (Child et al. 1968). As expected tsessebe, white rhino and warthog showed (Table 4.3) no seasonal change in group size – this is in agreement with others findings for white rhino (Owen-Smith op. cit.) and warthog (Rodgers op. cit.). Kudu did show a reduction in group size in the dry season and although this might not be expected given their closed family structure, it is in agreement with other's findings (Wilson 1965, Underwood 1978) and may related to decreased visibility in browse (Perrin op. cit.). Zebra also showed a reduction but here this is in contrast to other's findings where no seasonal reduction was observed (Smuts 1972). A possible explanation for this finding may be that as sampling generally occurred on higher ground and the, in winter, more desirable bottom lands were not sampled as intensely, the smaller zebra group size is simply a consequence of sampling less successful stallions, who presumably occupy the less favourable habitat in winter, with their smaller harems.

Influences of the breeding cycle

-Herd composition-

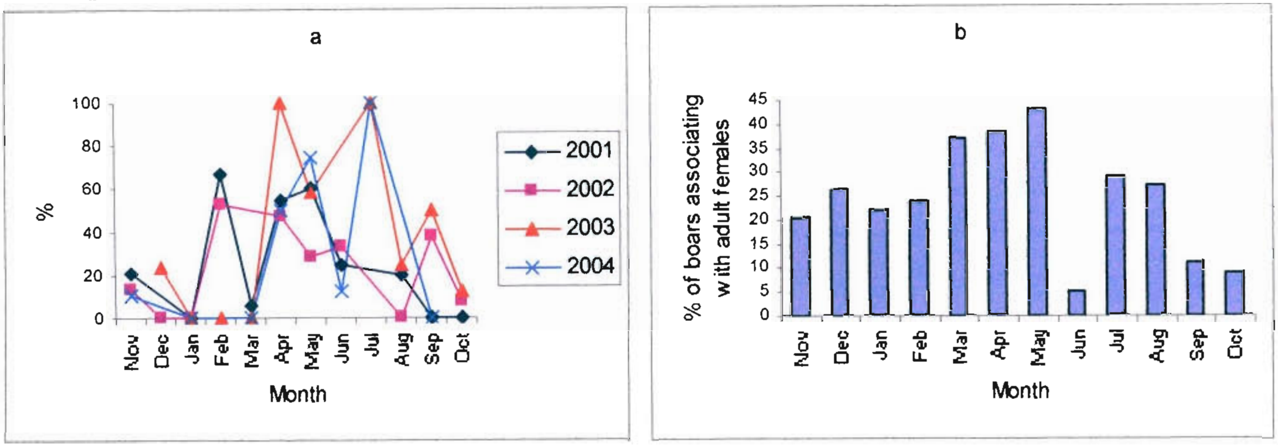
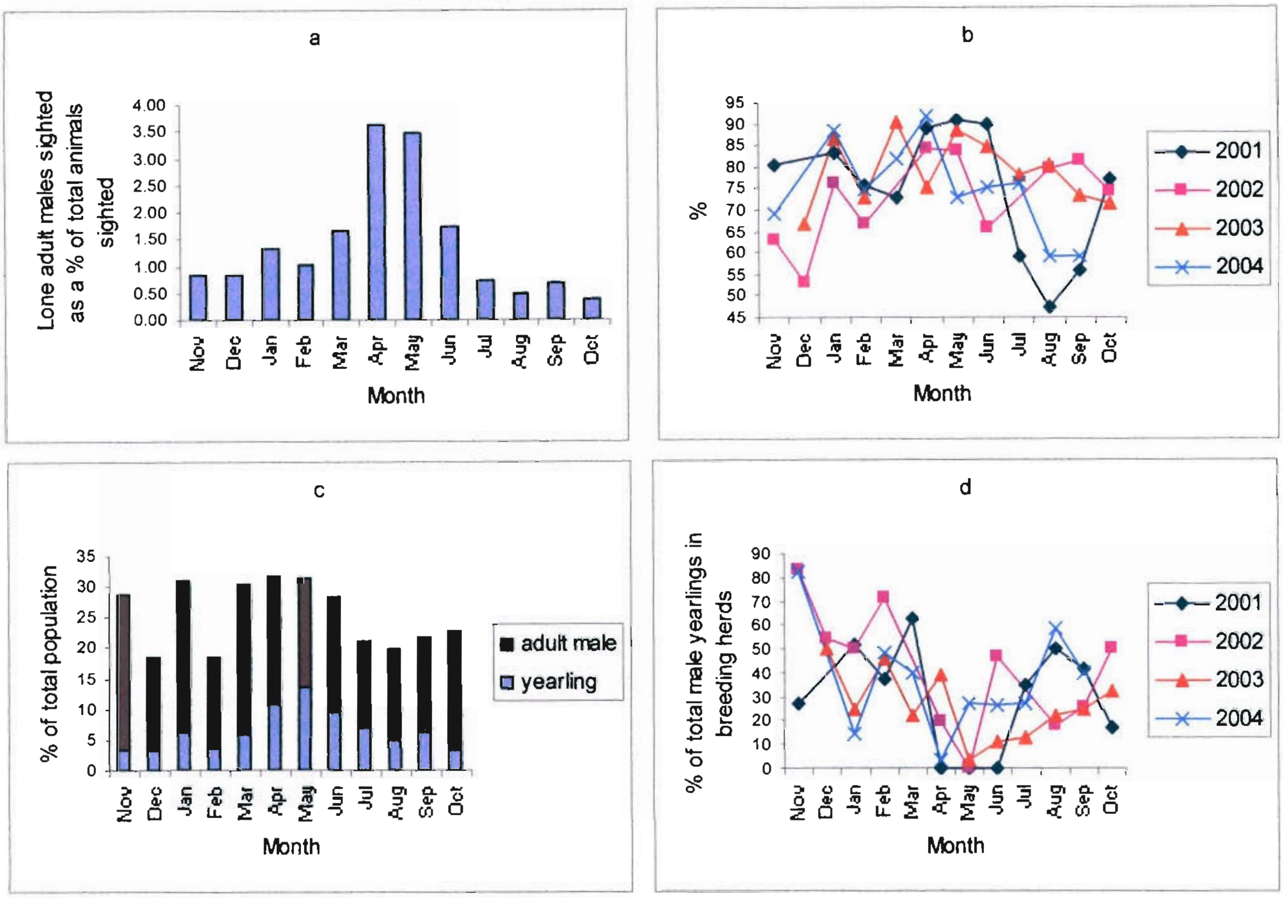


Fig 4.8: % of adult males associated with adult females by month. a = kudu 2001 to 2004 and b = warthog 2003 to 2004 (averaged).

In southern Africa the kudu is a seasonal breeder with the rut occurring around April/May (Owen-Smith 1984b). The percentage of adult males associating with breeding herds was seen to rise over this period (Fig 4.8a); this is in keeping with the findings of a ten year study on kudu in the Kruger National Park (Owen-Smith 1993) and of a two year study in the Eastern Cape Province (Perrin 1999). Warthog are also seasonal breeders where ever there are marked seasonal changes, as is the case in South Africa, and boars are said to only accompany sounders containing oestrous females (Cumming 1975, Estes 1997). Although, allowing for sample variability, an increase in percentage of boars associating with females is seen (Fig 4.8b) over the ~ May rut (i.e. when sows are in oestrous), boars are also seen to associate with females, albeit at lower levels, throughout the year in Ithala.

In East Africa male yearling wildebeest are cut out of the breeding herds soon after the next year's crop of juveniles are born i.e. when they are 12+ months old – by the time the next rut arrives four months later 90% are in bachelor herds (Estes 1969). In Hluhluwe – Umfolozi young males were not cut out until a year later i.e. when they were 24+ months old; male yearlings being seen in bachelor herds was an exceptional event (Attwell 1977). Findings here are in accordance with those of Attwell; only 4% (57 of 1299) of yearlings were seen in bachelor herds overall and specifically at the time of the rut, April, only 2% (3 of 143) were in bachelor herds. Both Estes and Attwell, although expulsion was occurring a year apart, noted that it occurred in relation to calving rather than the rut itself. This led Estes to suggest it occurred due to the newly arrived calves unsettling the yearlings' relationship with their mothers, in turn causing the bulls, who generally do not tolerate disturbances in the herd, to chase the yearlings from the herd. Attwell suggest the expulsion of yearlings approaching adulthood (i.e. 24 months old) was related to possible 'competition' between themselves and bulls over attentions to parturient (i.e. ones that have just calved) females; he did not offer any explanation as to why Estes mechanism did not seem to apply in his southern African population. Given the considerable effort (i.e. cost) put into expelling unwanted younger males by bulls (pers. obs.), Attwell's explanation does not seem to provide a compelling enough reason (i.e. benefit) for the bulls efforts. Attwell determined that 'spermatogenesis commences at two years of age' in wildebeest. As bulls 'in or out of season are always ready and willing to mate' (Estes), it seems more likely the expulsion of yearlings at 24 months in southern Africa relates to their onset of fertility.



Figs 4.9: Impala herd composition. a = lone adult males sighted per month 2001 to 2004 (averaged), b = % of adult/yrl males in bachelor herds by month, as a % of total adult or yearling males, c = composition of bachelor herds by month 2001 to 2004 (averaged) and d = % of male yearlings in breeding herds by month.

In southern Africa impala limit vigorous territorial behaviour to a few months around the time of the rut (Anderson 1972, Murray 1982a) which, in Ithala, is ~ April. Although impala territories are less obvious in the field than those of wildebeest (due to impala often inhabiting denser habitats), this is indeed seen in the marked peak in lone adult males over the time of the rut (Fig 4.9a). In contrast to East Africa where juvenile males are cut out of the breeding herd by territorial males, young males in South Africa are not cut out until the rut during their second year of life i.e. as yearlings (Jarman and Jarman 1973, Murray 1982b). The rise in the percentage of adult/yearling males in bachelor herds (Fig 4.9b), the rise in numbers of yearlings in bachelor herds (Fig 4.9c) and the fall in the percentage of male yearlings in breeding herds (Fig 4.9d) over the time of the rut are all reflections of this cutting out of yearlings (and any bachelor males in the vicinity) by territorial males. Jarman and Jarman (op. cit.) explained the delay in cutting out in southern populations as being a consequence of the shorter calving season, as this means territorial organization disintegrates 'before juvenile horns develop'. As juvenile horns are clearly visible in Ithala from March onwards (pers. obs.), this cannot be the explanation in this reserve. A more acceptable explanation would seem to be that as juveniles are not weaned until four and a half months (Estes 1997), they are still suckling (after the November/December calving season) at the onset of the rut and consequently mothers are unlikely to tolerate, for obvious functional reasons, separation from their calves at such a stage. Different reproductive strategies in terms of retention of offspring relating to biennial versus annual breeding, as found in mountain goats (Dane 2002), could conceivably also be involved. Although the extended breeding season in East Africa will mean there are a proportion of juveniles over the rut who *have* been weaned, the functional advantage to the territorial males of cutting out these individuals is unclear. As males only achieve fertility as yearlings (Fairall 1972), the reason cannot be related to any threat of impregnation by juveniles. Nor can it be related to ensuring that impregnated females suffer less competition for resources, as juveniles cut out return after the rut for some months (Jarman and Jarman op. cit.) – this was also seen to be the case in this study (Figs 4.9b/c/d). Since there appears to be no advantage in the removal of juveniles *per se*, possibly the removal has a secondary effect on females' fertility – perhaps it stimulates ovulation? A similar explanation may be the underlying reason as to why wildebeest bulls don't tolerate the disturbances to the breeding herd caused by young yearlings observed by Estes (see above). However unclear the strategy of the east African territorial impala may be, it is unlikely to be anything other than optimal given the extreme length of time, almost unique amongst the original African antelope, it has had to adapt to its environment (Vrba 1983, Mooring 1999, Matthee and Davis 2001).

Sex ratios

-Secondary sex ratios-

Polygynous mating systems involve competition between males, leading to the evolution of sexual dimorphism through sexual selection (Darwin 1871). Variation in mammalian adult sex ratios (ASR) is striking both intra- and inter-species; Darwin suggested that causes of variation might include competition between males for females and predation, and recognized that the degree of competition might be related to the extent of sexual dimorphism. In African antelope species Jarman (1974) proposed a series of relationships between habitat use, food dispersion and social behaviour, and hypothesised a series of evolutionary steps (Perez-Barberia et al. 2002) leading to sexual dimorphism in body size through sexual selection.

Although this straightforward link between sexual dimorphism and mortality has been widely discussed/presumed (Alexander et al. 1979, Clutton-Brock et al. 1980, Clutton-Brock et al. 1982, Andersson 1994, Owens and Bennett 1994, Weckerly 1998), recent studies where the effects of common ancestry have been removed by computing phylogenetically independent contrasts failed to detect this link (Berger and Gompper 1999, Toigo and Gaillard 2003). It seems, rather, that species life-history traits predispose sexes to differential mortality and that these characteristics are shaped, at a proximate level, by environmental conditions (including predation).

Table 4.4: Giraffe, kudu, wildebeest and impala annual adult sex ratios. P value refers to Chi Square Test applied to null hypothesis of parity of adult sex ratios. Significant results P< 0.05, NS = not significant (P>0.05). Adjusted ratio = annual adult sex ratio adjusted for management's removals (live and dead).

Species	Year	Adult male : adult female	P value	Adjusted ratio	P value
Giraffe	2001	113 : 100	0.34, NS	112:100	0.37, NS
	2002	121 : 100	0.14, NS	137:100	0.04
	2003	70 : 100	0.012	77:100	0.058, NS
	2004	66 : 100	0.009	81:100	0.16, NS
Kudu	2001	54 : 100	< 0.0001	57:100	< 0.0001
	2002	55 : 100	< 0.0001	59:100	< 0.0001
	2003	41 : 100	< 0.0001	47:100	< 0.0001
	2004	42 : 100	< 0.0001	54:100	< 0.0001
Wildebeest	2001	53 : 100	< 0.0001	58:100	< 0.0001
	2002	54 : 100	< 0.0001	57:100	< 0.0001
	2003	57 : 100	< 0.0001	59:100	< 0.0001
	2004	52 : 100	< 0.0001	55:100	< 0.0001
Impala	2001	67 : 100	< 0.0001	68 : 100	< 0.0001
	2002	56 : 100	< 0.0001	61 : 100	< 0.0001
	2003	63 : 100	< 0.0001	63 : 100	< 0.0001
	2004	74 : 100	< 0.0001	80 : 100	< 0.0001

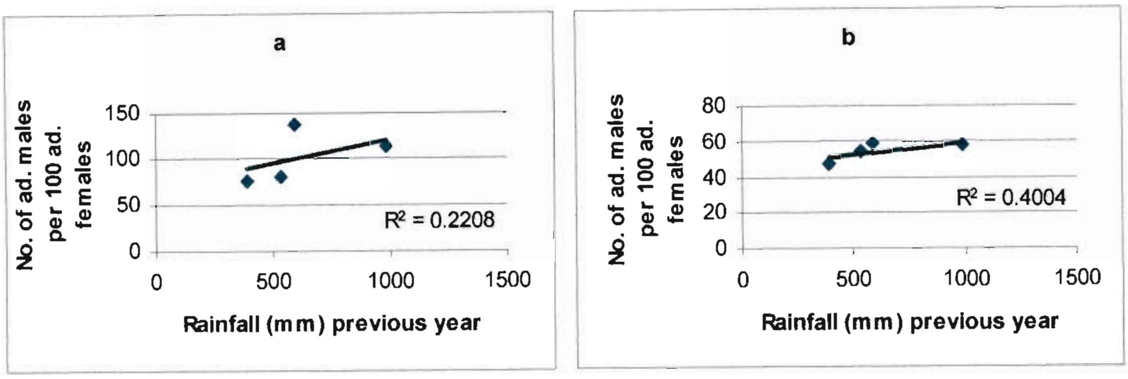


Fig 4.10: Adult sex ratio versus rainfall regressions, previous year's rainfall and adjusted for management removals (live and dead). a = Giraffe (2001 n = 251, 2002 n =243, 2003 n =206, 2004 n =159), b = kudu (2001 n = 463, 2002 n =367, 2003 n =340, 2004 n =334).

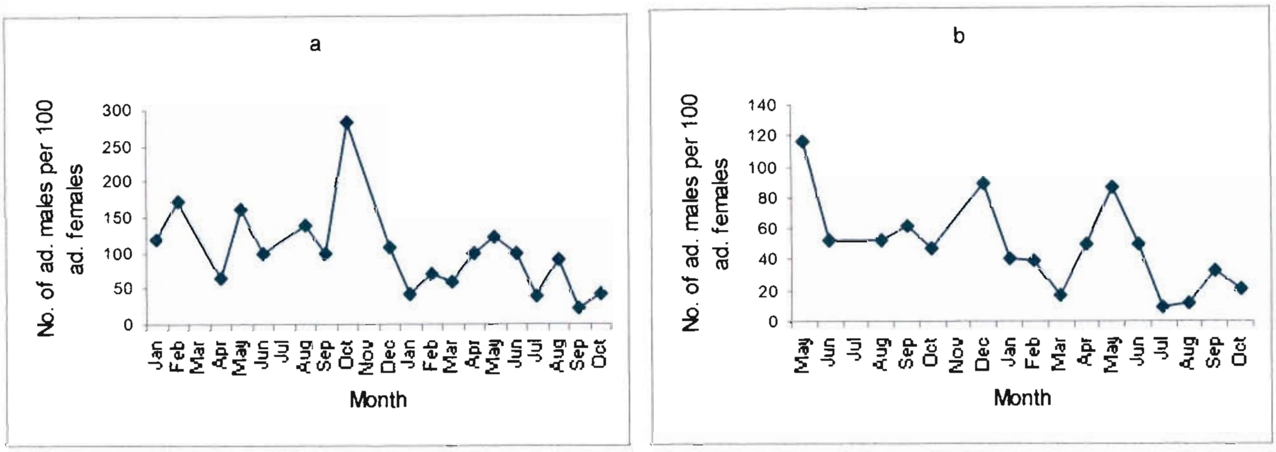


Fig 4.11: Number of adult males per 100 adult females, by month 2002 and 2003. a = giraffe and b =kudu.

Considering variations in the ASR (here taken as the number of adult males per 100 adult females) over the period of the study, giraffe and, to a lesser extent, kudu show a reduction in the ASR after 2002 (Table 4.4). Regressions of ASR against annual rainfall show a weak link with the previous year's rainfall (Fig 4.10). Analysis of ASR by month over the period (Fig 4.11) shows, especially for giraffe, that the reduction occurred ~ January 2003. Toigo and Gaillard (2003), reviewing research on a wide range of polygynous ungulates, concluded that in food-limited environments the survival of males relative to that of females was lower than in good environments, suggesting a cost of large size for males facing harsh conditions; Owen-Smith (1993) observed that male kudus were more susceptible to malnutrition. The spring rains (i.e. total for October/November/December) were below levels of surrounding years (Fig 1.1); browse shows a delayed response to rainfall (Hughes pers. comm.) and consequently the effects of this relative failure of the spring rains may not have been felt by the browsing guild until some weeks later, when, presumably, the larger males suffered proportionally greater mortality. Although the size of the reduction in ASR for giraffe is complicated by the non-significant deviation from parity in ASR in 2001 and 2002 (Table 4.4), the reduction does seem to be substantially larger for giraffe than kudu. This appears to be further evidence that giraffe are food limited in Ithala.

Wildebeest ASRs showed no link with rainfall on either an annual or monthly basis. As wildebeest in the reserve are at an unusually high density (Chapter 3), if males were subject to increased costs in harsh conditions one would expect this to be apparent during the depths of winter or a relative drought– hence the most parsimonious explanation of these findings is simply that rainfall variation, and hence its influence on habitat quality, does not cause differential male/female mortality in wildebeest in Ithala. This may be because wildebeest ASR is not affected *per se* by rainfall variation or, alternatively, that it is but only down to a certain lower level of male: female, below which the influence of underlying life-history traits is such that increased costs suffered by males as a result of lower rainfall are offset by advantages incurred by their relative scarcity – and that this lower level has been reached in Ithala consequent on the high density. In a severe drought in the Kalahari male wildebeest showed greater mortality than females (Knight 1995).

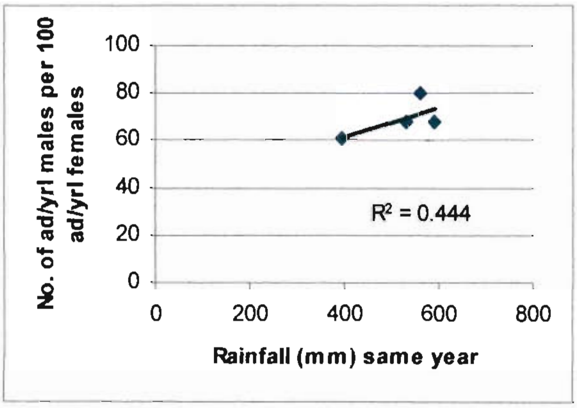


Fig 4.12: Impala adult sex ratio versus rainfall regressions, same year's rainfall and adjusted for management removals (live and dead). 2001 n = 2639, 2002 n =2672, 2003 n =3656, 2004 n =3413.

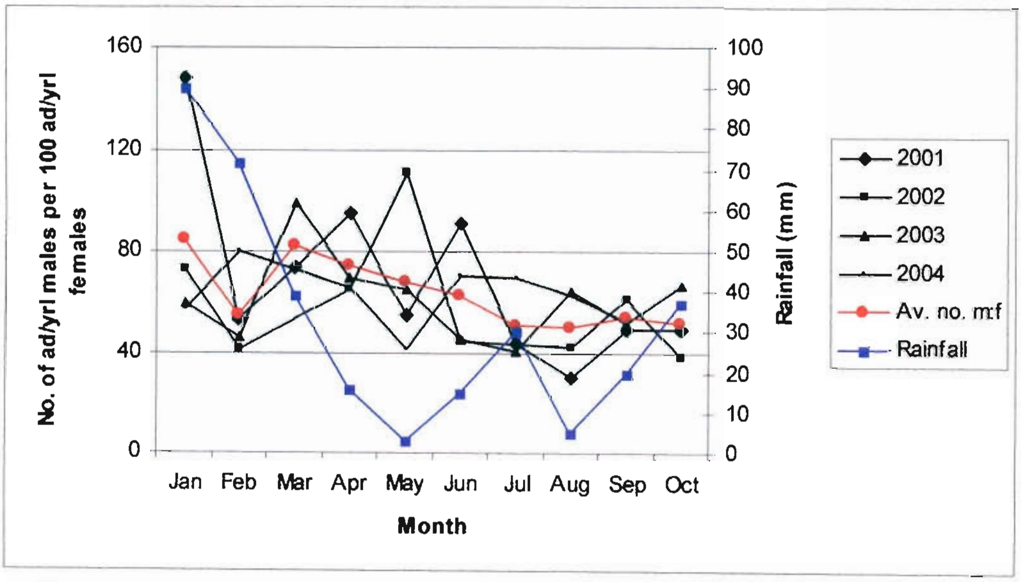


Fig 4.13: Impala, number of adult/yearling males per 100 adult/yearling females by month 2001 to 2004, with average monthly ratio and average monthly rainfall 2001 to 2004.

Impala ASR appears, in contrast, to be influenced by both (same year) annual (Fig 4.12) and monthly (Fig 4.13) variations in rainfall, with males showing a relative decline in comparatively harsh conditions.

Considering actual ASR, rather than annual/monthly variations, removals by management since the reserve's foundation in 1973 (Appendix 8) have been intentionally approximately at parity. If sex ratios in a given population differ from parity, as is the case with most herbivores in Ithala, removals at parity will reduce the minority sex disproportionately. However the numbers removed from Ithala, considered over thirty years, are too small to have noticeably affected ASRs – hence existing ASRs in the reserve are the result of natural processes at work, rather than human interference (poaching is minimal). Berger and Gompper (1999), reviewing a wide range of ungulates, concluded that the presence or absence of predators had no consistent effect on ASR, whilst acknowledging that at a proximate level it directly affects sex ratio variations – this emphasises the importance of, where possible, using similar study sites when comparing sex ratios.

Giraffe, although there appears to have been a trend towards proportionally fewer males over the study period, did not show any significant deviation from sex parity except in 2002 when there were significantly more males than females (Table 4.4). Most other studies have recorded more females than males (Innis 1958, Foster 1966, Child 1968, Berry 1973, Hall-Martin 1975, Hirst 1975, Dagg and Foster 1976, du Toit 1988). Foster (1966) and Foster and Dagg (1972) observed that adult males keep to forested regions more than females and this may account for variations in sex ratios between different studies. In this study a representative sample, including both plains and wooded areas, of a relatively small enclosed reserve was covered by vehicle; areas inaccessible were mainly wooded so it seems reasonable that a totally accurate/complete count would not reduce the observed male bias - if anything it would increase it. Small calves are very vulnerable with 50% - 75% subject to hyena and lions dieing in the first few months of life (Foster and Dagg op. cit., Moss 1975, Dagg and Foster 1976, Pratt and Anderson 1982, Pellew 1984b). Male calves move much farther away from their mothers especially in their second year as yearlings (Pratt and Anderson op. cit.); presumably this translates into greater male mortality from predation. Adult males, possibly due to their more lonely/nomadic existence following females in oestrous and to their feeding at full neck-stretch, are also more prone to predation (du Toit 1990). Pienaar (Pienaar 1969) found that out of 93 adult giraffe killed by lions over a two year period in the Kruger, the cow: bull ration was 1:1.8. The bias towards males in predator sparse Ithala would seem to emphasise the role of predation in maintaining a female bias; interestingly the only other location cited as showing a bias towards males (Fleur de Lys) also lacks significant predators. As discussed above, below average rainfall, through its affect on primary production, appears to have been responsible for greater male mortality in early 2003; it would be expected, therefore, for the overall poor quality/quantity of forage available to giraffe to have the overall affect of comparatively reducing the adult male component compared to reserves where giraffe are not resource limited. That this is not apparent suggests the importance of predation in determining the underlying ASR.

Kudu, like giraffe, showed a noticeable drop in the proportion of males over the period of the study (Table 4.4); ASRs before this drop are slightly less female biased, whilst those after are very similar to a range of values from across southern Africa reviewed by Owen–Smith (1993). At Timbavati lion preferred male kudu (Hirst 1969); Owen–Smith (op. cit.) observed that whilst lion in nearby Kruger National Park also showed a strong prey preference for male kudus, the population sex ratio of kudus seemed to be equally female-biased in areas where lion were less abundant or absent, leading to the conclusion that predation, although influencing ASR, was not of paramount importance and that excess mortality incurred by male kudu was caused by multiple factors. Results in this study would seem to be in agreement with these broad comments; lack of predation relates to a slightly higher male proportion but this is modified by environmental factors. Tick infestation was often noticed to be particularly heavy on kudu (Appendix 5, Plate 4); it has shown to be heavier in browsers (Gallivan and Horak 1997) and there may be sex differences in intensity of infestation (Horak et al. 1992, Gallivan et al. 1995).

Wildebeest ASRs (Table 4.4) are noticeably more biased towards females than those found in the most comparable reserve, Hluhluwe-Umfolozi, by Attwell (1977). Predation is heavier in that reserve, suggesting it is not a factor in causing greater male mortality in the region; indeed Attwell (1982) observed that the sex ratio of recorded kills of wildebeest (95% due to lion) in a sample of 175 showed no sex selection. A more general comparison of ASRs, mainly from southern Africa, also suggests that predation does not play a major role in causing differential wildebeest male mortality (fig 4.14), although the assessment of level of predation is a highly subjective one. Wildebeest ASRs showed no response to rainfall during the study, suggesting, despite their high density and therefore possible resource limitation, that harsh conditions are not instrumental in the relatively low proportion of males. However, as discussed above, an alternative, although intuitively less attractive, hypothesis implies that wildebeest adult males are disproportionately affected by harsh environmental conditions but only down to a certain lower ratio of male: female determined by the influences of underlying life-history traits. If this were the case, then inferences of the lack of influence of predation on ASRs for wildebeest in Ithala may be invalid i.e. the affect of resource limitation on ASRs is masking any affect of lack of predation.

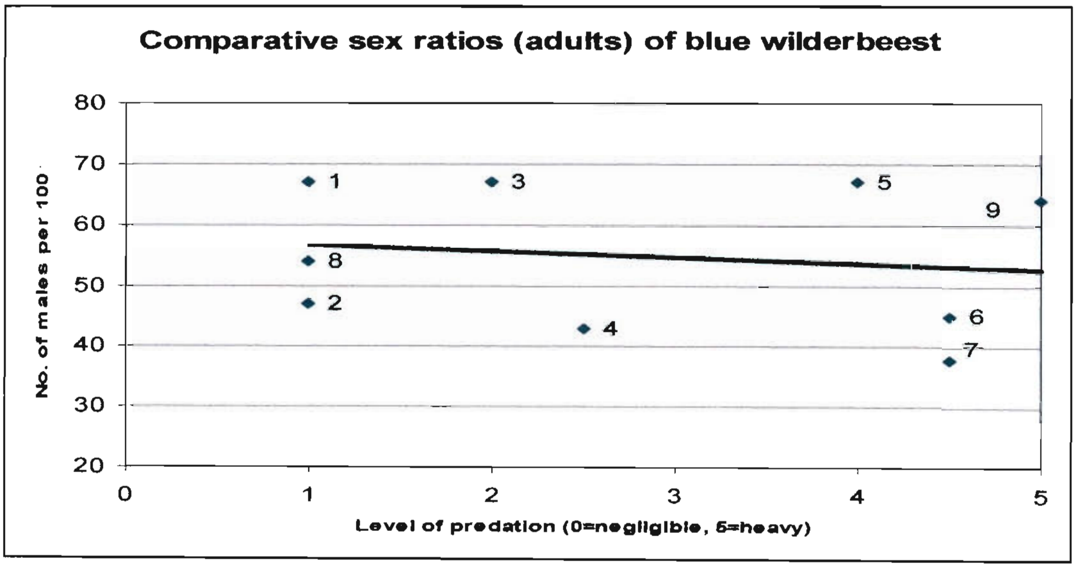


Fig 4.14: Comparative sex ratios of adult wildebeest. Note that the assessment of the level of predation is not by the cited authors, but is a subjective one based on the opinions of individuals with experience of the relevant reserves as to the predation level pertaining at the time of the cited papers.

1	*Mkuzi, R.S.A.*	*1972-1973*	*(Brooks 2001)*
2	*Mkuzi, R.S.A.*	*1973-1974*	*(Attwell 1977)*
3	*HGR-UGR Complex, R.S.A.*	*1974*	*(Attwell 1977)*
4	*Makarikari, Botswana*	*1965*	*(Estes 1965)*
5	*Ngorongoro*	*1963*	*(Talbot and Talbot 1963)*
6	*Kruger, Central District, R.S.A.*	*1972*	*(Braak 1973)*
7	*Hwange, Zimbabwe*	*1966*	*(Anderson 1967)*
8	*Ithala, R.S.A.*	*2001-2004*	*This study*
9	*Etosha, Namibia*	*1976-1978*	*(Berry 1980)*

Impala males, in contrast, have been observed to be preferentially selected by predators in general in the Timbavati Private Nature Reserve (Hirst 1969), and by lion in particular in both the Kruger National Park (Pienaar 1969) and Kafue National Park (Mitchell et al. 1965). Comparison of the results from this study with areas where lion are present or absent (fig 4.15) suggests that lion do indeed depress the male population; thus the absence of these large predators may help explain the relatively high proportion of males. Impala ASRs were seen (see above) to be lowered by the relatively harsher conditions of winter and 2002 in general; equally the *overall* favourable conditions in the reserve for a highly adaptable mixed feeder like impala (Dasmann and Mossman 1962a, Smithers 1983) may favour the males – Toigo and Galliard (2003) found in ungulates a tendency for the survival of males relative to that of females to increase in good environments. Additionally, vigilance behaviour in impala and wildebeest has been shown to be markedly increased in the presences of predators (Hunter and Skinner 1997). Reduced time spent in vigilance in the absence of predators must translate into energy saving and, as herd size and vigilance behaviour show a negative correlation for both species (op. cit.), this will disproportionately benefit males as bachelor groups are smaller than breeding groups. It seems reasonable that this additional influence of lack of predation will apply to any ungulate that herds, although it is likely that impala will be amongst the most affected due to their superior vigilance behaviour and extreme alertness (Mooring 1999, Power 2002). As an additional point of interest, Pienaar (op. cit.) observed that cheetah preferred female impala (ratio of 2:1) and Brooks (1975) also recorded that cheetah showed a slight but significant (P> 0.05) preference for adult females in Mkuzi Game Reserve. The sex ratio obtained at Ithala does not differ noticeably from areas where cheetah are present but this may reflect in these areas light predation or the suggested preference cheetah have for female impala being masked by other predators. The planned future introduction of cheetah into the reserve (Rushworth pers. comm.) will cause a perturbation enabling verification of this preference, especially since cheetah do well in the absence of other predators (Laurenson 1995), and herbivore populations not exposed to significant predation over as few as several generations appear to loose some of their antipredator behaviour (Blumstein 2002).

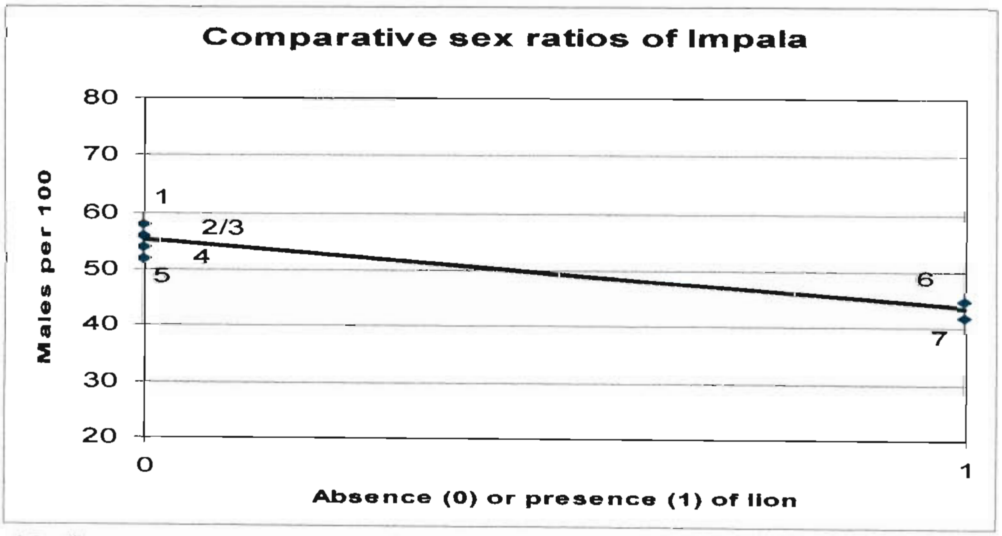


Fig 4.15: Comparative sex ratios of impala ad/yrls in presence or absence of lion.

1	Ithala, R.S.A.	2001-2004	This study
2	Henderson Ranch, Zimbabwe	1959-1960	(Dasmann and Mossman 1962a)
3	Mkuzi, R.S.A.	1970	(Brooks 1975)
4	Hluhluwe, R.S.A.	1961-1962	(Vincent 1972)
5	Mkuzi, R.S.A.	1963	(Brooks 1975)
6	Fort Tuli, Zimbabwe	1959-1960	(Dasmann and Mossman 1962a)
7	Hwange, Zimbabwe	1967	(Anderson 1967)

ble 4.5: Reedbuck, warthog, waterbuck, white rhino and zebra annual adult sex ratios. P value refers to Chi uare Test applied to null hypothesis of parity of adult sex ratios. Significant results P< 0.05.

Species	Year	Adult male : adult female	P value
Reedbuck	2003	67 : 100	0.012
	2004	70 : 100	0.023
Warthog	2003	37 : 100	< 0.001
	2004	49 : 100	< 0.001
Waterbuck	2003	63 : 100	0.037
	2004	55 : 100	0.002
White rhino	2003/2004	80: 100	0.074, NS
Zebra	2003	101 : 100	0.86, NS
	2004	107 : 100	0.4, NS

th species on whom only two years (2003 and 2004) of ASR data is available, formal regressions with rainfall are little meaning. However since 2002 was a comparatively dry year, if males did suffer disproportional mortality in t year, higher ASRs might be expected in 2004 compared to 2003 as the male population returned to more rmal' levels in response to more normal rainfall. No significant change in ASR was seen in either reedbuck (P = 5) or waterbuck (P = 0.57) in 2004 compared to 2003, but in both cases numbers sampled (163 and 115 pectively) were small. Warthog, however, did show a significant rise (P<0.01, n = 448) in ASR in 2004 compared 2003, suggesting that males do suffer more in harsher conditions in this species. Although his sample sizes were all, Mason (1990a) recorded a noticeably lower ASR, compared to subsequent years, amongst warthog following failure of the spring rains at the start of the 1982/83 wet season in the Kruger National Park. Zebra did not show a nificant change (P = 0.45) and in this species larger numbers (576) were sampled. Energetically costly intra-sexual npetition and males decreasing feeding time during the breeding period (Braza et al. 1986, Apollonio et al. 1989, mers et al. 1994, Loison 1995) result in males entering winter with diminished body reserves and are likely to count for differentially higher male mortality (Toigo and Gaillard 2003). Marked competition between male zebra s noticeably absent in Ithala (pers. obs.) and the peaceful manner in which injured, sick or old stallions are usurped been reported (Klingel 1974); additionally zebra in poor condition were, compared to other herbivores, rarely n in the reserve (pers. obs.). These observations may thus explain the apparent absence of both any change in ASR 4 compared to 2003 and any differential male mortality *per se* amongst zebra in Ithala (see below).

nsidering actual ASRs (Table 4.5), warthog ASRs recorded in both Zululand (Mason 1982) and the Kruger tional Park (Mason 1990a) showed a preponderance of females. Actual values varied widely, most probably ause sample size was small, and therefore comparison with this study's results should be treated with caution, ough the ASRs recorded here do fall within the range of Mason's studies. Additionally, results from this study uld themselves be treated with caution as it was assumed that an adult warthog in the presence of juveniles was a ale, whilst single adults were not assumed to be male. Therefore the data may contain a bias towards females. ite rhino ASR is complicated by the species longevity (Owen-Smith 1988b) as a normal range of age classes uld not be expected to exist yet in Ithala given their recent, in terms of their life span, introduction (Owen-Smith s. comm.). However, the degree of bias towards females is comparable to that Owen-Smith (1973) found in nearby hluwe-Umfolozi Game Reserve. Zebra ASRs in the Kruger National Park, although generally showing a female s, were noted to be related to the degree of depredation; high density of predators in the Northern District was ted to a smaller proportion of males compared to the Crocodile Bridge area which has fewer predators (Smuts 76). Smuts (1974) commented 'there can be little doubt that behaviour of an adult stallion renders it more prone to predation than is the case with adult mares'. No significant departure from parity of sex ratios was recorded in er year in this study; this is in contrast to both Smuts (op. cit.) findings and those of Mentis (1970) and of bertson (1993a) in Umfolozi Game Reserve, Zululand which also showed a female bias. Lack of predation, ether with the behavioural and nutritional aspects discussed above, would seem to account for this difference. ormation on ASRs of reedbuck and waterbuck was not found in the literature.

Summary

Rs of different species in Ithala show different responses to environmental conditions, ranging from impala, where Rs are apparently influenced by both rainfall and associated primary production/habitat quality and by levels of dation, to wildebeest, where ASRs are not obviously influenced by either of these factors. This in turn suggests an r-species range for the extent to which underlying life-history traits, as opposed to environmental conditions, ermine ASR

-Primary sex ratios-

To determine primary sex ratios (PSR) of a species in the field, both sufficient numbers of juveniles and easily distinguishable juvenile sexes are required; impala were the only species counted in this study where these criteria applied.

Fisher (1930) showed that natural selection favours those parents who invest equally in both their sons and daughters. Trivers and Willard (1973) later argued that, under certain well defined conditions, natural selection favours deviations away from a 50/50 ratio and that these deviations cancel out in the local breeding population. They hypothesised that mothers in comparatively better condition would gain from a reproductive strategy where they biased the production of their young towards males, whilst those in a comparatively poorer condition would bias production towards females – the underlying reasoning being that the condition of the young tends to correlate with that of the mother during the period of parental investment and male offspring in superior condition are reproductively more successful, due to intra-sexual competition, whilst female offspring tend to reproduce whatever their condition. At the time Trivers and Willard hypothesised that such a bias might be effected by the female adjusting either the birth sex ratio or maternal investment after birth; evidence in ungulates for the former is equivocal at best and, rather, supports the latter (Hewison and Gaillard 1999).

Since, as Trivers and Willard emphasised (Saltz 2001, Hewison et al. 2002, Saltz and Kotler 2003), it is not environmental conditions *per se* which are predicted to influence PSR but rather individual maternal condition *relative* to that of other mothers in the population, in studies such as this where an overall sex ratio of a population is obtained no affect of environmental conditions of PSR would be expected to be detected. However, the Trivers and Willard model requires that a mother be able to assess her condition relative to those mothers around her, so as to 'decide' on her reproductive strategy during that breeding season – if such an ability is accepted as theoretically possible, it seems reasonable to propose additional abilities of mothers to assess other aspects of their local population with regards to parental investment decisions. I propose, all things being equal, it would 'pay' a mother to invest more heavily in daughters if, in the absence of predators differentially reducing the number of males reaching sexual maturity, large numbers of sons were unable to 'have their turn' in establishing territories/having access to reproductive females i.e. were surplus, functionally, to requirements. Such a situation, given the high ASR, may currently exist with impala in Ithala. The window of opportunity for confidently assigning sex to all juveniles seen in the field is small (April); in the months immediately following the Nov/Dec births horn buds in the males, once they appear, are only seen close up (leading to a bias in recorded males as this is the only sex one can, when occasionally close enough, assign) and by May female juveniles, due to their almost equal size, are bracketed with adult/yearling females. However, it is interesting that the juvenile ratio in each year during April was biased (Table 4.6), although not to a significant extent. Combining the four years ratios, albeit it a dubious statistical exercise, gives a juvenile male: female ratio of 101:126 (departure from parity significance: P=0.1). If such a mechanism does exist, it would presumably be effected via an endocrinal response in the female related to excessive adult male territorial aggression/density. Equally, however, all things may not be equal in that the increased number of males due to lack of lion predation may have translated into stronger competition amongst the sexually mature males leading to a faster turnover of territories/smaller territories; in such a case the mother would need to continue to produce her crop of sons to enter into this increased competition and would not gain from switching to more daughters. Although territory size appears to decrease with increasing overall population density (Estes 1997), there appears to be no analysis in the literature of territory size/time held in specific relation to concentration of adult males.

Table 4.6: Juvenile sex ratios for impala in April. Significance refers to the departure from parity.

Year	Male juveniles	Female juveniles	Significance
2001	18	25	P=0.29
2002	47	56	P=0.38
2003	14	20	P=0.3
2004	22	25	P=0.67

Sexual segregation

Three hypotheses are generally discussed in the literature (Main et al. 1996, Conradt 1997, Gross 1998, Main 1998, Ruckstuhl and Neuhaus 2002) to try and explain sexual segregation; the forage-selection hypothesis suggests that females will select habitat based on food quality, while males should prefer high forage biomass, the predator-risk (or reproductive-strategy) hypothesis suggests that females will use relatively predator-safe habitats, while males are predicted to use habitats with higher predation risk but better food quality and the activity budget hypothesis suggests that with increasing dimorphism in body size males and females will increasingly differ in the time spent in different activities.

The scramble competition hypothesis was forwarded as a variation of the forage-selection hypothesis and implies that females graze the vegetation in high-quality forage habitats too low for males to be able to obtain sufficient forage intake rates in these habitats, and males are thus forced by indirect female competition into marginal habitats with lower forage quality but higher forage biomass (Clutton-Brock et al. 1982, Clutton-Brock et al. 1987).This 'indirect-competition' hypothesis effectively extends Jarman's (1974) and Bell's (1971) argument for explaining inter-specific competition between different sized herbivore species to intra-specific competition between different sized sexes of a species. However, removal of females on the Isle of Rum did not result in males increasing their use of preferred habitat as predicted by the hypothesis (Conradt et al. 1999), leading researchers to conclude that sex differences in body size within a species are, in spite of theoretical considerations (Illius and Gordon 1992), not large enough for the Jarman-Bell principle to apply and, consequently, the hypothesis was rejected. In a general revue of the literature on sexual segregation Main *et al* (op. cit.) concluded that most evidence supported the reproductive-strategy hypothesis, whilst in a later and more rigorous review Ruckstuhl and Neuhaus (2002) showed that there is considerably more evidence supporting the activity budget hypothesis – in fact out of 23 studies, in 22 the predictions of the hypothesis were confirmed.

Earlier studies often did not make clear whether they were discussing habitat segregation or social segregation or both, leading to confusion in the literature over the definition of sexual segregation (Main et al., op. cit.), with some studies discussing habitat segregation between the sexes (Tierson et al. 1985) whilst others discuss sexual segregation in terms of separation between sexes occupying the same habitat/area (McCullough et al. 1989). It is important that the type of sexual segregation being discussed is defined. Further confusion occurs over the near avoidance of the role of territoriality. This may be because most studies on sexual segregation have been done in northern temperate regions (Clutton-Brock et al. 1987, Main and Coblentz 1990, Miquelle et al. 1992, Bleich 1993) where territoriality is confined to a short, pronounced rut – sexual segregation occurring outside of the rut is thus not related to territoriality. This is not the case with certain ungulates in southern Africa – wildebeest maintain territories all year round except in the depths of winter (Attwell 1977), whilst zebra, although not defending an actual territory, vigorously repel other adult males from their harems all year round (Smuts 1974, 1976). In such cases clearly the behaviour of the dominant male keeps the bachelor groups separate from the breeding herds and is the immediate cause of sexual segregation, whether with concomitant habitat segregation (wildebeest) or without (zebra). However, once territoriality stops, it is the persistence of sexual segregation, as also occurs in the northern hemisphere cervids, which is the interesting puzzle. In Ithala, wildebeest and impala bachelor groups in the absence of territoriality (i.e. mid-winter for wildebeest, outside of the pre-rut and rut for impala) did not show any habitat segregation (Chapter 2) but maintained social separation from the breeding herds (Figs 4.9c and 4.16). Frequently the two groups, although clearly separate, were seen in close proximity (pers. obs.) – thus dispelling any fears that the lack of habitat segregation was an illusion due to insufficient resolution consequent on the scale used to determine habitat selection (Main et al. 1996). Of the three hypotheses outlined above, only the activity budget hypothesis allows for sexual segregation without concomitant habitat/area segregation and is thus the only one which could explain these patterns of association/segregation.

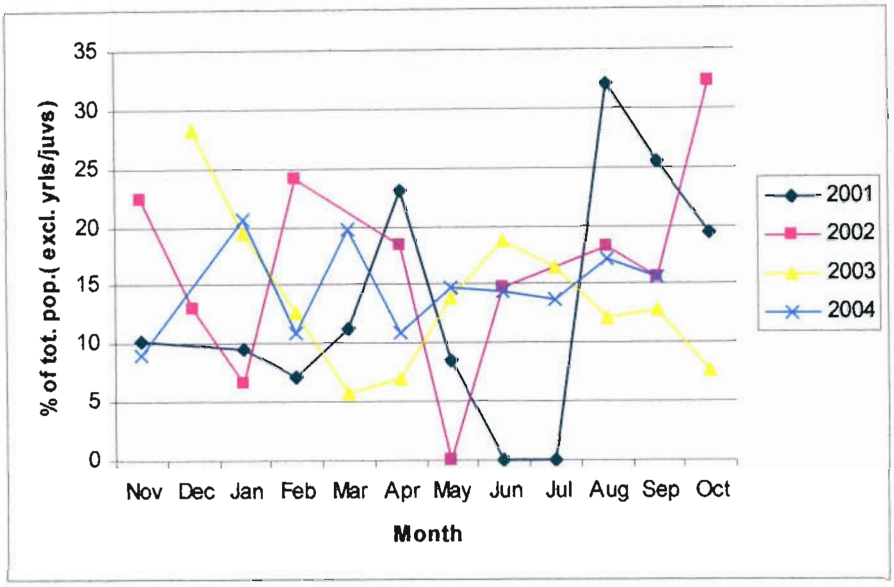


Fig 4.16: Wildebeest, bachelor herds as a percentage of total population (excluding yearlings and juveniles), by month 2001 to 2004.

Kudu do not show territoriality at all (Owen-Smith 1984a, b, Perrin 1999) but do show habitat segregation between the sexes over the calving and postnatal period (du Toit 1995) – du Toit argues that this results from females occupying habitats where their calves are less at risk from predation i.e. an example of a reproductive-strategy causing habitat segregation. In winter male and female kudu live in the same habitat (du Toit, op. cit.) but still remain, compared to the rut, physically apart (Perrin, op. cit.). Warthog do not show territoriality either and both sexes occupy the same habitat throughout the year but are separated except when sows are in oestrous (Estes 1997). Again, in such circumstances were sexual segregation exists without habitat segregation, only the activity-budget hypothesis offers an explanation. Thus although the immediate cause of habitat segregation between the sexes varies according to different strategies adopted by different species (territorial dominance by bulls in wildebeest and impala, selection of habitat with lower predation risk by kudu mothers), once these no longer apply and the sexes live in the same habitat, sexual social segregation appears to be maintained by differences in activity budgets.

An attraction of the activity budget hypothesis is that, whilst the functional advantage for dominant bulls of excluding bachelors (wildebeest/zebra/impala) or for kudu cows with calves avoiding predation is clear, it provides a convincing functional explanation for the persistence of bachelor groups even when bachelors are not forced to remain as such – namely that differences in activity budgets would increase the costs of synchrony necessary to maintain group cohesion in a mixed sex group. Main *et al* (op. cit.) observe that the universal nature of sexual segregation among polygnous ungulates suggests this behaviour is the product of selective pressures from a similar evolutionary background and, moreover, that it would be more profitable to understand sexual segregation in terms of selective pressures that influence reproductive success across taxa, rather than to concentrate solely on separate species- or site-specific explanations. The success of the activity-budget hypothesis in explaining the empirical data from different species adopting different reproductive strategies, suggests it is the underlying mechanism at work.

Du Toit (op. cit.) comments that support for his suggestion that seasonal habitat segregation between the sexes in kudu relates to predation, would come from an experiment where predators were removed - if sexual habitat segregation eventually disappeared this would support the hypothesis. Although the pre-removal phase has never existed in Ithala, the virtual absence of predation since the reserves formation approximates to the conditions of this suggested experiment. Interestingly, females were not seen (Chapter 2) to select the more open habitats in the wet season but preferred the more closed habitats that the males also selected, lending support to his predation risk hypothesis. Sexes were, however, seen to retain their physical separation (Fig 4.8a) outside of the rut as per other reserves. Blumstein (2002) discusses antipredator behaviour and its retention/loss overtime in the absence of predation, observing that economic thinking tells us to expect that costly antipredator behaviour should be lost if it is no longer beneficial. He observed that visual predator recognition is strongly retained despite no exposure to predators but that other behaviours (e.g. flight distance) are less 'hard wired' and are reduced over time in the absence of predators. Females choosing a habitat more suited to predation risk appears to be an example of a behavioural pattern rapidly lost without exposure to predation – this is logical since its continuance, given that it places the females and her calf in a habitat less nutritious for a browser, carry considerable disadvantages. It would also be in accordance with various correlation studies (Greenwood 1980, Switzer 1995, 1997) that have shown that an individual's past reproductive success often increases its breeding site fidelity (i.e. the tendency to return to a previously occupied location), suggesting that individuals use their reproductive experience to assess habitat quality.

Assessment of technique

Ultimately, assessment rests on whether the results are compatible with others findings, make biological sense and variations can reasonably be explained by established/likely ecological processes. Broadly, as discussed in depth above, this was the case. Additionally data may be cumulatively plotted against number of observations (Appendix 11). Once such a graph has levelled out and is consistent this implies the underlying value in the field has been determined (Goodman 1980); an indication of the number of observations, and hence hours in the field, required to reach that situation is also provided. In the case of adult sex ratios, hours required in the field (Table 4.7) were, not surprisingly, related to species density and ease of sighting and were similar to those required in nearby Mkuzi Game Reserve by Goodman (op. cit.).

Table 4.7 Sampling of adult (+-yearling) sex ratios. The number of observations, and corresponding hours in the field, for plots of sex ratios against number of observations to level out (see text) are given.

Species	No. of observations	Hours in the field
Giraffe	150	210
Kudu	140	190
Reedbuck	100	265
Waterbuck	50	285
Warthog	150	75
White rhino	35	135
Wildebeest	140	60
Zebra	150	60
Impala	150	60

Summary

A wide range of demographic data was obtained and analysed. Differences in ease of sighting, sexing and ageing between the large herbivore species, together with wide variations in their prevalence, lead to inter-species differences in demographics analysed.

Environmental factors influencing species demographics were habitat quality, competition and predation. Inter- and intra-species variations in how these fundamental environmental determinants affected demographics were reflections of varying life-history traits.

Rainfall, via its effect on habitat quality, was, unsurprisingly, of paramount importance. The seasonal cycle of a wet and then dry season affected juvenile mortality (which increased as drier conditions prevailed), wildebeest territoriality (which waxed and waned in relation to rainfall), group size (which decreased for most species in the dry season) and impala adult sex ratios (where male mortality differentially increased in the dry season). Rainfall also influences the timing of the breeding cycle which, in itself, affects demographics as seen by the links between herd composition and the rut and calving. The affect of inter-annual variations in rainfall highlighted differences in diet between species. During the study period only one year (2002) had noticeably less rainfall and wildebeest, the only pure grazer studied over the full four years, were the only species noticeably affected (showing reduced fecundity and increased juvenile mortality). Browsers (giraffe and kudu) and mixed feeders (impala) were not similarly affected. Interestingly, however, wildebeest did not show any response in terms of annual rainfall affecting adult sex ratios whilst, to varying extents, giraffe, kudu and impala showed male mortality increasing in relation to lower rainfall.

Habitat quality is not only determined by rainfall. The inter-play between density of animals utilising a habitat and the nature of that habitat also affects its quality. Uniquely within the reserve, giraffe are alien species and consequently appear unable to achieve a balanced co-existence with a large portion of the reserves browse. This, combined with their high density, has resulted in degradation of their food source to an extent whereby they are showing abnormally low fecundity related demographics virtually irrespective of annual rainfall variation. The high density of wildebeest, by putting excessive pressure on the grasslands, may be the cause of the atypical increase seen in their (and other's) group size in the dry season and of tsessebe's generally low fecundity.

As high density results in increased competition for food, there is clearly a link, which is partially one of semantics, between density and competition and how they affect habitat quality. Competition for another resource, females, also affected demographics. Territorial behaviour, virtually year round by wildebeest bulls and over the rut by impala bulls, imposed spatial sexual segregation between breeding and bachelor herds in these species. Outside of these periods, and generally in species not exhibiting territoriality, social sexual segregation was maintained and appeared to relate to differing activity budgets – in themselves examples of intra-specific competition for forage.

Very low levels of predation in the reserve appeared to result in giraffe, zebra and impala adult sex ratios being comparatively less biased towards females; contrastingly, wildebeest adult sex ratios seemed unaffected by predation. More subtle affects suggested included altered impala primary sex ratios and affects on upper group size. The most obvious likely affects of lack of predation, namely reduced mortality especially amongst juveniles, could not be assessed due to a lack of data from other similar reserves for comparison.

Where comparisons could be drawn with other reserves, differences were explained in terms of variations in habitat quality, competition and predation.

Findings may thus be summarised:

1) Giraffe and tsessebe fecundity-related demographics were persistently low.
2) Wildebeest showed lower fecundity-related demographics in response to lower rainfall; rainfall over the period of early lactation seemed most important.
3) Other herbivores' fecundity-related demographics were normal during the study period; taken with the above findings, this suggested a range of resource limitation amongst the reserves' herbivores.
4) Wildebeest juvenile mid-winter mortality increased over the driest and coldest winter; this was not seen with impala.
5) Impala juvenile early-winter mortality increased over unseasonably cold weather; this was not seen with wildebeest.
6) Wildebeest territorial bulls, whose numbers peaked over the rut, were seen to abandon their territories in the depths of winter and re-occupy them soon after the return of the rains.
7) Herbivores which have an open social structure showed a change in seasonal group size. Compared to the wet season, average dry season group size was lower, except with wildebeest and hartebeest who showed increased average dry season group size. Herbivores with a closed social structure showed no change, except kudu and zebra who showed a decrease in average dry season group size.
8) Wildebeest yearlings were expelled from breeding herds at ~ 24 months of age in relation to calving at that time; impala yearlings at ~ 18 months of age in relation to the rut.
9) Giraffe, kudu, warthog and impala showed, to varying degrees, increased adult male mortality in response to harsher conditions.
10) Giraffe, zebra and impala adult sex ratios were comparatively less biased towards females, most probably as a result of minimal predation. Wildebeest adult sex ratios were not, suggesting predation is not relevant.
11) There was a suggestion of impala primary sex ratios being biased towards females – this might relate to the excess of adult males.
12) Territorial behaviour by wildebeest and impala bulls imposed sexual spatial segregation, but in the absence of this proximal cause sexual social segregation remained. The absence of sexual spatial segregation in kudu in the reserve may relate to minimal predation.

Implications for conservation management are as follows:

1) Giraffe and tsessebe are breeding at an abnormally low rate.
2) An isolated year of lower rainfall is likely to negatively affect only grazers.
3) Wildebeest juvenile mortality is particularly sensitive to rainfall during early lactation.
4) Giraffe, zebra and impala adult sex ratios are excessively biased towards males. This should be born in mind and corrected, over time, when planning game removals (live and dead).

CHAPTER FIVE

SUMMARY

Habitat occupancies, numbers and demographics for most of Ithala Game Reserve's large mammalian herbivores were determined.

Statistically significant selections, both positive and negative, for a range of habitat types by herbivores were shown. Species preferences generally corresponded to well established patterns, namely browsers occupied habitats plentiful in browse, grazers occupied the grasslands and mixed feeders selected both types of habitat. Differences in habitat selection between social groups were also shown, principally between bachelor and breeding groups in wildebeest and impala.

Statistically significant changes in habitat selection between wet and dry season were demonstrated. In response to deteriorating habitat quality in the dry season animals, in general, showed movement down-slope and into the water-courses, with movement onto heavier, nutrient rich soils being demonstrated in some species (giraffe, wildebeest and possibly impala). Changes in species' range between seasons were also apparent. The extent and nature of these changes appeared to correlate with the species dependence on quality versus quantity of forage during times of resource limitation. Thus non-ruminants (zebra) showed a broadening of both habitat types and the total range occupied, ruminant browsers (kudu) showed an unchanged dispersion, whilst ruminant grazers (hartebeest, tsessebe, reedbuck and wildebeest) showed markedly increased selectivity, mainly in the total range occupied. These findings are in general agreement with current models of optimal foraging for ungulates. Exceptions to these trends were explained by species behavioural (warthog), digestive (white rhino) or situational idiosyncrasies (giraffe).

Certain species (hartebeest, warthog, wildebeest and impala) were strongly attracted to grass flushes following winter burning. Surface water in itself did not, due to the extensive network of rivers and streams available throughout the year in the reserve, influence species' habitat occupancy.

Inter-specific resource competition and the lack of predation possibly accounted for non-seasonal details of habitat occupancy. Thus the high density of wildebeest may be restricting habitat available both to other grazers (hartebeest, tsessebe and white rhino), resulting in these species having an unusually restricted range, and to impala, resulting in their unexpected under-utilisation of grasslands. Impala's year round attraction to browse habitats may be related to very low levels of predation and may in turn be depriving wildebeest of grazing in closer habitats. Lack of predation may also account for atypical habitat selection by giraffe and kudu breeding groups.

Replicated road strip counts described in this study produced cost effective, acceptable estimates of population numbers for most of the larger herbivores in Ithala Game Reserve. In most cases these appeared to be more accurate than those provided by aerial counts. Consequently both the level of stratification, as defined by the routes covered and the range of habitats defined, and the level of replication, being six counts in both the wet and dry seasons, were appropriate, both for numbers estimation and determination of habitat occupancies. This GIS based technique is relevant to other reserves with similar topographical problems, its ease of application depending on the range of GIS data currently available. Estimates for reedbuck, warthog and waterbuck were less satisfactory, primarily due to the level of stratification being inappropriate for these species.

Most species populations are stable or increasing, with the exception of giraffe and tsessebe which appear to be in decline. The high effective density of giraffe and their alien nature to the reserve's vegetation appear to be putting them under marked resource limitation. Tsessebe's decline may relate to the high density of wildebeest in the reserve, possibly depriving tsessebe of forage both generally and in terms of 'sward capture', and/or to recent drier conditions. Giraffe, wildebeest and zebra high densities are most probably due to negligible predation.

Persistently low fecundity-related demographics were seen with giraffe and tsessebe, probably due to year-round low quantity and/or quality of forage available to these species. Wildebeest, the only ruminant grazer at unusually high density, showed reduced fecundity in response to the one drier year; particularly in relation to early post-natal rainfall. Other species showed more normal fecundity-related demographics.

Seasonal variation in habitat quality was seen to influence wildebeest bulls' territoriality, with bulls abandoning some territories in the depths of winter, and herbivores' group size, with wildebeest and hartebeest showing an atypical increase in group size in the dry season. The influences of the breeding cycle, itself linked to habitat quality, were seen with the peaking of territory establishment by wildebeest and impala over the rut, and with the expulsion of yearling wildebeest and impala from breeding herds in relation to calving and the rut respectively.

Giraffe, zebra and impala adult sex ratios were comparatively more biased towards males, most probably as a result of minimal predation. Wildebeest adult sex ratios were not, suggesting predation is not relevant to differential mortality in this species. Territorial behaviour by wildebeest and impala bulls imposed sexual spatial segregation, but in the absence of this proximal cause sexual social segregation was seen to remain.

Animals' choice of habitat, their numbers and demographics are seen to be influenced by the inter-related factors of habitat quality, competition and lack of predation. The varying degrees to which these environmental determinants affect one species compared to another, and sub-groups within a species, are reflections of differing evolutionary histories and consequent present-day strategies. The effects of habitat quality are generally marked – whether where quality is persistently poor for a species (e.g. giraffe's marked reduction in area selectivity in the dry season, declining numbers and low fecundity), where it is temporarily, but at a critical juncture, poor (e.g. wildebeest's reduced fecundity in response to failure of early spring rains), where it is temporarily but uniformly attractive for a guild of herbivores (e.g. dry season grass flushes) or where generalised seasonal changes occur (e.g. dry season moves down the slope, group size changes). More subtle changes are also seen, such as differing inter-sexual adult mortality and inter-species juvenile survival in response to harsher conditions. Generally less obvious are the possible influences of competition and predation. Via inter-specific resource competition, the high density of wildebeest may be instrumental in tsessebe's declining numbers and low fecundity, other grazers' restricted year round (hartebeest and tsessebe) or dry season (white rhino) range and impala's summer under-utilisation of the grasslands. Intra-specific competition amongst the numerous wildebeest may account for their dry season increase in group size and decrease in area used. Another aspect of intra-specific competition, male dominance, whether territorial (e.g. wildebeest and impala) or harem based (e.g. zebra), also affects habitat selection (sexual spatial segregation) and/or demographics (sexual social segregation). Lack of predation appears to be instrumental in habitat selection decisions (impala and giraffe and kudu females), in abnormally high densities (giraffe, wildebeest and zebra), and in reduced differential adult male mortality (giraffe, zebra and impala).

Where differences in habitat occupancy, densities or demographics existed between the findings in this study compared to other localities, these were explained in terms of these fundamental environmental determinants of habitat quality, competition and predation.

Findings of the study may be summarised:

1) G.I.S.-based ground count method produced acceptable population estimates and, consequently, realistic habitat occupancy data for the reserve's giraffe, kudu, hartebeest, tsessebe, white rhino, wildebeest, zebra and impala. Sampling frequency required in Ithala equates to ~ 150 man hours and 1,600Kms driven per year. The technique is applicable to other similar reserves.
2) Gross vegetative selection by herbivores was broadly in keeping with their established preferences, with browsers concentrating in open and closed woodlands and grazers on grasslands.
3) Deterioration in habitat quality in the winter, consequent on lower rainfall, generally led to changes in habitat selection. The extent and nature of these changes appeared to correlate with the species dependence on quality versus quantity of forage during times of resource limitation.
4) Generally species showed a move down-slope in the dry season moving, in some cases, onto heavier soils.
5) Surface water did not directly influence herbivore distribution.
6) Hartebeest, warthog, wildebeest and impala were strongly attracted, zebra less so, to grass flushes following winter burning.
7) Giraffe (~1.8 km^{-2}), wildebeest (~6.0 km^{-2}) and zebra (~5.6 km^{-2}) densities are high compared to other reserves, probably due to minimal predation.
8) Giraffe showed marked reduction in area selectivity in the dry season, declining numbers and persistently low fecundity-related demographics, all implying marked resource limitation. This is likely to be due to their detrimental effect on the upper browse and their high density.
9) Tsessebe numbers also appear to be in decline and their fecundity-related demographics were persistently low. This may relate to the high density of wildebeest in the reserve and/or drier conditions.

10) The high density of wildebeest, via inter-specific resource competition, may be having an adverse effect on other grazers, principally tsessebe, hartebeest and white rhino. It may also be instrumental in the unexpected under-utilisation of the grasslands by impala in summer; by the same mechanism impala may be depriving wildebeest of grazing in closer habitats.
11) Wildebeest showed lower fecundity-related demographics in response to lower rainfall; rainfall over the period of early lactation seemed most important.
12) Other herbivores' fecundity-related demographics were normal during the study period; taken with the contrasting findings above, this suggested a range of resource limitation amongst the reserves' herbivores.
13) Wildebeest territorial bulls, whose numbers peaked over the rut, were seen to abandon their territories in the depths of winter and re-occupy them soon after the return of the rains.
14) Herbivores which have an open social structure showed seasonal change in group size. Average dry season group size was smaller, except with wildebeest and hartebeest where group size unexpectedly increased. Herbivores with a closed social structure generally showed no change.
15) Wildebeest yearlings were expelled from breeding herds at ~ 24 months of age in relation to calving at that time; impala yearlings at ~ 18 months of age in relation to the rut.
16) Lack of predation in the reserve may also be contributing to impala's year round attraction to closer, browse habitats and additionally may be affecting giraffe and kudu breeding herds' habitat choice.
17) Giraffe, zebra and impala adult sex ratios were comparatively less biased towards females, most probably as a result of minimal predation. Wildebeest adult sex ratios were not, suggesting predation is not relevant.
18) Territorial behaviour by wildebeest and impala bulls imposed sexual spatial segregation, but in the absence of this proximal cause sexual social segregation remained. The absence of sexual spatial segregation in kudu in the reserve may relate to minimal predation.

The GIS based technique utilised in this project, as well as producing satisfactory results here, is easily replicated by relatively untrained reserve staff. All that is required is that the individual follow the routes as described, at a similar rate and record which vegetation (a skill rapidly learnt) a sighting occurs in. As the areas being sampled have been determined, densities within each vegetation type (providing habitat occupancy data), and from that absolute population numbers, are easily obtained. A less satisfactory aspect of the project related to the question of scale in the GIS layers. The primary layer for comparison with herbivore spatial data, the vegetation layer, was generally not detailed enough and, as a result, only very general deductions could be made about habitat preferences. A GIS layer containing a lot more detail on vegetation type and structure would have revealed nuances of herbivores' preferences, which are likely to be of relevance to the ecosystem. At the other end of the scale, soil types vary over such short distances (Fig 1.4) that, combined with some inevitable inaccuracy in determining an herbivore's position, over-lay operations in the GIS are likely to produce inaccuracies. This may explain why, despite a sizeable workload, analysis of soil types produced expected results in only a few species. The successful application of GIS to analysing ecological spatial data therefore depends on employing layers of appropriate, and compatible, scale. Another criticism of the study is that it was trying to cover too broad a subject, despite the three main themes being closely inter-related. This inevitably led to certain areas of the study (e.g. group size, distance to water) being covered too superficially.

Although four years of demographic data provided a reasonable sample size, another wet and dry season's worth of positional data would have added authority to the habitat occupancy and numbers results and their interpretation. The poor performance of the tsessebe population indicates an area for further research, possibly using the causes suggested by this study as a starting point. The possible effects of wildebeest's high density on the reserve's ecosystem also warrant further investigation. A more detailed investigation of the implications of long term minimal predation, both for Ithala and reserves in general, would be of relevance to conservation. This would especially be the case in the context of South Africa, where a considerable proportion of game reserves are too small to carry significant numbers of predators. Additionally, should predators ever be re-introduced into Ithala, this would provide the opportunity of studying the effects of such a perturbation.

The relevance of the findings of this study and their implications for conservation management may be summarised:

1) A vehicle based method for determining animals' numbers, demographics and habitat choices has been described, assessed and found to be cost effective for most of the reserves' large herbivores. The technique should be applicable to other reserves, with similarly diverse topography, where current techniques (e.g. aerial survey, *Distance*) are inappropriate.
2) Habitat occupancies, numbers and demographics of most of the reserves larger mammals have been determined.
3) Some species have attained abnormal densities, probably due to negligible predation.
4) Giraffe densities are abnormally high, their numbers are declining and their fecundity is abnormally low; findings complimenting previous work which concluded they were destroying the upper browse. Their continuing alien presence in such high densities may be expected to impinge on lower browse, and hence black rhino, at some point.
5) Wildebeest densities are also abnormally high and, although the species itself does not appear to be suffering any significant consequences at present, they may be having a detrimental effect on other grazers including the rare tsessebe and white rhino.
6) Tsessebe numbers are in decline and their fecundity is abnormally low.
7) An isolated year of lower rainfall is likely to negatively affect only grazers.
8) Giraffe, zebra and impala adult populations are comparatively less biased towards females, most probably because of negligible predation. This highlights the need in such reserves of removing animals in a ratio of sexes which simulates the effect of predation, thus retaining natural adult sex ratios in the population.
9) Any future introduction of predators would be expected to affect herbivores' habitat preferences. Leopard in particular, as they hunt in closed habitats, would

be expected to shift impala preferences out into the grasslands thus putting further pressure on this resource.

10) The importance of grass flushes in mid-winter to hartebeest, warthog, wildebeest and impala is shown. Successful sprouting of the grass does, however, require rain to fall relatively shortly after the burning and therefore, since winter rainfall in the reserve is sporadic and unpredictable, burning should be spread over the winter and not bunched at the end, otherwise flushes will be absent during those months were grazing is at its poorest (as occurred in 2004).
11) The winter move down the slope, shown by most species, highlights the need for topographical variety to provide such areas of reserve forage in an enclosed park.
12) Various more minor aspects of how species are differentially affected by weather patterns (e.g. wildebeest versus impala mid-winter juvenile mortality in response to dry and cold conditions) have been highlighted; such effects would be expected to be modified by intra- and inter-species' densities.

The following specific recommendations are made to management:

1) Stop the aerial census of herbivores.
2) Implement, using the vehicle based GIS technique described in this study, a regular annual census of herbivore numbers; this will concomitantly provide habitat occupancy data. Which, if any, demographic data is collected may, as this imposes a further burden on resources, be tailored to the situation (e.g. re-determination of giraffe, zebra and impala adult sex ratios would be desirable after a few years of male biased removals).
3) Considerably reduce the numbers of giraffe in the reserve.
4) Reduce the numbers of wildebeest in the reserve.
5) In general, when removing giraffe, zebra and impala, remove a greater proportion of males than females to realistically simulate predation. Specifically, a programme should be implemented to gradually bring the currently abnormal adult sex ratios pertaining in these species, back to values recorded in reserves with the full suite of predators.
6) Ensure winter burning is effective in providing grass flushes by spreading it over the winter months.
7) Record rainfall, minimum and maximum temperatures in the reserve on a reliable, daily basis.

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Appendices:

Appendix 1: Vegetation structure

Physiognomy of woody species was based on the following criteria from Kotze (op. cit.)

Continuous	Tree layer of touching or interlocking crowns.
Closed	Tree layer with crowns < one diameter apart or touching.
Open	Trees spaced > one crown diameter apart (not > five crown diameters apart).
Sparse	Discontinuous tree layer, individuals spaced > five crown diameters apart.

Appendix 2: Field trip dates.

Field trip no.	Start date	End Date	Number of days
1	15 January 2001	18 January 2001	4
2	20 February	23 February	4
3	6 March	9 March	4
4	23 April	26 April	4
5	29 May	1 June	4
6	30 July	2 August	4
7	20 August	23 August	4
8	17 September	20 September	4
9	8 October	11 October	4
10	13 November	16 November	4
11	10 December	13 December	4
12	14 January 2002	17 January 2002	4
13	11 February	14 February	4
14	25 February	28 February	4
15	8 April	11 April	4
16	1 May	4 May	4
17	17 June	20 June	4
18	5 August	8 August	4
19	2 September	5 September	4
20	28 October	31 October	4
21	2 December	5 December	4
22	6 January 2003	9 January 2003	4
23	3 February	6 February	4
24	3 March	6 March	4
25	14 April	17 April	4
26	12 May	15 May	4
27	2 June	5 June	4
28	30 June	3 July	4
29	21 July	24 July	4
30	25 August	28 August	4
31	15 September	18 September	4
32	13 October	16 October	4
33	10 November	13 November	4
34	24 November	28 November	5
35	5 January 2004	8 January 2004	4
36	16 February	19 February	4
37	1 March	3 March	3
38	29 March	1 April	4
39	26 April	29 April	4
40	24 May	27 May	4
41	21 June	24 June	4
42	19 July	22 July	4
43	2 August	5 August	4
44	20 September	23 September	4

Appendix 3: Field data sheet

Spp=species, W.P.= waypoint, Act=activity, We=weather, Tp=temperature, Wi=wind, Hb=habitat (=vegetation type), Fl=flush, Rt=route.

Date	Spp.	W.P.	Bear.	Dist.	Total	Male					Female					Unclassified					Act 1	Act 2	Act 3	We.	Tp.	Wi.	Hb.	Fl.	Rt.	G.P.S.
						Ad.	SA	Yrl.	Juv	Unc	Ad	SA	Yrl.	Juv	Unc	Ad	SA	Yrl.	Juv	Unc										

Appendix 4: Soil characteristics (produced by Prof. Hughes, University of KZN).

CLASS_NAME
Ag Augrabies - essentially a calcareous Oakleaf on lower footslopes. High base status. Moderate WHC
Alluvium - variable depending on source material
Ar Arcadia - heavy black clay; high base status and high WHC; smectitic
Av Avalon - moderately clayey soil with soft plinthite (intermittent wetness) at depth; lower slope soil
Bd Bloemdal - essentially a Hutton (often on colluvial material) that is periodically wet at depth)
Bo Bonheim - heavy black clay soil; rich in smectite (if Arcadia is a 5 then this is a 4)
Bv Bainsvlei - essentially a Hutton with intermittent wetness (shown by soft plinthic material) at depth
Cf Cartref - light sandy, washed out soil; low WHC and low base status
Cf/Vf 60/40 - see individual soil forms
Cg Coega - very shallow soil over calcrete; high base status; low WHC (due to depth)
Ch Champagne - organic (peat-type) soil in vleis
Cliffs & Scree - self explanatory - no soil!
Ct Constantia - light, sandy soil with sometimes increasing clay with depth; if Cartref is a 1 then this would be a 1.5
Cv Clovelly - depends on parent material, position and age
Cv/Gs 40/60 - see individual soil forms
Dr Dresden - very shallow soil; just a topsoil on hard plinthite
Du Dundee - variable dependent on source of alluvium
Du/Sn - see individual soil forms. Steendal (Sn) has a black topsoil with high base status and WHC over a calcareous subsoil; often not very deep
E Erosion - self explanatory - no soil
Es Estcourt - sodic soil often; duplex soil - sandy topsoil over a very heavy sodic clay subsoil; lower footslopes often on shales
Fw Fernwood - light very sandy soil' very low base status and WHC
Gf Griffin - depends on parent material, position and age
Gs Glenrosa - young soil on steepish slopes; often shallow (essentially a partially weathered

CLASS_NAME
Mispah)
Gs/Cv/Bo 70/25/5 - see individual soil forms
Gs/Hu 70/30 - see individual soil forms
Gs/Hu 80/20 - see individual soil forms
Gs/Ms 60/40 - see individual soil forms
Gs/Ms 65/35 - see individual soil forms
Gs/Ms 70/30 - see individual soil forms
Gs/Ms 80/20 - see individual soil forms
Gs/Ms + Ms/Gs - see individual soil forms
Gs/R 40/60 - see individual soil forms
Gs/R 50/50 - see individual soil forms
Hu Hutton - depends on parent material, position and age
Hu/Gs - see individual soil forms
Hu/R 70/30 - see individual soil forms
Hu/Sd - see individual soil forms
Ik Inhoek - black, often quite clay-rich and base rich soil; moderate WHC
Ka Katspruit - valley bottom, wet soil
Kd Kroonstadt - valley bottom wet soil; often sandier near surface than Katspruit
Ky Kimberley - essentially a Hutton underlain by calcareous rich subsoil
Lo Longlands - holds water at depth (soft plinthite) but often coarser textured near surface; lower slope soil commonly
Ms Mispah - very shallow soil on steep slopes
Ms/Gs 60/40 - see individual soil forms
Ms/Gs 70/30 - see individual soil forms
Ms/Hu 40/60 - see individual soil forms
Ms/R - see individual soil forms
Ms/R 20/80 - see individual soil forms
Ms/R 25/75 - see individual soil forms

CLASS_NAME
Mw Milkwood - essentially a blacker, more heavy textured version of Mispah with higher base status and WHC
My Mayo - blacker, more heavy textured version of Glenrosa with higher base status and WHC
Nb Namib - light very sandy soil, very low base status and very low WHC
Ns Not surveyed - self explanatory
Oa Oakleaf - variable; often moderately clayey with moderate base status and WHC
Oa/Va 60/40 - see individual soil forms
Oa/Va/Du 50/25/25 - see individual soil forms
R Rock - self explanatory
R/80% - presumably mostly rock
Red Gs - as for Glenrosa - just a colour distinction
Red Oa - as for Oakleaf - just a colour distinction
Rg Rensburg - black, heavy clay soil; wet at depth; smectitic; very high base status and WHC; valley bottom soil
Shu - don't know what this is - ?shallow Hutton?
Sd Shortlands - red, moderate to high base status and WHC; moderate to high clay content; normally on base-rich rocks in a semi-arid climate
Se Sepane - valley bottom soil, clay-rich; wet at depth; often quite high base status and WHC
Se/Sw/Mw - see individual soil forms
Ss Sterkspruit - duplex soil; may be sodic or saline; very strong subsoil structure; high subsoil clay content; often on lower slopes over shale
Sw Swartland - shallow upslope soil often on convex slopes; clay-rich subsoil (often thin); base-rich; lowish WHC due to depth
Tu Tukulu - essentially an Oakleaf that is wet at depth
Va Valsrivier - essentially a Sepane that is dry throughout the profile
Vf Vilafontes - generally sandy soil with some increase in clay (and therefore base status and WHC) with depth
We Westleigh - shallow soil on lower slopes; soft plinthite (intermittent wetness) near to surface

Appendix 5: Photographs referred to in the text.

Plate 1: Showing lone territorial wildebeest bull associating with tsessebe herd.

Plate 2: Showing high browse line typical of Ithala Game Reserve.

Plate 3: Showing giraffe browsing on small bushes in open grasslands.

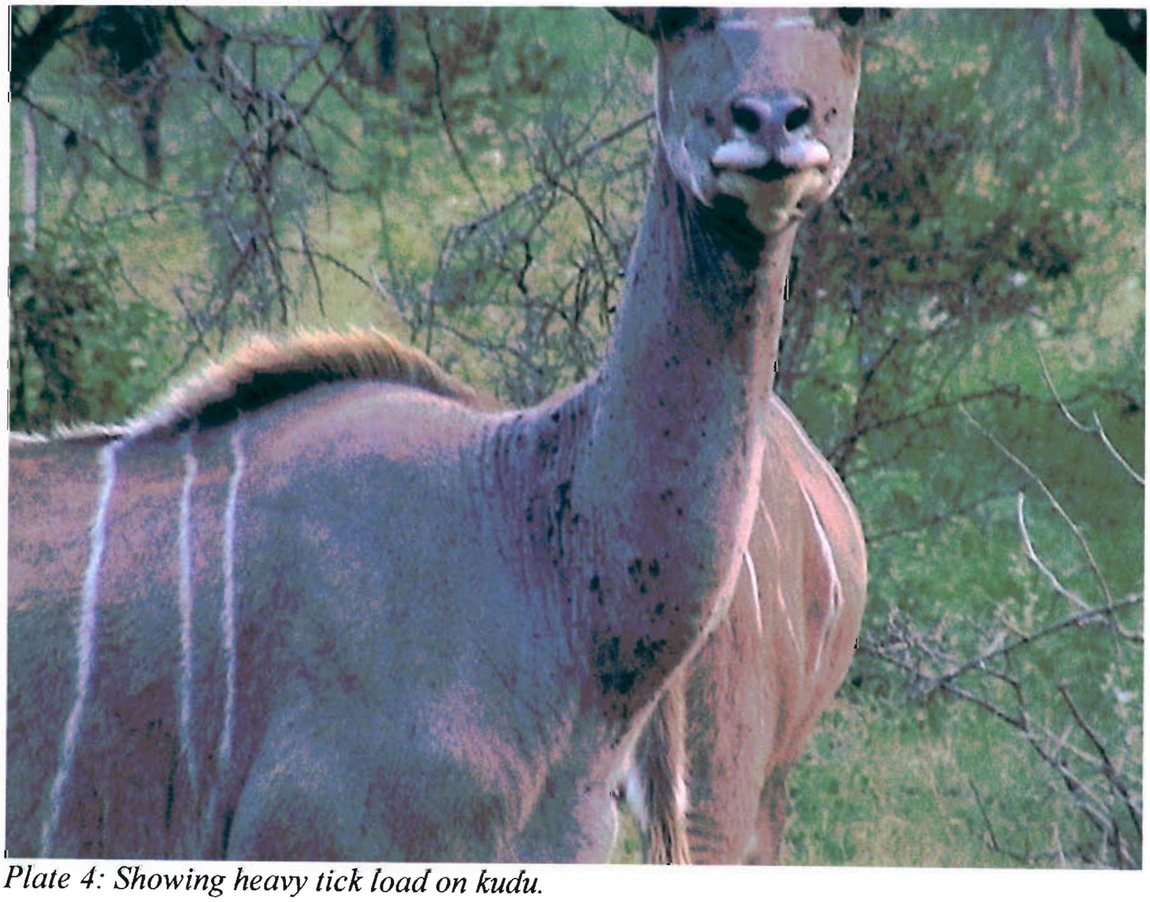
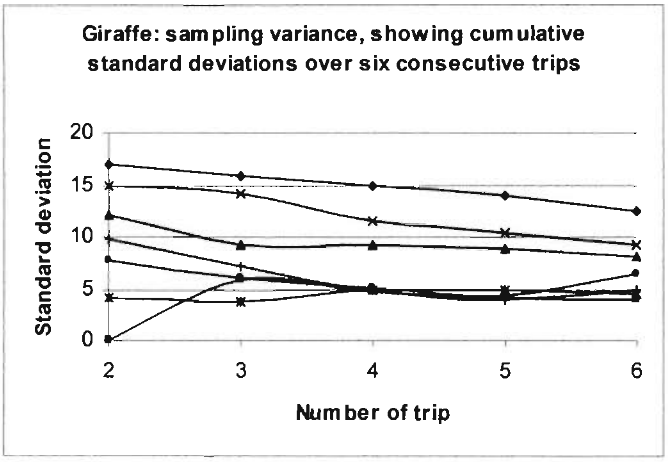
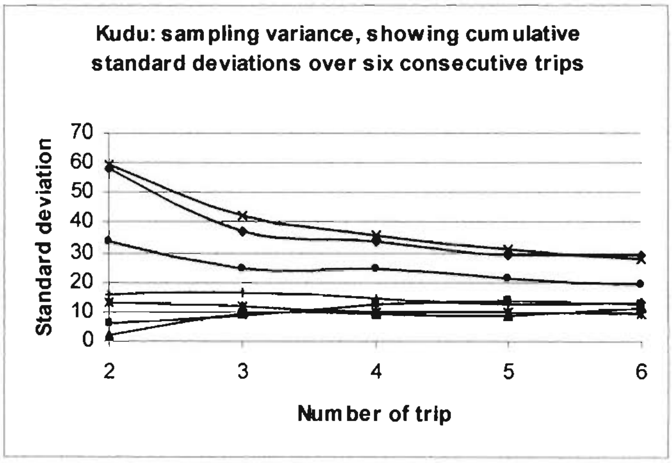
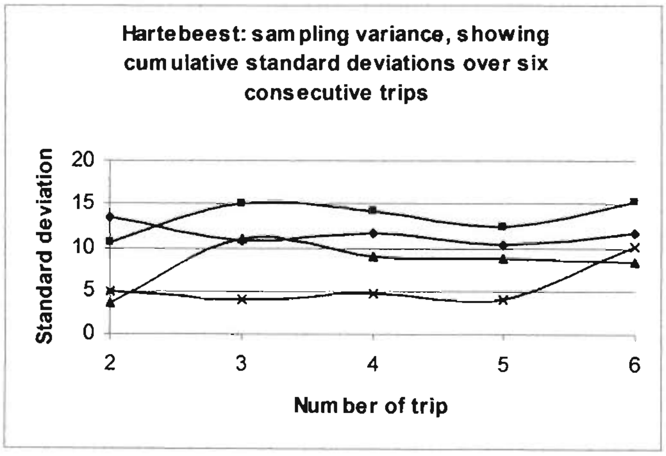


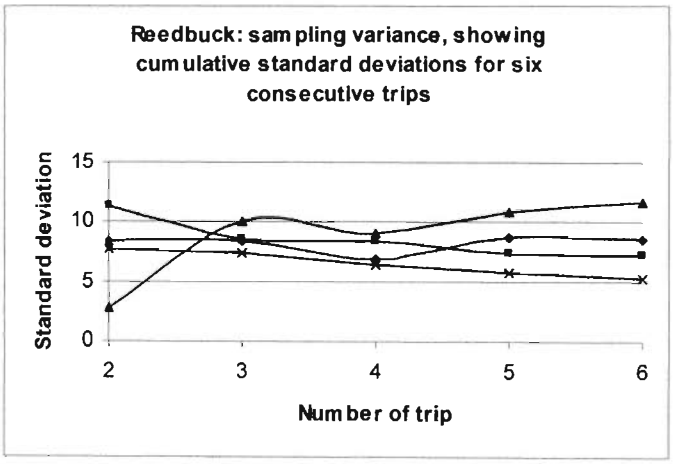
Plate 4: Showing heavy tick load on kudu.

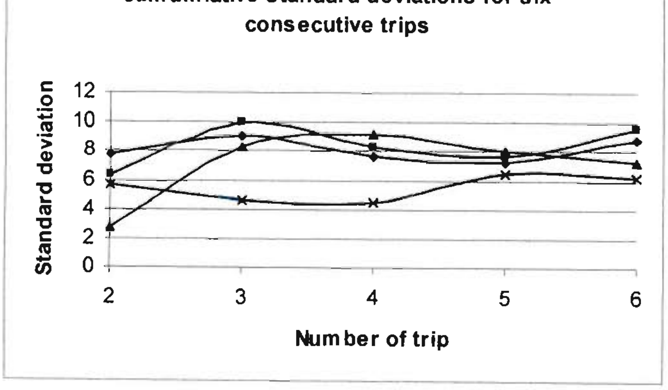
Appendix 6: Sampling variance, showing cumulative standard deviations for number of animals sighted over six consecutive trips. For species studied for 42 months, there are seven 'six trip blocks', for species studied for only 24 months four 'six trip blocks'.

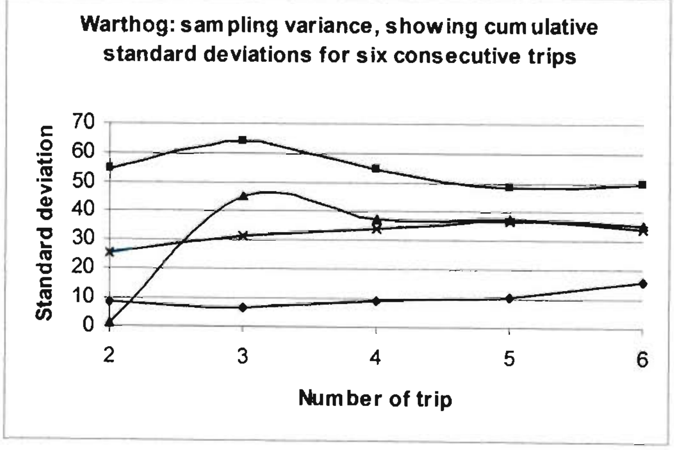

Giraffe: sampling variance, showing cumulative standard deviations over six consecutive trips

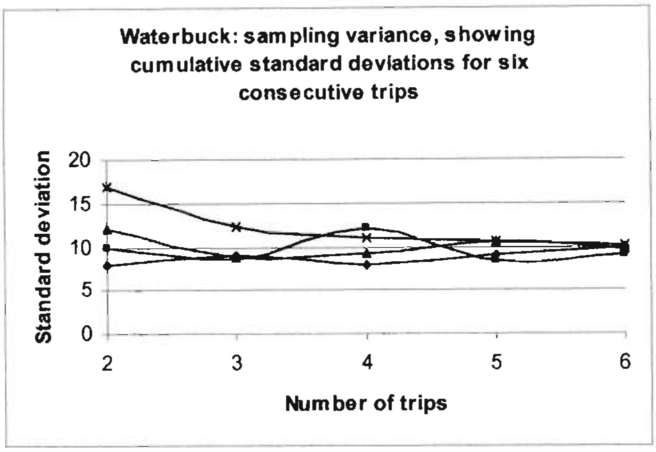

Kudu: sampling variance, showing cumulative standard deviations over six consecutive trips

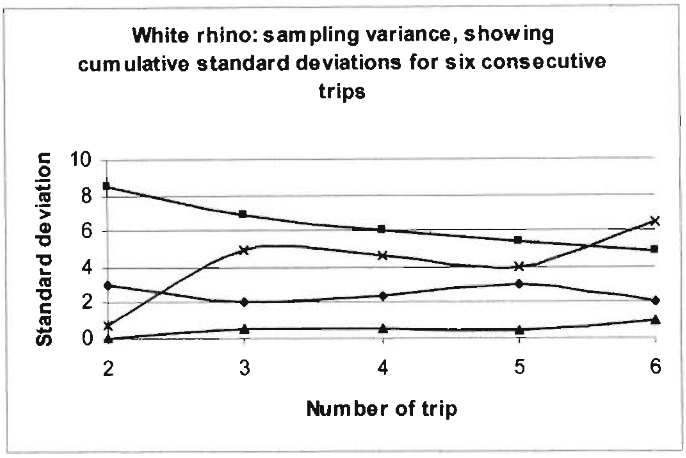

Hartebeest: sampling variance, showing cumulative standard deviations over six consecutive trips

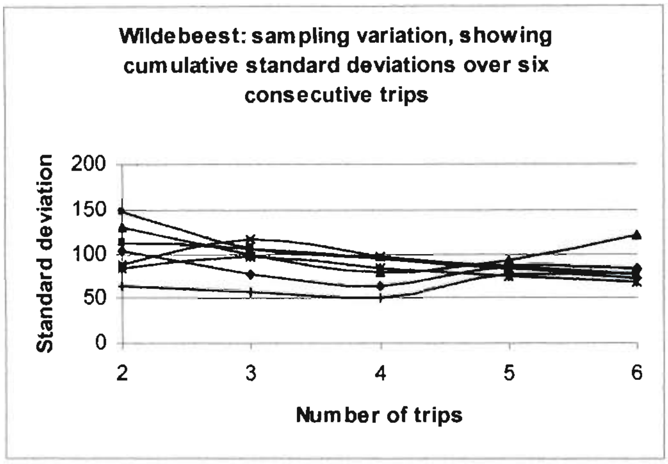

Reedbuck: sampling variance, showing cumulative standard deviations for six consecutive trips

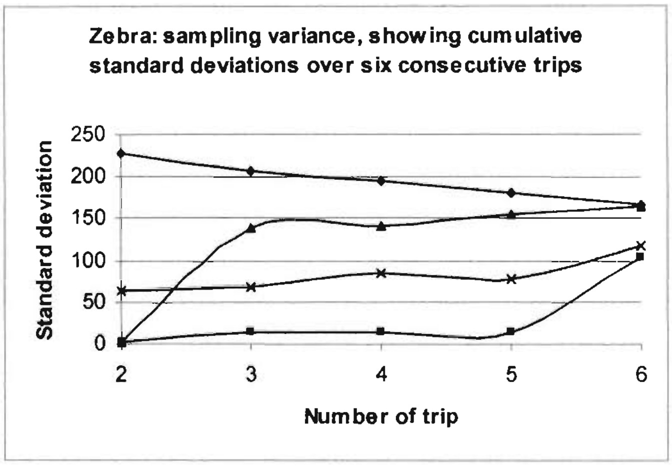

Tsessebe: sampling variance, showing cumumlative standard deviations for six consecutive trips

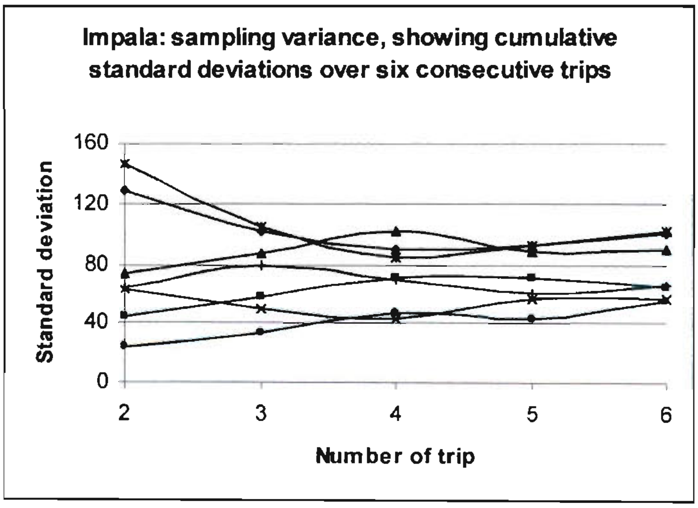

Warthog: sampling variance, showing cumulative standard deviations for six consecutive trips


Waterbuck: sampling variance, showing cumulative standard deviations for six consecutive trips

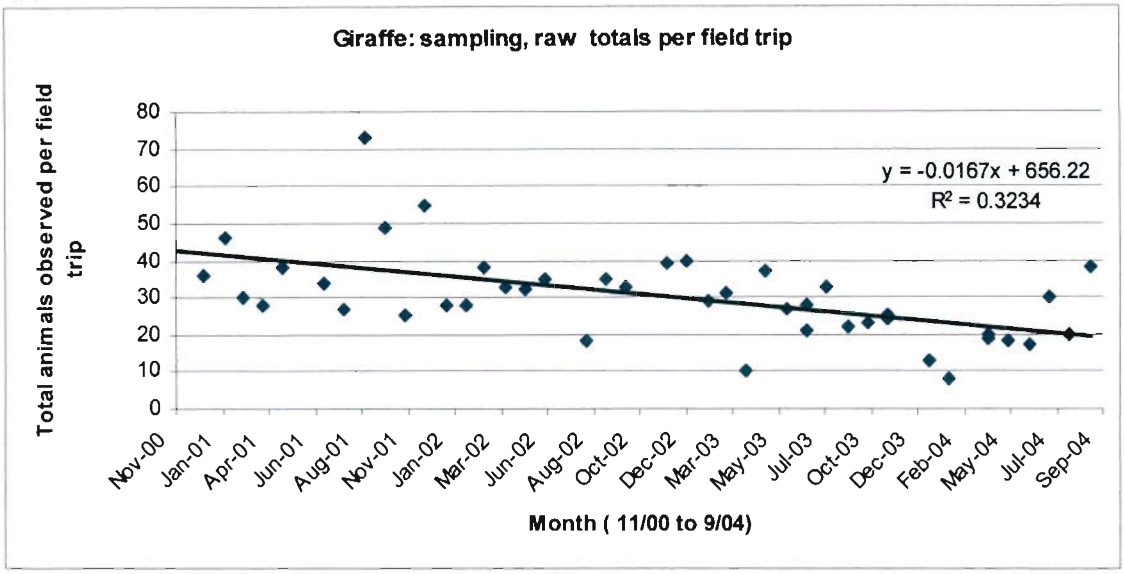

White rhino: sampling variance, showing cumulative standard deviations for six consecutive trips

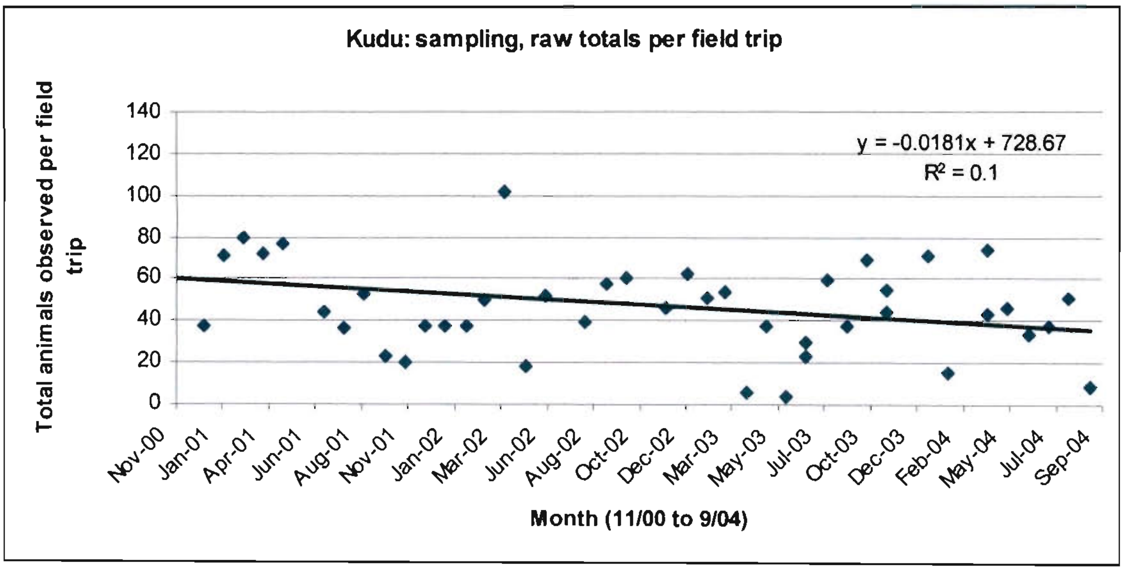

Wildebeest: sampling variation, showing cumulative standard deviations over six consecutive trips

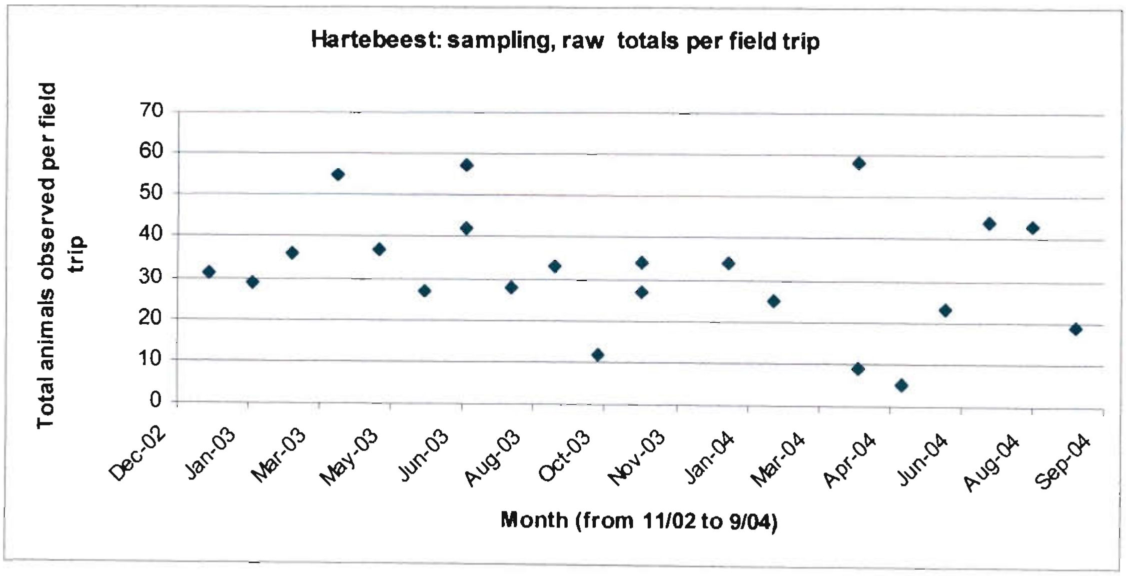

Zebra: sampling variance, showing cumulative standard deviations over six consecutive trips

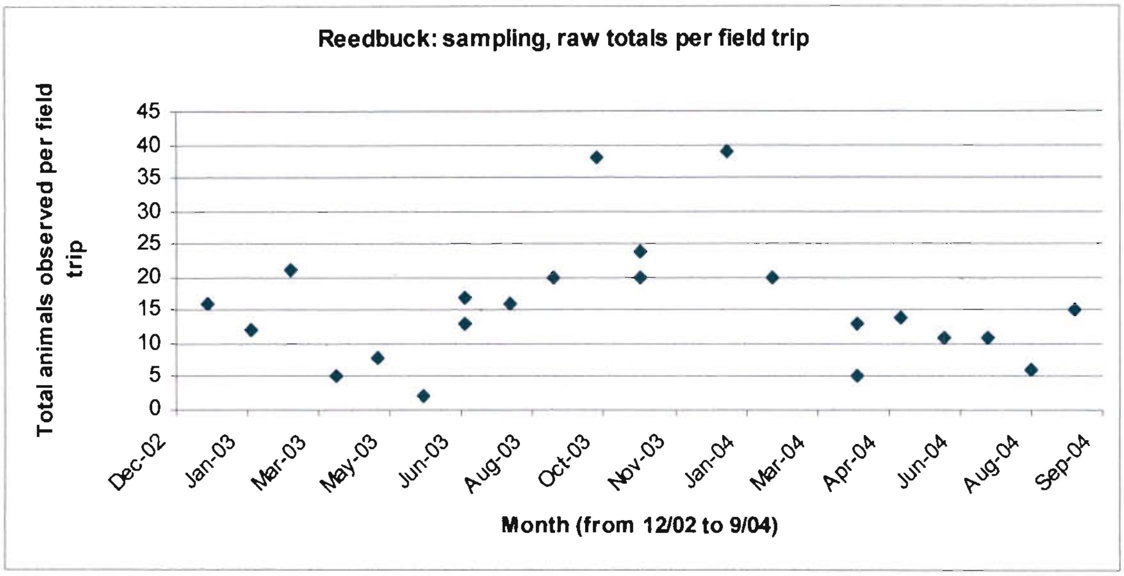

Impala: sampling variance, showing cumulative standard deviations over six consecutive trips

Appendix 7: Raw totals per field trip

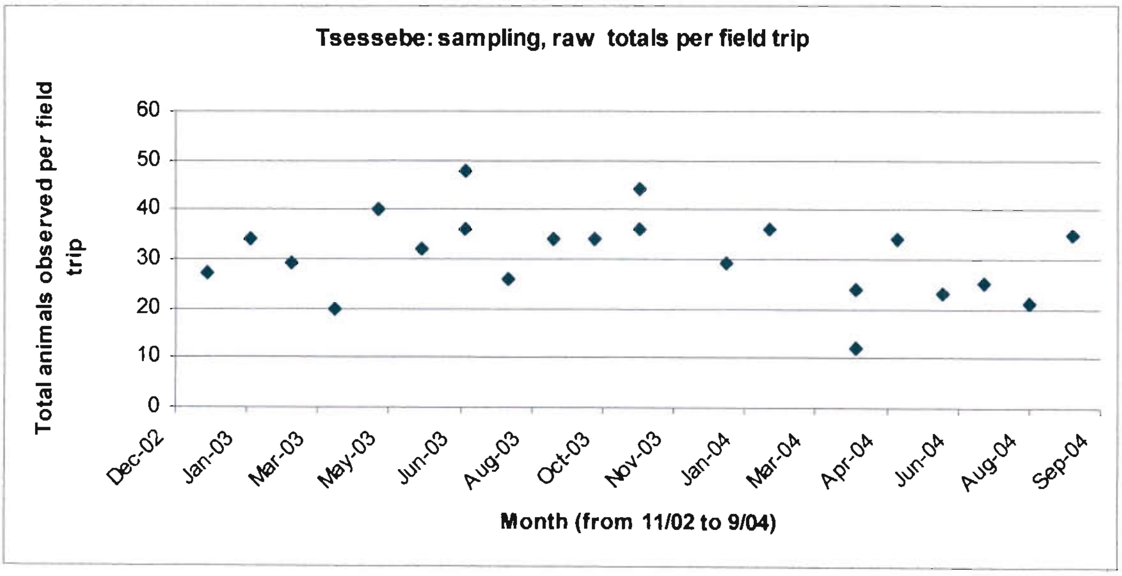




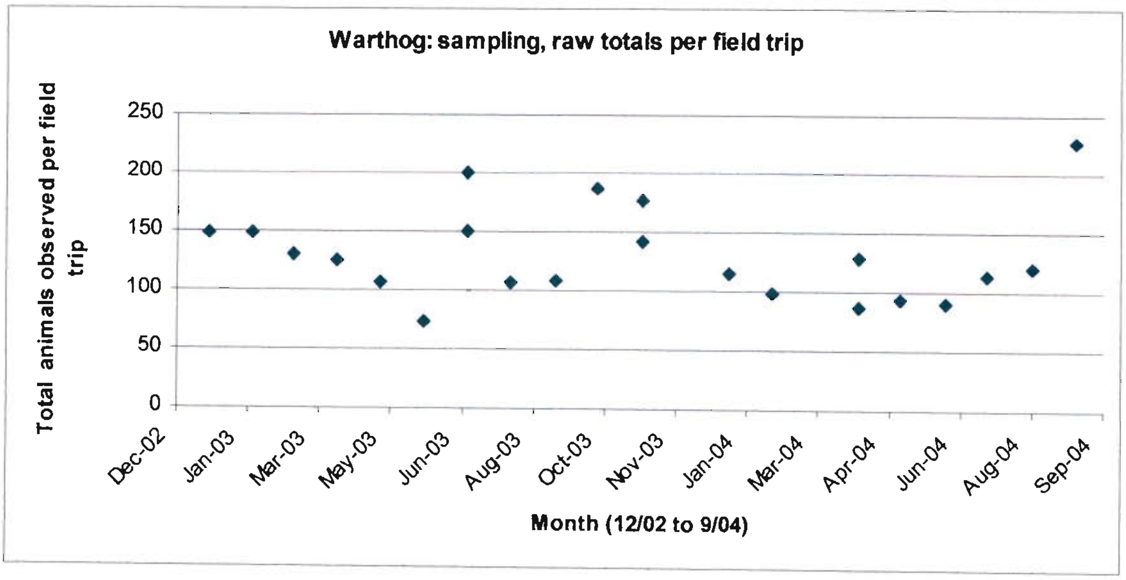




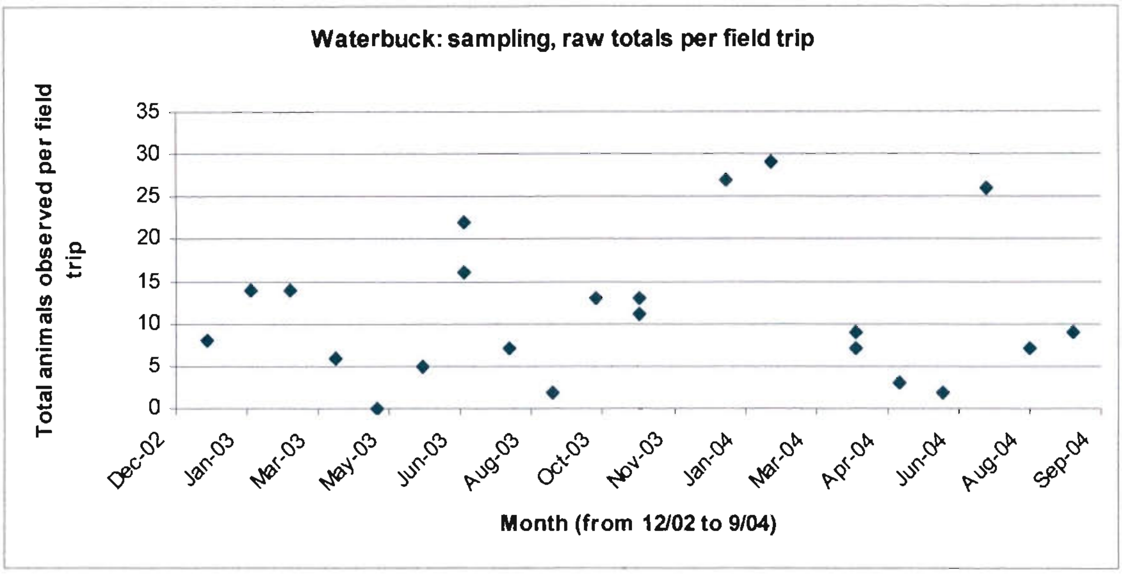
Reedbuck: sampling, raw totals per field trip

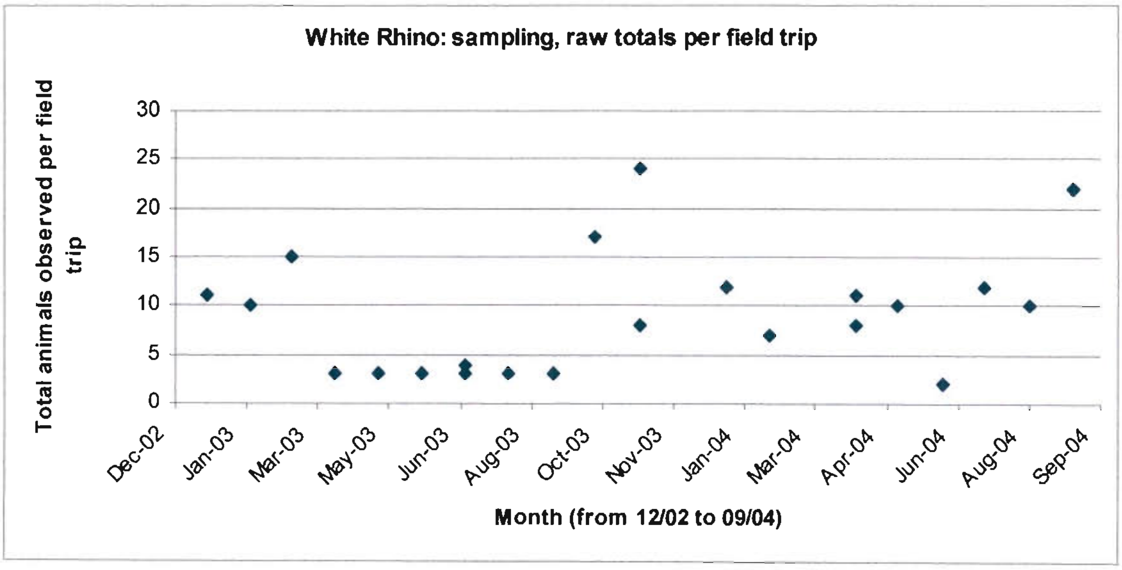


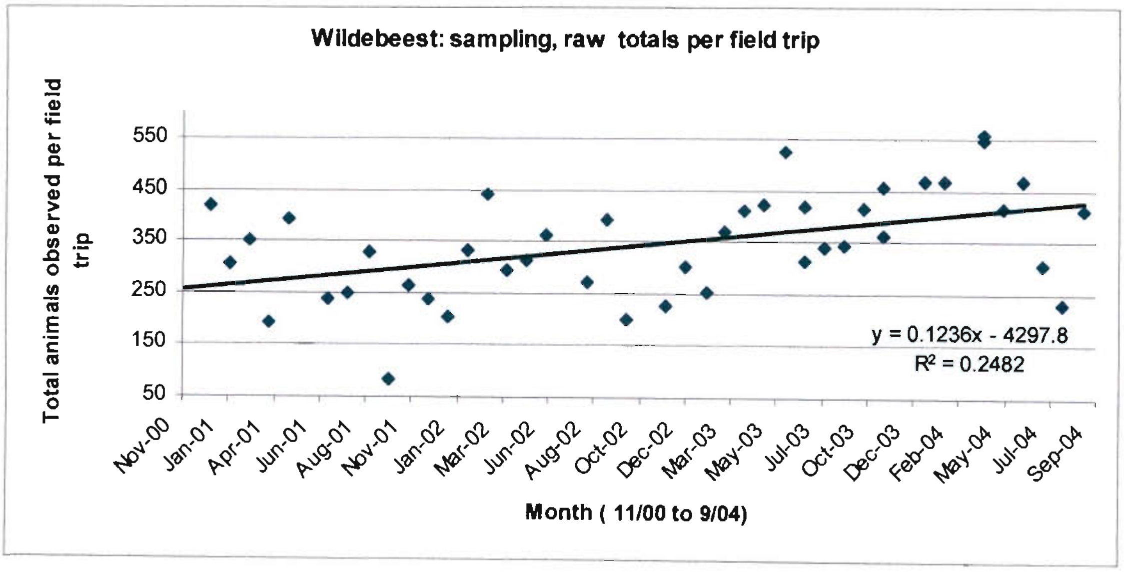
Tsessebe: sampling, raw totals per field trip



Warthog: sampling, raw totals per field trip


Waterbuck: sampling, raw totals per field trip
Total animals observed per field trip
35
30
25
20
15
10
5
0
Dec-02
Jan-03
Mar-03
May-03
Jun-03
Aug-03
Oct-03
Nov-03
Jan-04
Mar-04
Apr-04
Jun-04
Aug-04
Sep-04
Month (from 12/02 to 9/04)


White Rhino: sampling, raw totals per field trip
Total animals observed per field trip
30
25
20
15
10
5
0
Dec-02
Jan-03
Mar-03
May-03
Jun-03
Aug-03
Oct-03
Nov-03
Jan-04
Mar-04
Apr-04
Jun-04
Aug-04
Sep-04
Month (from 12/02 to 09/04)


Wildebeest: sampling, raw totals per field trip
Total animals observed per field trip
550
450
350
250
150
50
y = 0.1236x - 4297.8
R² = 0.2482
Nov-00
Jan-01
Apr-01
Jun-01
Aug-01
Nov-01
Jan-02
Mar-02
Jun-02
Aug-02
Oct-02
Dec-02
Mar-03
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Jul-03
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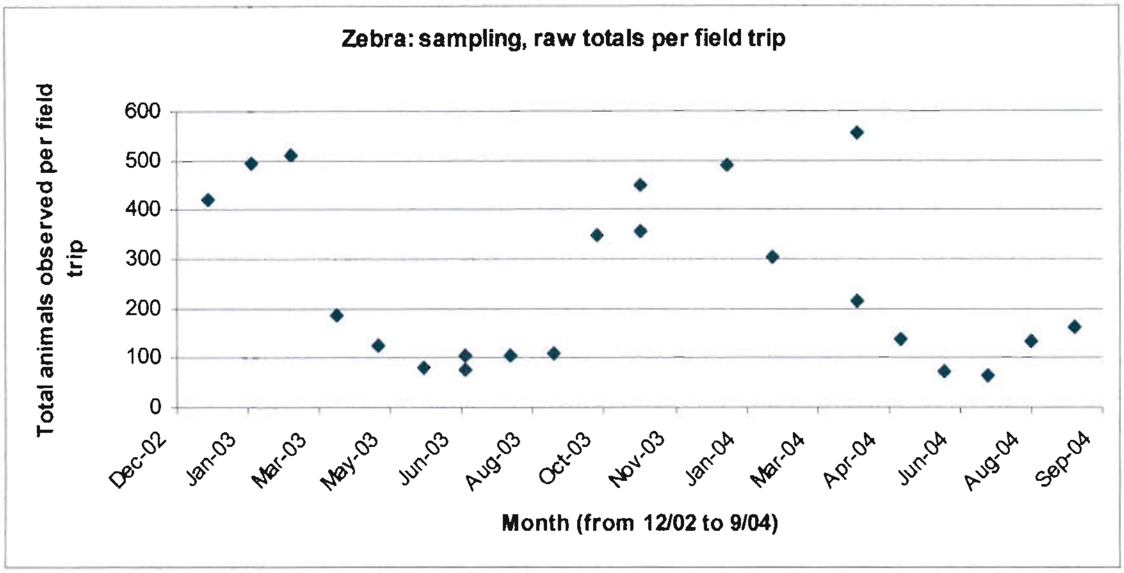
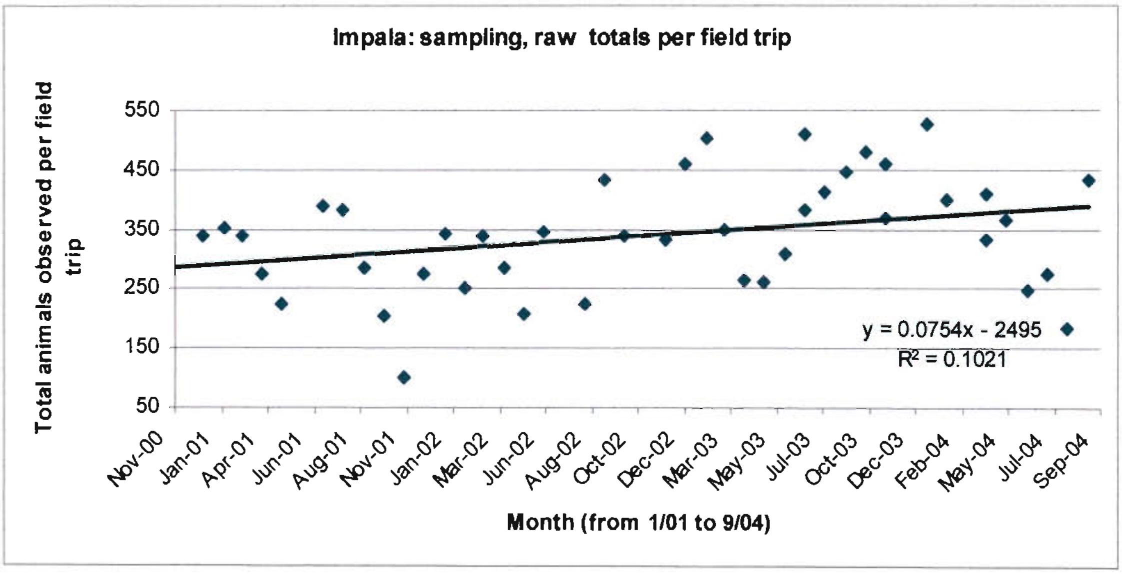
Dec-03
Feb-04
May-04
Jul-04
Sep-04
Month (11/00 to 9/04)


Zebra: sampling, raw totals per field trip
Total animals observed per field trip
600
500
400
300
200
100
0
Dec-02
Jan-03
Mar-03
May-03
Jun-03
Aug-03
Oct-03
Nov-03
Jan-04
Mar-04
Apr-04
Jun-04
Aug-04
Sep-04
Month (from 12/02 to 9/04)


Impala: sampling, raw totals per field trip
Total animals observed per field trip
550
450
350
250
150
50
y = 0.0754x - 2495
R² = 0.1021
Nov-00
Jan-01
Apr-01
Jun-01
Aug-01
Nov-01
Jan-02
Mar-02
Jun-02
Aug-02
Oct-02
Dec-02
Mar-03
May-03
Jul-03
Oct-03
Dec-03
Feb-04
May-04
Jul-04
Sep-04
Month (from 1/01 to 9/04)

Appendix 8: Management removals of animals

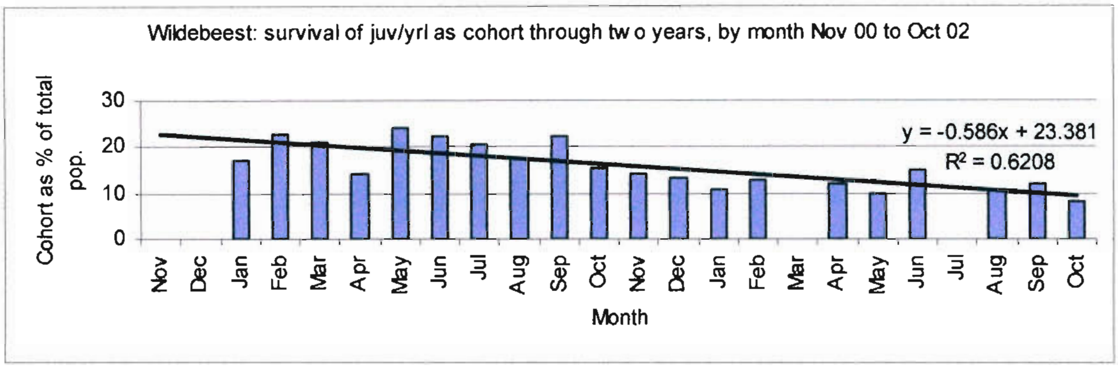
a) Records of management's removals (live and dead) by sex for 2000 to 2003. Only animals where significant numbers (compared to their total number) have been removed are included.

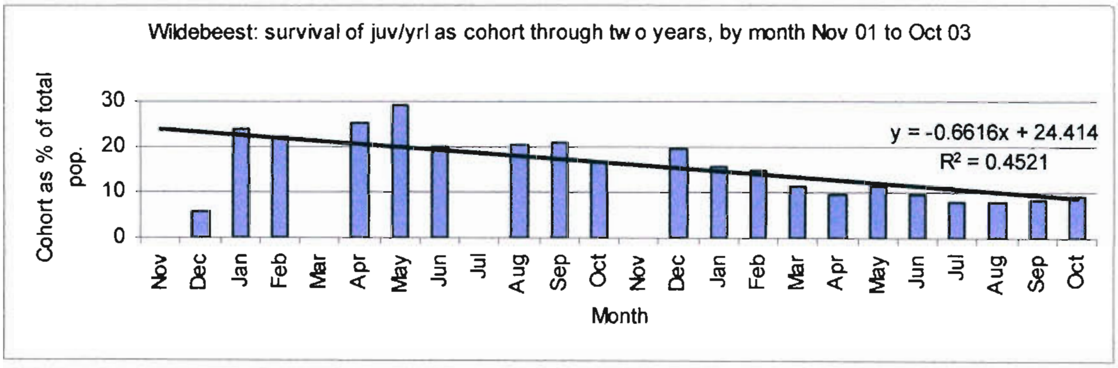
	Year			
	2000	2001	2002	2003
Species	Male\Females removed	Male\Females removed	Male\Females removed	Male\Females removed
Giraffe	23\21	26\12	26\27	27\21
Kudu	46\49	77\93	80\103	108\93
Wildebeest	95\76	100\121	29\20	33\7
Impala	192\265	203\240	92\131	147\56

b) Records of management's total removals (live and dead) by sex from 1973 to end of 2003.

Species	**Male**	**Female**	**Unknown**
Giraffe	138	119	0
Kudu	459	578	0
Reedbuck	0	0	0
Waterbuck	0	0	0
Warthog	670	844	0
White Rhino	11	8	0
Wildebeest	1082	1127	200
Zebra	124	142	11
Impala	1168	785	12

Appendix 9: Wildebeest and impala cohort survivorship





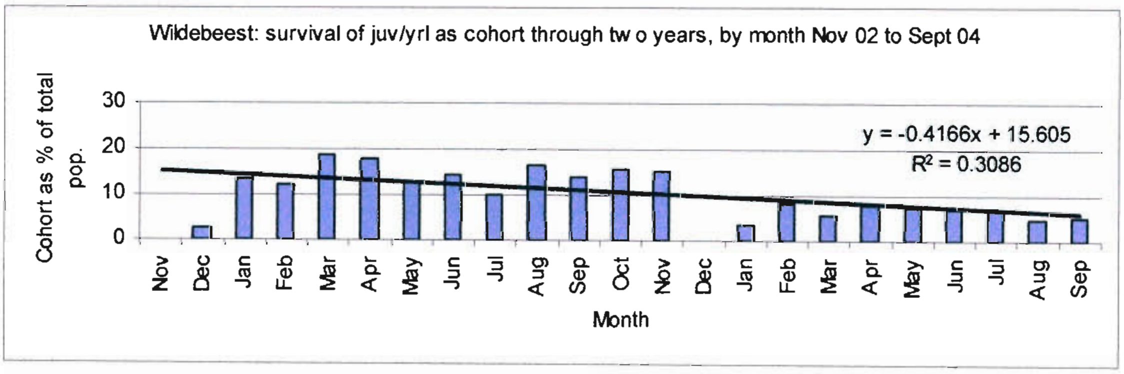


Fig A.9.1: Wildebeest, cohort survivorship. Showing juveniles (which become yearlings as of 1st November in the second year) as a percentage of the total population over a two year period. The survival of three consecutive cohorts of juveniles (i.e. those born 2000, 2001 and 2002) are shown. These figures are 'filtered'.

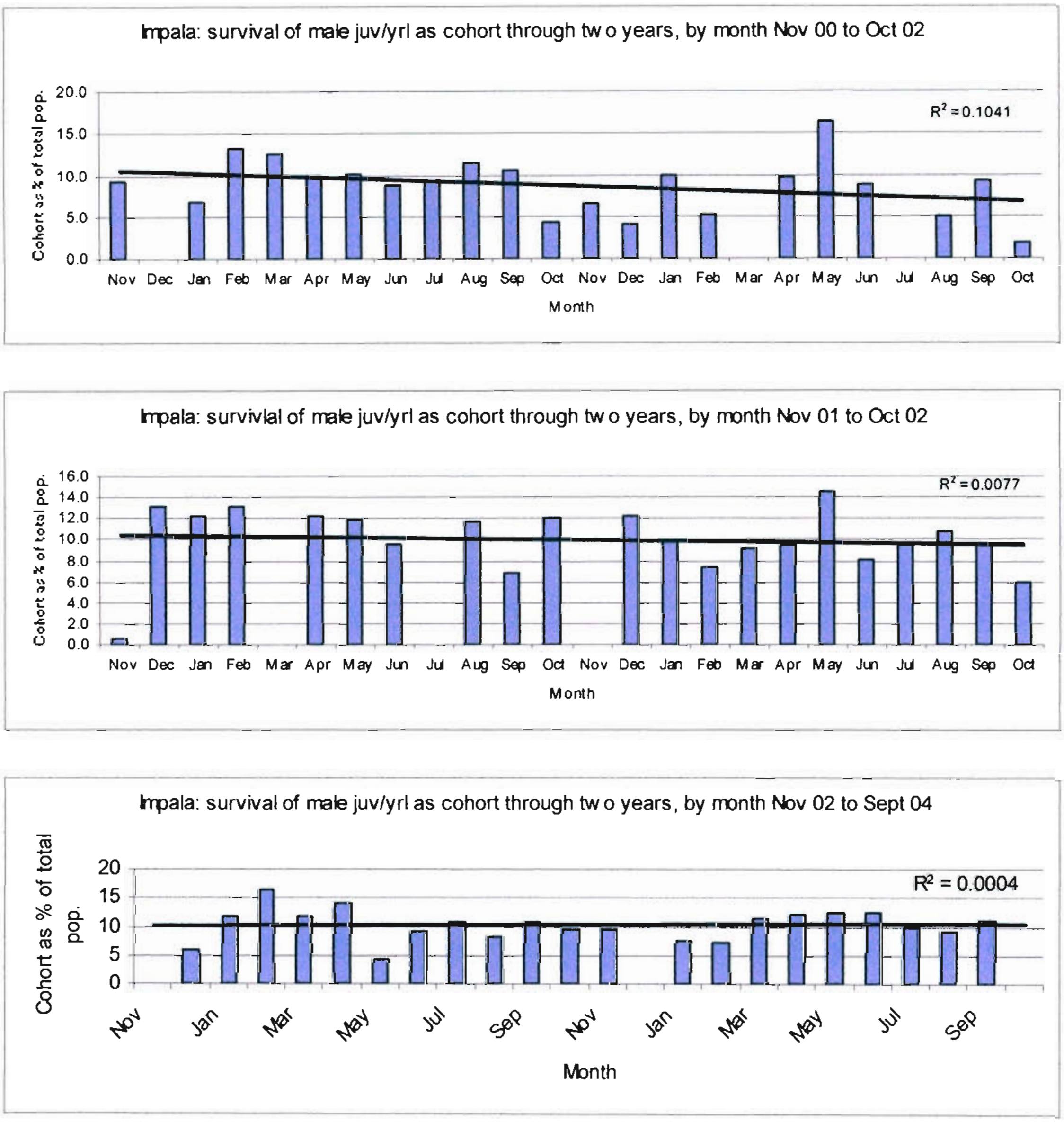
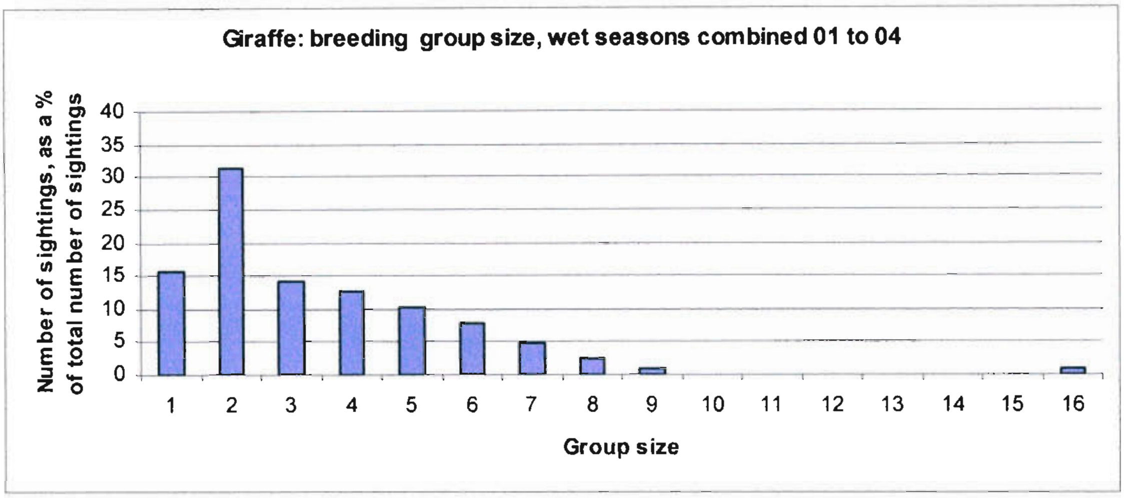
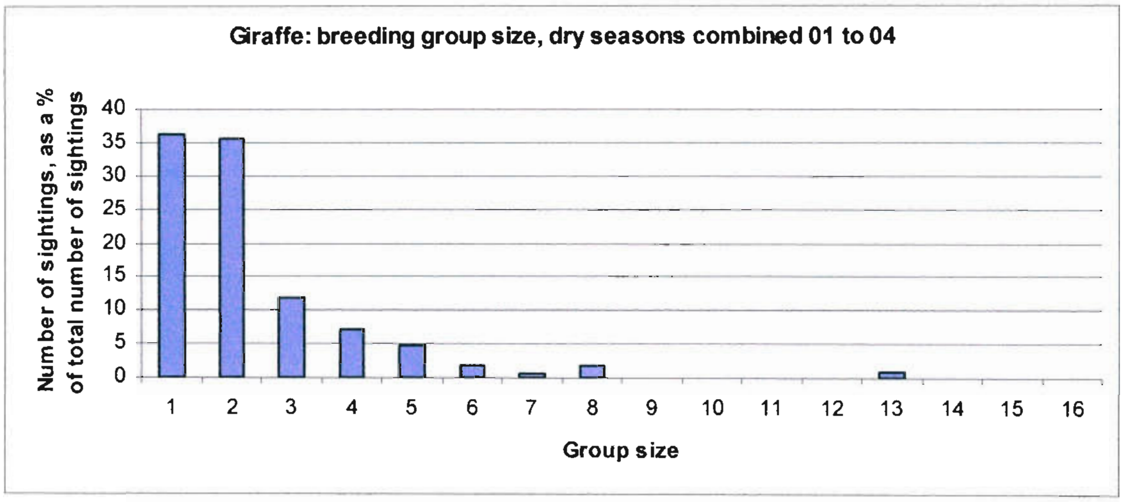
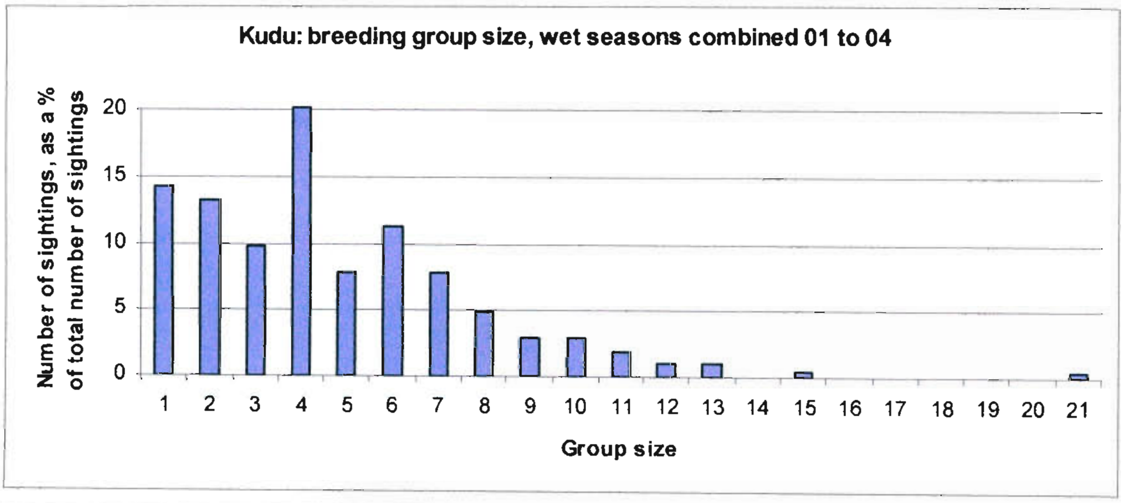


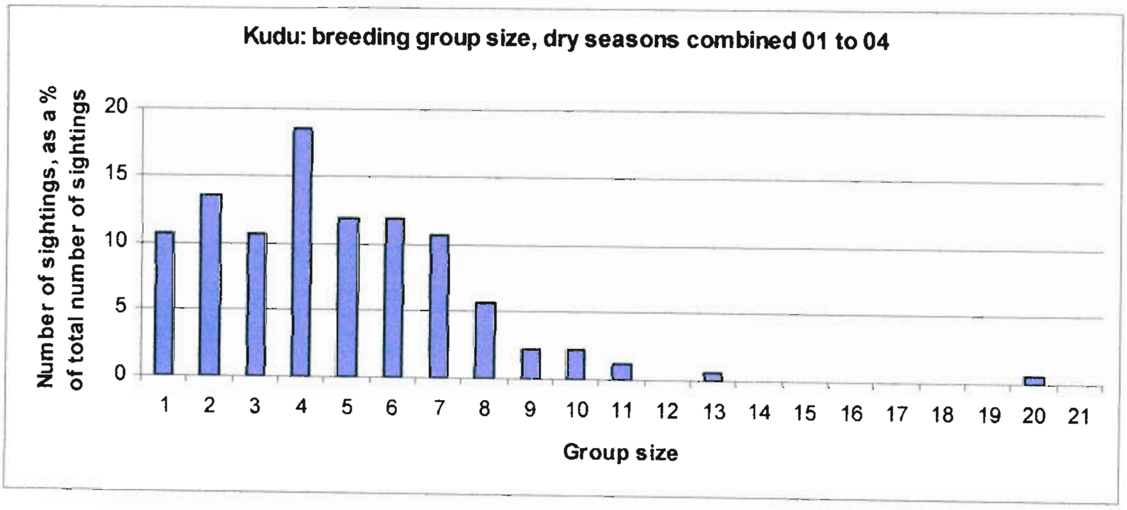
Fig A.9.2: Impala, cohort survivorship. Showing survival of male juveniles (which become yearlings in the second year) over a two year period. The survival of three consecutive cohorts of juveniles is shown. These figures are 'filtered'.

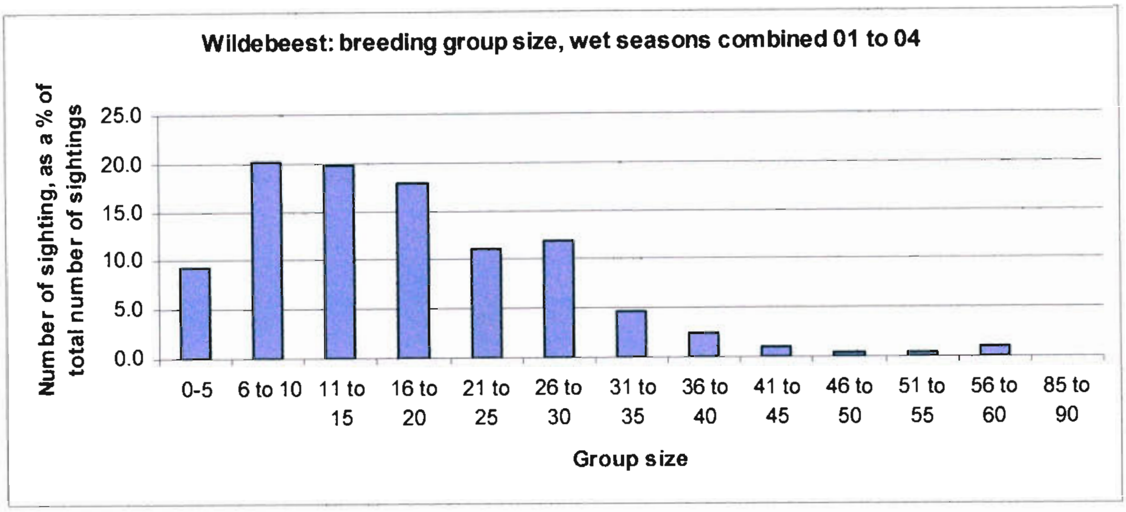
Appendix 10: Breeding group size by season.

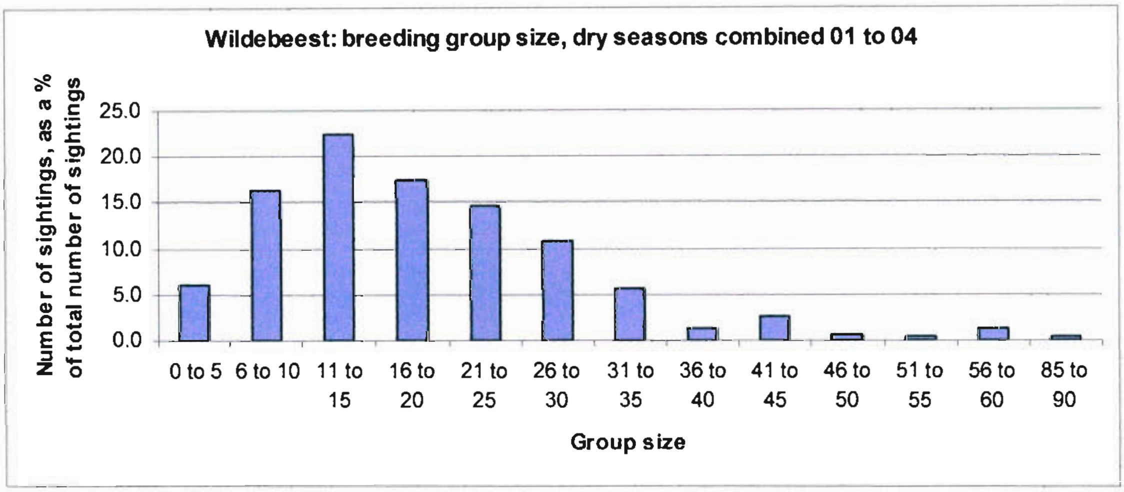


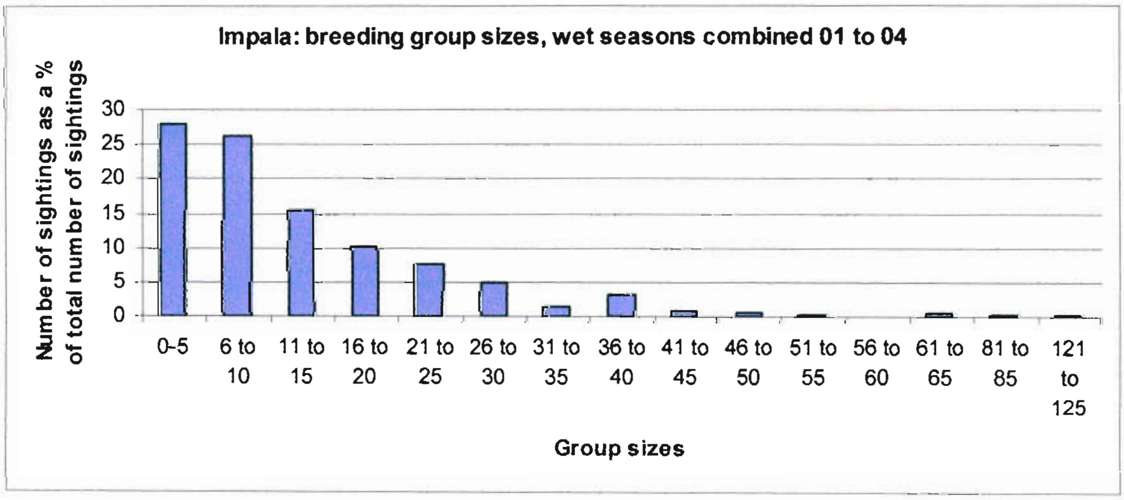


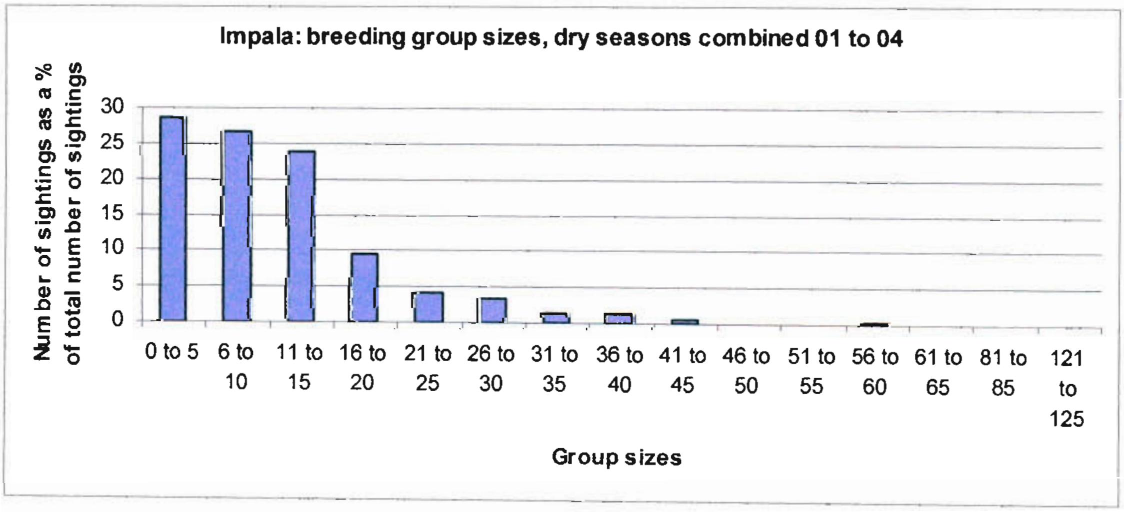




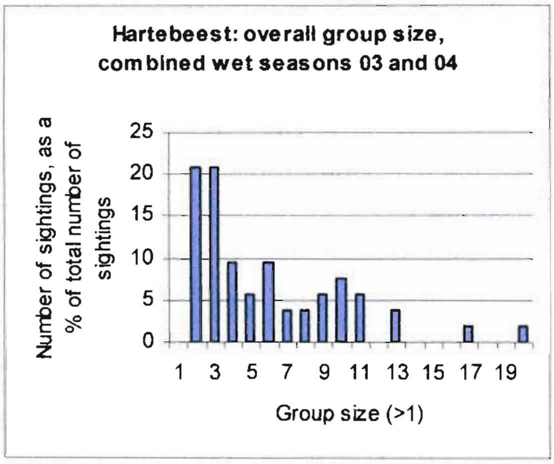

Wildebeest: breeding group size, wet seasons combined 01 to 04
Number of sighting, as a % of total number of sightings
25.0
20.0
15.0
10.0
5.0
0.0
0-5
6 to 10
11 to 15
16 to 20
21 to 25
26 to 30
31 to 35
36 to 40
41 to 45
46 to 50
51 to 55
56 to 60
85 to 90
Group size

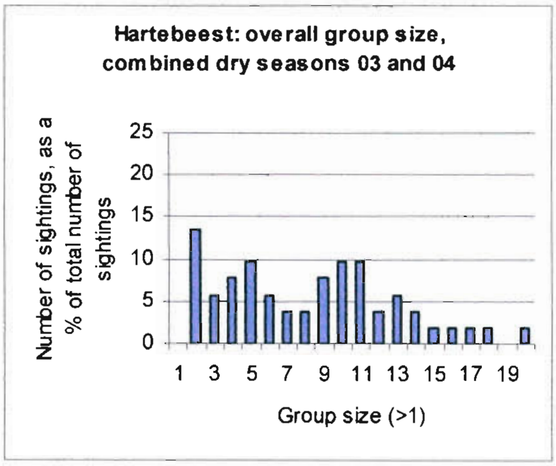

Wildebeest: breeding group size, dry seasons combined 01 to 04
Number of sightings, as a % of total number of sightings
25.0
20.0
15.0
10.0
5.0
0.0
0 to 5
6 to 10
11 to 15
16 to 20
21 to 25
26 to 30
31 to 35
36 to 40
41 to 45
46 to 50
51 to 55
56 to 60
85 to 90
Group size

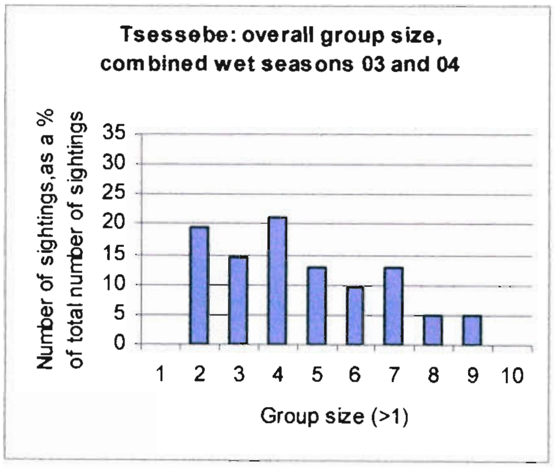

Impala: breeding group sizes, wet seasons combined 01 to 04
Number of sightings as a % of total number of sightings
30
25
20
15
10
5
0
0-5
6 to 10
11 to 15
16 to 20
21 to 25
26 to 30
31 to 35
36 to 40
41 to 45
46 to 50
51 to 55
56 to 60
61 to 65
81 to 85
121 to 125
Group sizes

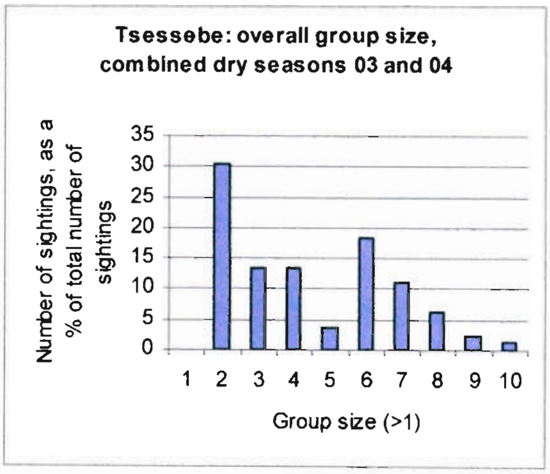

Impala: breeding group sizes, dry seasons combined 01 to 04
Number of sightings as a % of total number of sightings
30
25
20
15
10
5
0
0 to 5
6 to 10
11 to 15
16 to 20
21 to 25
26 to 30
31 to 35
36 to 40
41 to 45
46 to 50
51 to 55
56 to 60
61 to 65
81 to 85
121 to 125
Group sizes

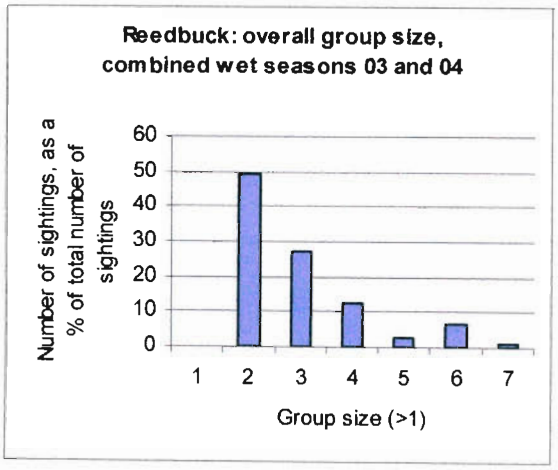
For species on who there is only two years data histograms are shown reduced in size.

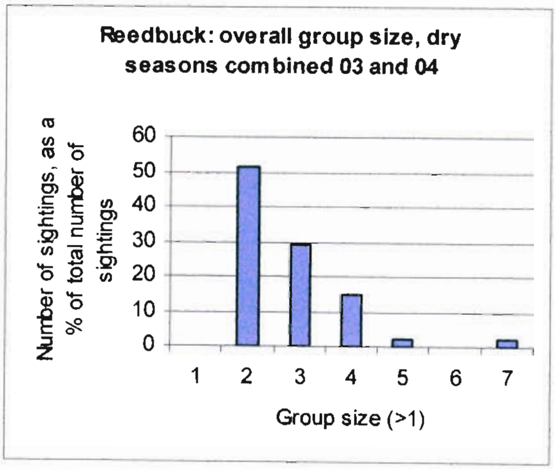

Hartebeest: overall group size, combined wet seasons 03 and 04

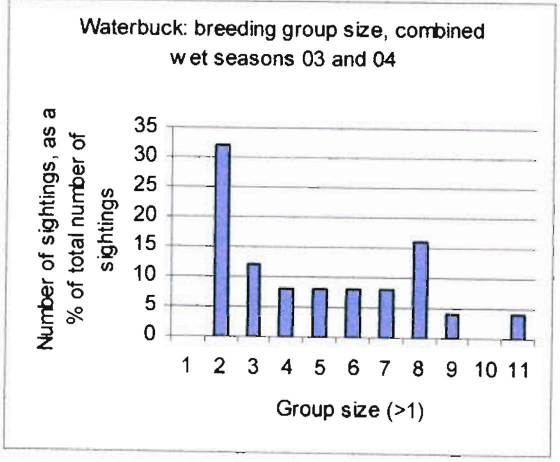

Hartebeest: overall group size, combined dry seasons 03 and 04

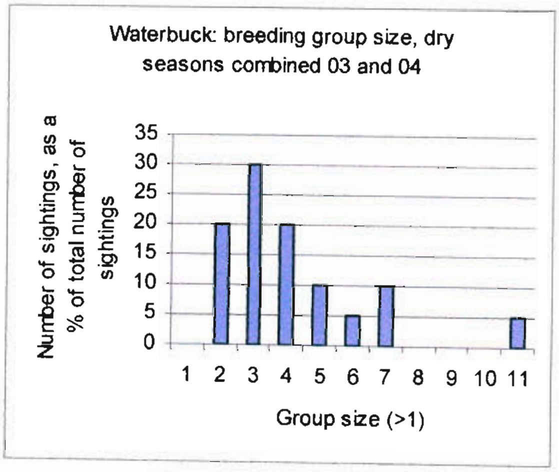

Tsessebe: overall group size, combined wet seasons 03 and 04

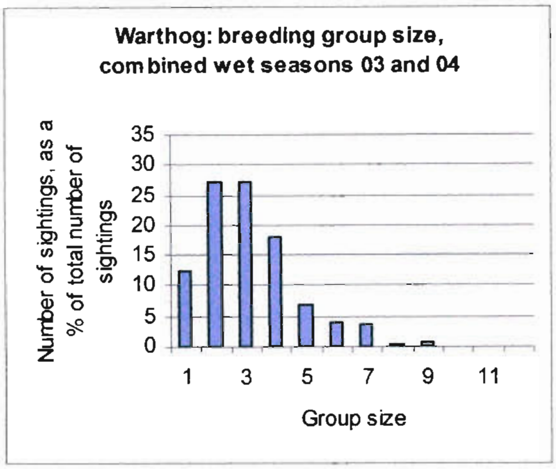

Tsessebe: overall group size, combined dry seasons 03 and 04

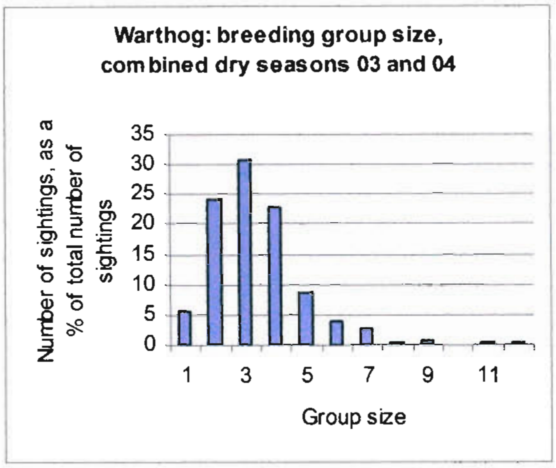

Reedbuck: overall group size, combined wet seasons 03 and 04

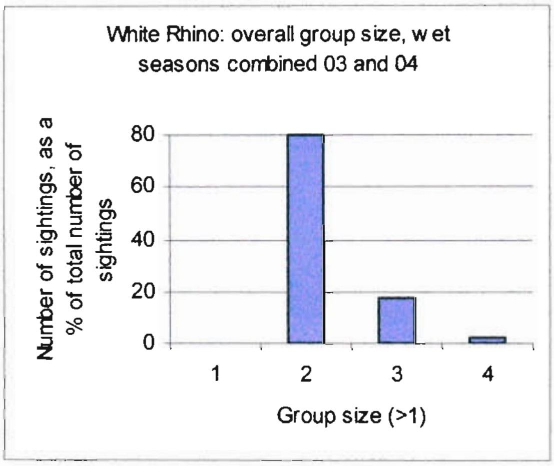

Reedbuck: overall group size, dry seasons combined 03 and 04

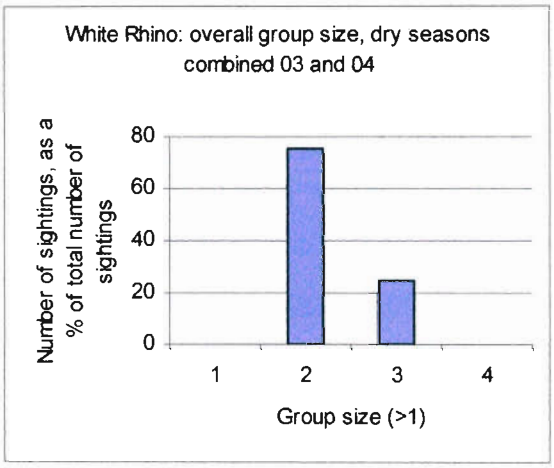

Waterbuck: breeding group size, combined wet seasons 03 and 04

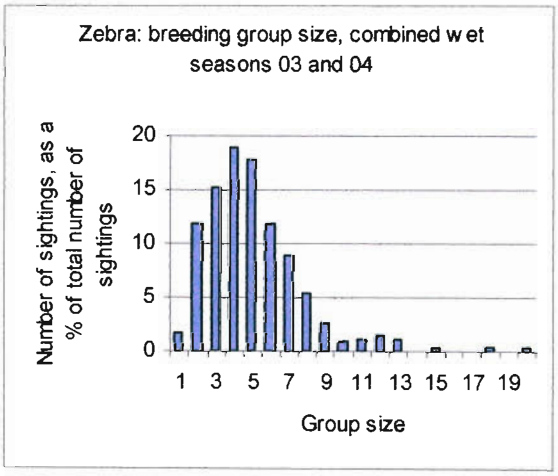

Waterbuck: breeding group size, dry seasons combined 03 and 04

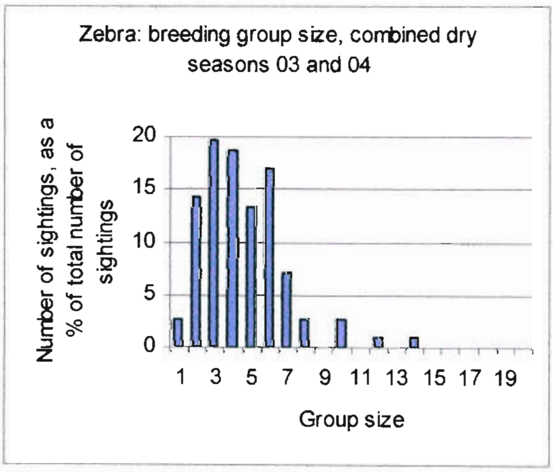

Warthog: breeding group size, combined wet seasons 03 and 04


Warthog: breeding group size, combined dry seasons 03 and 04

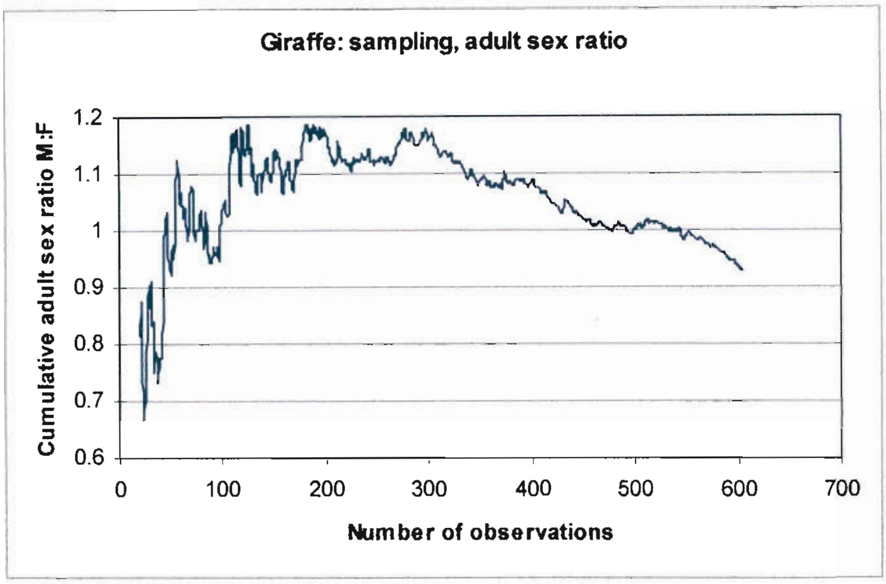

White Rhino: overall group size, wet seasons combined 03 and 04

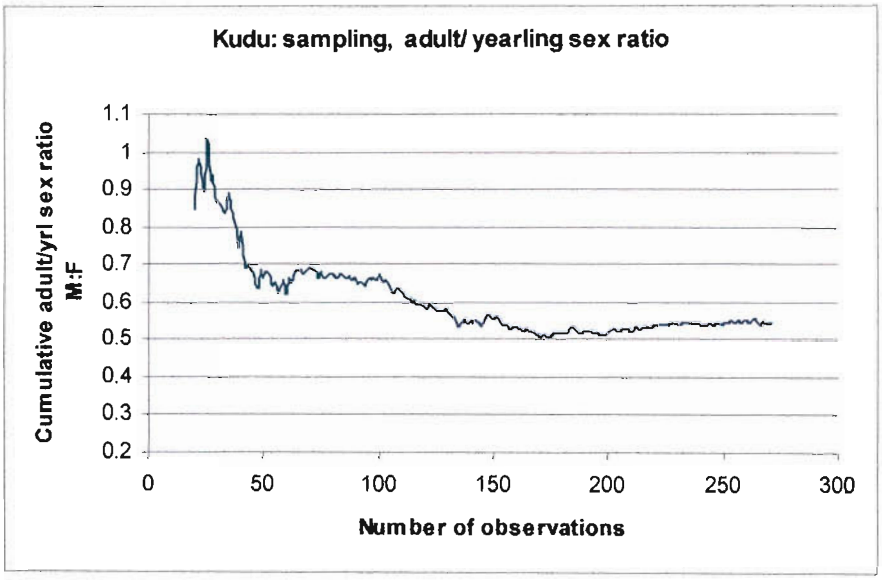

White Rhino: overall group size, dry seasons combined 03 and 04

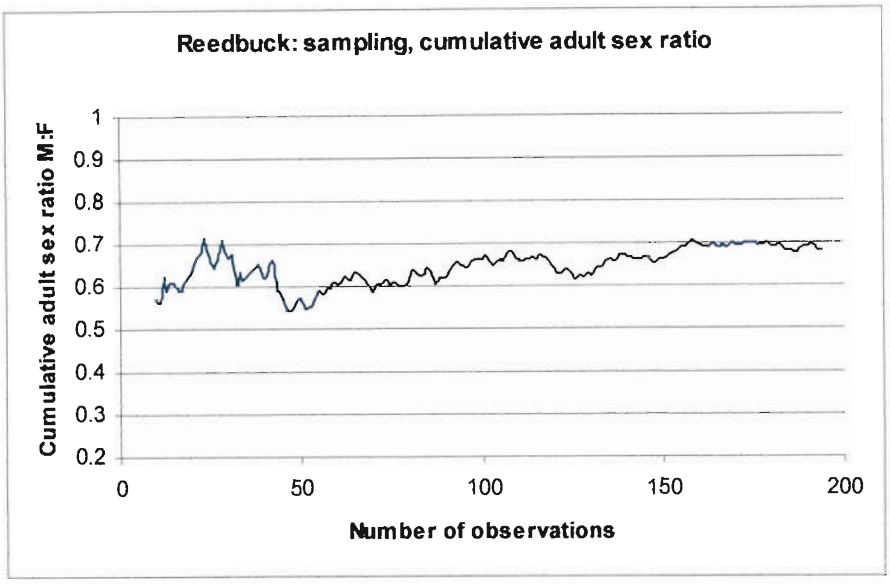

Zebra: breeding group size, combined wet seasons 03 and 04

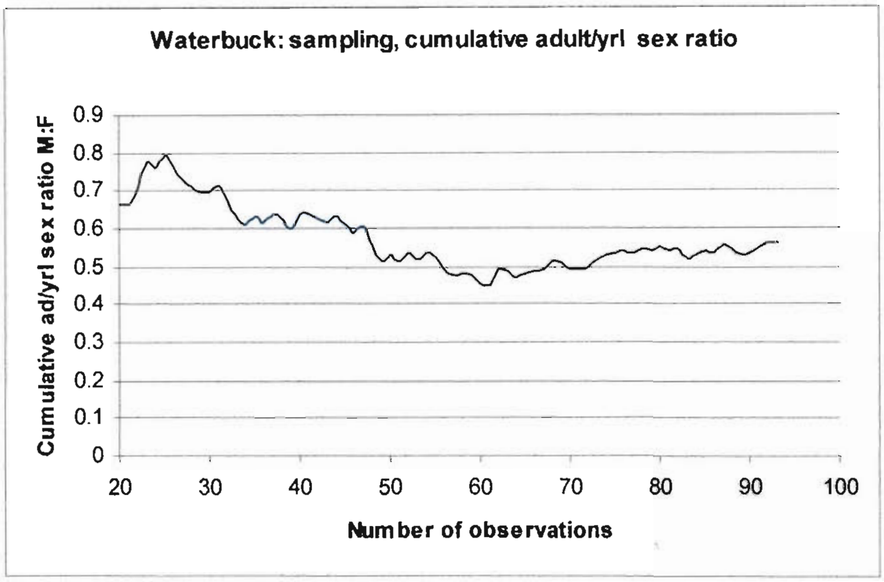

Zebra: breeding group size, combined dry seasons 03 and 04

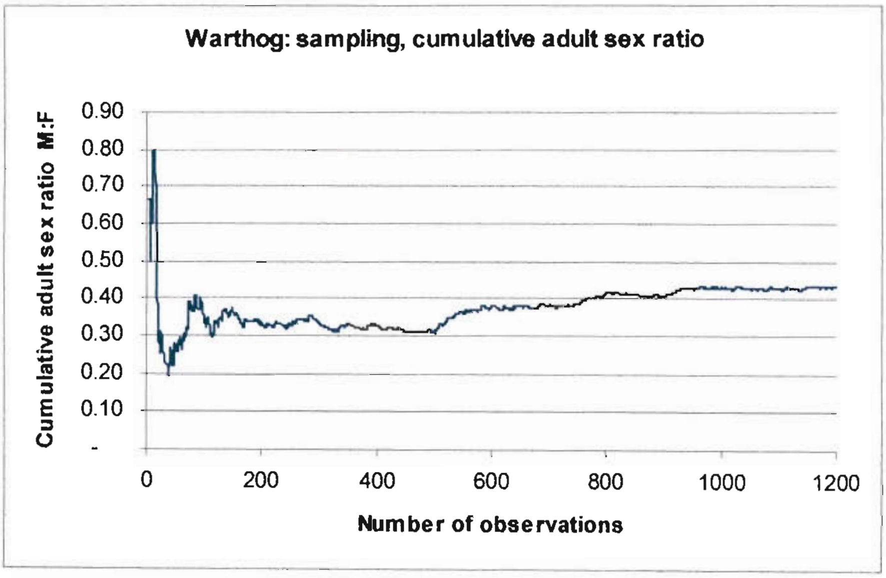
Appendix 11: Sampling of adult sex ratios.

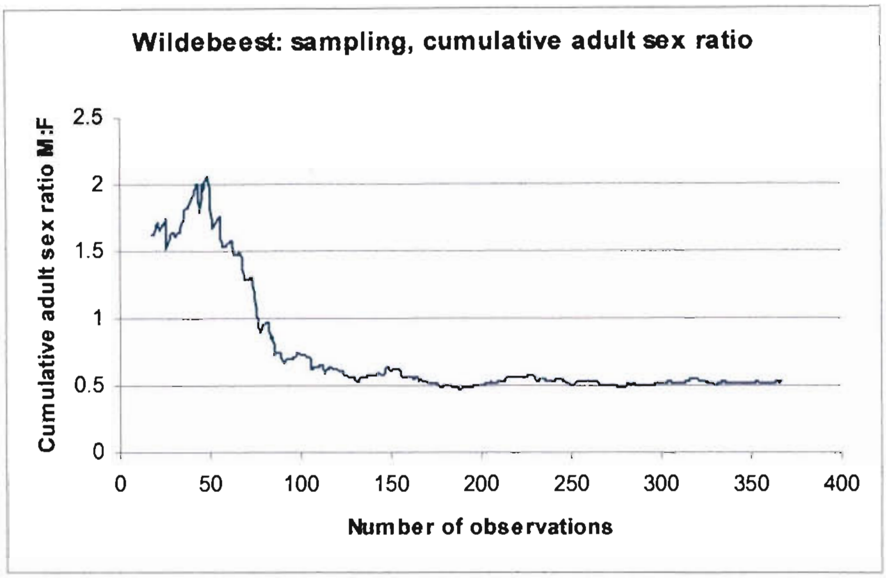




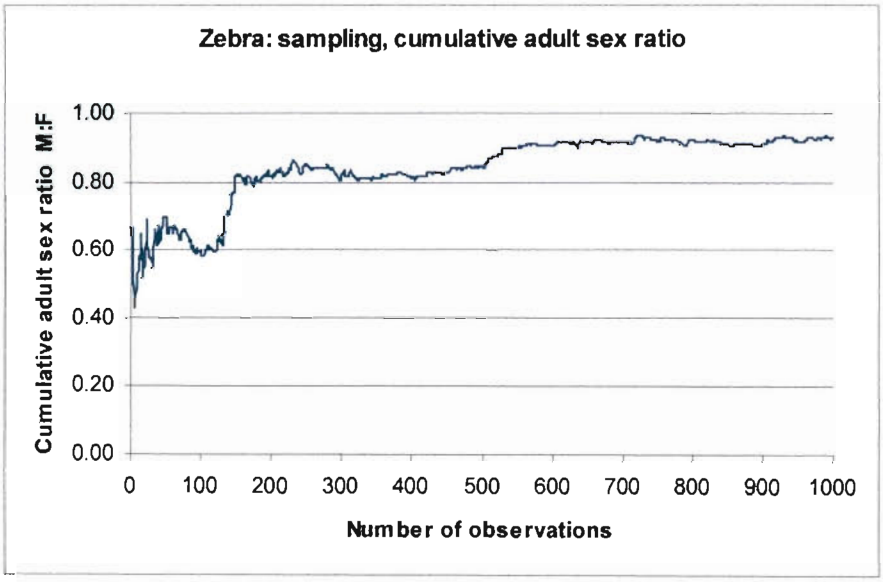

Reedbuck: sampling, cumulative adult sex ratio
Cumulative adult sex ratio M:F
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0
50
100
150
200
Number of observations


Waterbuck: sampling, cumulative adult/yrl sex ratio
Cumulative ad/yrl sex ratio M:F
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
20
30
40
50
60
70
80
90
100
Number of observations


Warthog: sampling, cumulative adult sex ratio
Cumulative adult sex ratio M:F
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
-
0
200
400
600
800
1000
1200
Number of observations



Wildebeest: sampling, cumulative adult sex ratio



Zebra: sampling, cumulative adult sex ratio