Grevy's zebra: ecology in a heterogeneous environment

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June 1998

Abstract

The aim of this study was to test the hypothesis that Grevy's zebra (*Equus grevyi* Oustalet) compete for critical resources with pastoral people and their domestic livestock. The study was conducted in three areas to approximate a manipulative experiment, with pastoralists and their livestock being excluded from one of the areas.

Forage was seasonally limited in the areas used by pastoralists. Although no single factor determined the space use of Grevy's zebra, the distribution of food - particularly in the pastoralist areas - and predators were important. Use of space by Grevy's zebra was constrained by their dependence on water and by the presence of the people in the pastoralist areas. Zebra dispersed from areas when food became limiting. Different sex classes exhibited different times of dispersal that may have been related to different thresholds for dispersal.

In the area where there were no pastoral people, temporal patterns of water use by Grevy's zebra were driven by avoidance of predation. In contrast, Grevy's zebra in the pastoralist areas drank at night to avoid the monopolisation of water by people and their domestic livestock by day. By drinking at night, the zebra, and particularly their foals, were probably more susceptible to predation.

Breeding patterns in Grevy's zebra were explained by condition dependent oestrus: oestrus and conception were highly dependent on stochastic patterns of climatic variation. Juvenile survival was related to the amount mothers move, and was lowest in areas used by pastoralists.

Grevy's zebra were found to compete for critical resources with pastoralists and their livestock. This highlighted the importance of protected areas to sustain recruitment into the population. Release from competition is, however, necessary to further improve the likelihood of persistence of Grevy's zebra in their natural range. To achieve this, pastoralist stocking rates must be reduced.

Acknowledgements

Although what is written in this thesis is the product of my own work and time, I am not under any illusion that I could have done it alone (although given these people, nor would I have wanted to). Without the help of numerous people these words would never have come into being. The range of assistance, offered and received, was phenomenal; I am deeply indebted to the generosity of these people.

What follows in these acknowledgements might read simply like a list of things that people did for me. The words to express gratitude are so few: a thesaurus might list grateful, thankful, appreciative, beholden and indebted. To the people here, and others that in the four years of the making of this thesis have escaped my mind, I am these and more. Thank you.

The Government of Kenya allowed this work to be conducted under research permit number OP.13/001/23C 2. The Permanent Secretary for Research in the Office of the President, Mr D. Kiua Nzioka was helpful in allowing me to start on the research by granting me a temporary research permit while the National Research Council of the Ministry of Science and Technology deliberated the full permit. The research was affiliated to the Department of Resource Surveys and Remote Sensing. Mr H. Mwendwa, Director of the DRSRS granted me the freedom of his Department, for which I am grateful.

The Kenya Wildlife Service supported the work, both officially and practically. This support came primarily from the staff of the Research and Veterinary Sections. Dr Jim Else provided good advice on how research clearance should be obtained,

facilitated the darting of the zebra and loaned me a liquid nitrogen tank. The support from the Research Section continued through Mr Wilbur Otichilo.

I am particularly thankful to the KWS Veterinary Service. Under Drs Richard Kock and John Wambua, they darted the Grevy's, stored specimens, allowed me access to equipment to do the faecal egg counts and assisted with dealing with the bureaucracy of exporting samples.

Mr Peter Ambenje of the Drought Monitoring Centre, part of the Kenya Meteorological Department in Nairobi gave me access to the climatological records of all the meteorological stations in northern Kenya. Mr Geoffrey Mungai, Herbarium Manager of the East African Herbarium at the National Museum in Nairobi accepted my plant samples for confirmation - though I will be more grateful when I receive the results!

The fieldwork in Kenya was funded by unconventional sources. The Institute of Zoology provided me with a stipend and funded much of the fieldwork. Other sources of funding included Dances for Elephants, the Eden Wildlife Trust, the Elsa Conservation Trust, Brookfield Zoological Society. Obviously without the support of these organisations and the people running them, the fieldwork would not have happened. For their support, I am grateful.

The radio-collars were funded by even less conventional means, with a group of individuals and organisations funding one or two collars each. These were Peter Moller, Kisima Farm Ltd, Chev Bateman, Serena Lodges and Hotels, United Touring Company, Tor Allen Safaris Ltd, Terry Mathews, Allan Earnshaw, Ms Phyllis Cole and Mr John Whittaker.

Doug and Lynn Walker, through the National Academy of Natural History in Philadelphia, USA were also extremely generous in their support of my fieldwork.

Support in kind came from many directions. Firestone (EA) Ltd gave me good reductions on tyres. Alick Roberts lent me a telescope for the duration of the fieldwork. Innumerable hours were spent staring at Grevy's zebra bums through that telescope. Ker & Downey Safaris Ltd allowed me the freedom of the workshops to get my car preened for its traumatic ventures through the road licensing offices. Rodney Elliott gave me some of his time to question him about the history of the protected areas in northern Kenya. Tony Dyer gave me a flight to track the collared females, albeit curtailed by a lack of fuel. Nonetheless I am grateful for the information that the flight provided but also for the smooth landing. Hanspeter Linger and the staff at the Laikipia Research Programme were generous in allowing me to use their facilities.

I had numerous people who helped with data collection over the course of the study. James Leng'aur was my research assistant in Barsalinga, collecting data on pastoralist ecology. Much of those data do not appear in this thesis, but I am grateful for his work and for the insights into Samburu culture that he provided. I am grateful to my other research assistants who collected the rainfall data: Matthew Lekermui and Lekuwan Lekumoisa. Shakil Visram did all the egg counts in the faecal samples. Although those data also do not appear in this thesis, I am grateful for his time and effort. Dr Truman Young took the time to confirm my plant samples for which I am grateful.

In September 1994 and July 1995, I had volunteers that collected data during the waterhole watches. In September 1994, they put up with being dropped in the field and abandoned to a rigorous and sleepless schedule. The volunteers in September 1994 were: Tom Henfry, Nancy and Ruth Moinde, Albert Mburu, Jill Pruetz, Yeme and Malaku Tassama, Ben Themen, Shakil Visram and Robyn Williams. Those in July 1995 had a more leisurely time, hampered only by bureaucrats. The volunteers were: Ibrahim Gitonga, Waweru Karemeri, James Leng'aur, Alex Onjie, Jill Pruetz, Yeme Tassama, Shakil Visram and Doug West.

I am deeply indebted to the various people who were exceptionally hospitable to me, putting up with my sporadic visits. Paddy and Pam Grattan put me (and Grevy's faecals) up on many occasions, but I am particularly grateful for the brusque care when I had malaria. Pete and Sarah Jenkins allowed me to use their storage space for

my camp on those occasions when I wasn't living in it. My visits to them were always unannounced but that never dampened their hospitality. Sophy Grattan and the staff at Cape Chestnut provided me with storage space, sandwiches and a fax machine when in Nanyuki.

The Isiolo County Council Warden and rangers of gave me the freedom of Buffalo Springs and Shaba. They were always welcoming and cheerful. I am particularly grateful for the permission to work at night for the waterhole watches. For that period, they willingly provided *askaris* for my volunteers, while KWS provided others for my camp.

I am especially grateful to the peoples of Barsalinga and Ngare Ndare. They welcomed me into these areas with warmth and without restraint when I was questioning their very philosophies and practices of existence. Their curiosity always delighted me, their unabashed vanity amused me, and their generosity astonished me. If they were sad to see the end of my fieldwork, then I am sure it is because tea stops in my camps are no longer.

All the staff at Samburu Serena Lodge made my time in Buffalo Springs that much more pleasurable. I was given a prime, cool spot to camp, the freedom of the Lodge including fridges and showers - which was welcome relief indeed from the bucket shower waving in the cold breeze in Barsalinga and Ngare Ndare.

In the UK, Robin Dunbar and Ruth Mace were both willing to take me aboard with few questions. The bureaucracy of UCL was made that much smoother for their help. At the Institute, I am grateful to my fellow ecologists. Between them they provided advice, read chapters, shared beer, and much, much more besides. I am particularly grateful to Tim Coulson and Steve Albon for the time they took in the task of guiding me through the delights of generalised linear models that are so central to the analyses in this thesis. They, with Josh Ginsberg, also took the sledgehammer to my writing to pummel it into the dry, inaccessible form to which we are forced to conform. My fellow PhD students, George, Theresa, Manuela, Isabelle, Daniella and Sarah shared tasteless take-aways and a forgotten summer within small, hot rooms. Anne Loison, a surging wizard, provided invaluable help with the analysis of juvenile survival for chapter 5. Pat Wisbey strained her eyes to proof-read the data chapters in an incredibly short time. Sarah Durant proof-read the introduction, and her help was invaluable with the revised versions of the thesis, while Sarah Cleaveland read the conclusion.

Among the many people that have helped me, there are a few whose contribution cannot be contained within a few sentences. To these people I will always be indebted.

In the days when I was setting out, both in London and in the field, Emma Dennis was unflagging in her support. Pookie, the dog, was a friend and companion, whose patience surpassed any human equivalent. Jill Pruetz provided companionship, intellectual stimulation and a friend with whom to travel many a dusty and bumpy road in East Africa, when with and without Grevy's zebra. Her contribution to this work was significant. Her training as a captive animal researcher honed the discipline with which the data in my fieldwork were collected; she also spent time collecting data, clipping grass, and sharing a seat with Pookie. I am extremely grateful for her support and friendship. Jane Wisbey made the writing up tolerable, providing the support on which these words were written. Her ear received my frustrations, both written and spoken.

Tana and Jet provided support, friendship and efficiency in dealing with the endless requests for things from Nairobi. Over the course of the fieldwork I rattled over sixty thousand kilometres in my car without any serious mishaps; that is testament alone to the care Jet put into its maintenance. Julie provided beds, beer and bags of grass. As the brother to these three people, I hope that one day I will be able to give as I took from them.

Special thanks are due to Josh Ginsberg, supervisor *in absentia.* Although I spent a total of five out of the forty-eight months of this PhD in the same country as Josh, his contribution and assistance was huge. When I was in the field, he acted as postman, provider of field goods for fieldworkers, secretary, guide for my thoughts and actions; when I was in London, he was only an e-mail away ...... Josh's support and belief in me were (and sometimes surprisingly) steadfast throughout.

Kunge Kiribhai's contribution was immense. Of all the people here, it was he that put up with my quirks in the field. His patience bore no measure, his friendship was warm, his stories frivolous, his ability to marry women incomparable.

The folks are as much a part of this work as I am. Without them, it would not have been done - not only during the fieldwork, but they brought me up with Grevy's zebra on our doorstep; with them it was conducted with comfort and smoothness only they could be capable of. It would be a futile task to try to list the things and ways they have contributed; for my time in the field, they have my express thanks.

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1. General introduction

The aim of this study was to test the hypothesis that Grevy's zebra (*Equus grevyi* Oustalet) compete for critical resources with pastoral people and their domestic livestock. Over the past 50 years, there has been a contraction in the range of Grevy's zebra in northern Kenya (Kingdon 1979), and between 1977 - 1988 a 70% decline in numbers within that range (Dirschl & Wetmore 1978; Grunblatt *et al.* 1989; Rowen & Ginsberg 1993). It is impossible to determine, unambiguously, the cause(s) of these declines because no study has examined the underlying processes over time. However, suggested explanations include habitat degradation (Herlocker 1992), competition for critical resources between zebra and pastoral people and their domestic livestock (Rowen & Ginsberg 1993), and the killing of Grevy's zebra for their skins (R. Elliott, personal communication). Although Rowen & Ginsberg (1993) have suggested that competition may have been important in the decline in numbers, no evidence exists as to whether competition occurs.

The results of this study are critical for the development of a comprehensive management plan for this endangered species as they determine whether competition is an important factor for limiting Grevy's zebra. The importance of this can be appreciated when considering that protected areas comprise only 0.4% of the range of Grevy's zebra in northern Kenya. Nonetheless, most previous studies have been conducted exclusively in protected areas (Ginsberg 1988; Rowen 1992; Rubenstein 1986). The single study conducted outside a protected area was purely ethological in its focus (Klingel 1974). In this study, data on the ecology of Grevy's zebra were collected both in and outside protected areas. Consequently, this study represents a significant extension of the knowledge of Grevy's zebra.

Interspecific competition

Before explaining how I tested the hypothesis that Grevy's zebra compete for critical resources with pastoral people and their domestic livestock, I first examine what is meant by interspecific competition.

Interspecific competition has been considered as one of the major kinds of interactions fundamental to structuring communities and determining the habitat use of species within a community (e.g., bird communities on New Guinean islands, Diamond 1975; the ungulate community of the Serengeti ecosystem, Sinclair 1979). In the 1970s, the prevalent view was that competition was of overriding importance in shaping communities (Cody 1975; Lack 1971; MacArthur 1975). However, non-equilibrial and stochastic forces are now also considered to be important (Diamond & Case 1986; Gee & Giller 1987). Nonetheless, it is thought that competition may determine the number of species that can coexist and the density that any one species can attain in an ecosystem (Keddy 1989).

The study of interspecific competition

Although other disciplines within ecology are founded on some underlying theoretical basis (for example, behavioural ecology has natural selection as its basis, Krebs & Davies 1987), competition has been based almost entirely on the many ways in which it can be investigated: from models to laboratory experiments, field observations to field experiments. Because of this, there exists a wide range of methodologies, evidence, end-results and underlying influences from which the general features of competition have been identified.

Much of the early work focused on investigating the principal underlying premise of competition: 'competitive exclusion' or 'Gause's' principle. Gause's Principle arose from laboratory work (Gause 1934; Gause 1935) that set out to test mathematical models developed by Volterra (1926) and Lotka (1932) that, in turn, examined the conditions that determine the various outcomes of competitive interactions. Gause's Principle states that if two competing species coexist in a stable environment, they do so as a result of niche differentiation (Keddy 1989). If there is no such differentiation, then one of the species will eliminate or exclude the other.

Following on from these laboratory experiments, work in the 1960s and 1970s centred on field observations and niche analyses investigating Gause's principle (e.g. Lack 1971; Levins 1968; MacArthur 1958). The ecological overlaps or similarities (or dissimilarities to explain coexistence) between studied species were described. The underlying premise was that sympatric species diverged due to interspecific competition, thus facilitating coexistence.

One such programme in East Africa set out to investigate the processes that facilitate the coexistence of its diverse ungulate community (Sinclair & Arcese 1995; Sinclair & Norton-Griffiths 1979). Niche differentiation was described for the ungulates at various levels: habitat (Bell 1970; Ferrar & Walker 1974; Jarman 1972; Lamprey 1963; Sinclair 1977); plants eaten (Field 1968; 1972; Jarman 1971) and plant parts eaten (Bell 1970; Gwynne & Bell 1968; Sinclair 1977). These observations led Sinclair (1979) to conclude that interspecific competition was the dominant structuring process in the Serengeti ungulate community.

The studies were largely descriptive and open to criticism. The link between the described overlaps (or differences) and the dynamic effects were not always justified: it may not have been limited resources that caused the described effects on population growth and/or densities (Bender *et al.* 1984). There may have been explanations that mimic the effects of competition (Connor & Simberloff 1979; Diamond & Gilpin 1982; Gilpin & Diamond 1982; Simberloff 1983; 1984). For example, Sinclair and Norton-Griffiths (1982) subsequently re-analysed the data on the Serengeti ungulate community to conclude that predation plays as much of a role as interspecific competition, thus explaining why the plains zebra (*Equus burchelli*) population (of 200,000 individuals) remained relatively stable while the wildebeest (*Connochaetes taurinus*) population expanded from 300,000 to 1.5 million between 1961 - 1985 (Sinclair *et al.* 1985). Moreover, as resource use and the resources were rarely, if ever, measured, competition could only ever be inferred. In undertaking such niche analyses, many of the null hypotheses and alternative hypotheses or explanations, including competition, could never be eliminated.

Other field-based, descriptive studies, described as 'natural experiments' by Diamond (1983), used competition as an explanation for recorded responses to natural perturbations or natural distributions of present populations. These studies included those which compared areas in which the potentially competing species were, naturally, sympatric and allopatric. For example, Diamond (1975) used the distribution of birds on New Guinean islands as evidence for competition, drawing conclusions that species that do not co-occur on islands compete. Such 'experiments' have the advantage of being natural, and are generally on a large scale. However, they suffer the serious defect of having no controls; Diamond (1983) states that control is exercised solely through the potentially subjective process of site selection.

Natural perturbation experiments rely on: 1) having data on a species; 2) a natural disturbance (for example, the colonisation by an exotic species); and 3) the ability to study the responses in the population dynamics of that species and all possible competitors. However, these experiments often ignored coevolution between species. Hence studies that invoke competition as the mechanism that structured present communities, or that determined the outcome of some past interaction, are prone to difficulties of interpretation. Past interactions between species can become so attenuated through coevolution, that present day interactions are weak or absent. Such communities may nonetheless remain structured by these interactions ('ghost of past competition' - Connell 1980).

More recently, the use of controlled experiments has largely replaced descriptive work. Indeed, such experiments are now considered not only sufficient but also necessary to demonstrate unambiguously competitive interactions (Bender *et al.* 1984; Reynoldson & Bellamy 1971). Generally, these experiments use perturbations that alter the density (usually to zero) of one of the potentially competing species, and record the subsequent changes in the density and/or behaviour of the second (or remaining) species. If appropriate, then the resulting dynamics were considered as conclusive proof of the presence or absence and the strength of the interactions.

Although manipulative experiments are considered necessary to demonstrate interspecific competition, they, too, are susceptible to problems. Examples include: 1) manipulated areas may not be equivalent because of the spatial heterogeneity of communities and environments; 2) temporal variation in resource availability results in fluctuation in competitive intensity; and 3) manipulative experiments are susceptible to time-lags, especially when dealing with species with low intrinsic rates of increase and of high longevity. In the case of large species, the ideal of manipulating densities of animals in ecologically similar areas is hampered by the impracticability of large home ranges and the length of the study necessary.

A definition of competition

In order to make predictions about the effects of competition, interspecific competition must first be defined in a way that identifies its operational parts - which are drawn from the above work.

Previously, competition has been defined in two ways which reflect the conflicting aims: thus, whether it be 1) to emphasise the postulated mechanisms of the interaction, or 2) to be more operational and to emphasise the responses to perturbations (Law & Watkinson 1989).

The first approach focuses on the causes - drawing attention to the resources and therefore require their quantification. Such definitions are in the spirit of Milne (1961): 'competition is the endeavour of two (or more) animals to gain the same particular thing, or to gain the measure each wants from the supply of a thing when that supply is not sufficient for both (or all)'. Two mechanisms of competition are recognised from this definition of competition. First, interference competition is direct conflict between individuals for resources. Second and in contrast, exploitative competition occurs when individuals interact with each other indirectly, responding to resource levels which have been depressed by competitors.

The second approach focuses on the effects of competition, particularly on an organism's population dynamics. This has the advantage of avoiding the potential for confusion in species rich communities in which demonstration of resource limitation could be very difficult. It also allows measurement of competition through manipulation of the densities of the potential competitors (Bender *et al.* 1984).

For the purposes of this study, I have used a hybrid definition of competition. Here, competition will be defined as occurring when:

> two or more species interact through their shared requirement for a limited resource. The consequence of such an interaction is a reduction of survivorship, growth and/or reproduction of one or both of the organisms concerned.

This reflects the widespread usage of the term 'competition' in contemporary literature (e.g., Law & Watkinson 1989). The definition is, however, not altogether satisfactory. First, indirect interactions that cause inhibition are not covered. Second, there is no measure of resource dynamics (Tilman 1982), and, therefore, this definition ignores fluctuating competitive intensities caused by a heterogeneous environment.

To make predictions about the effects of competition, the operational parts of the definition must be identified and emphasised. Therefore, interacting species must influence each other's access to or use of limited resources which results in negative effects upon one or both of the species.

To demonstrate the mechanism of competition - that organisms affect one another's access to or use of resources - can be difficult. It requires measurement of the resources themselves and the effect of the organisms on them. That resources are limiting can be measured indirectly by the way in which they are used by the animals (Duncan 1992; Mayes & Duncan 1986) and in the effect that they have on the mortality and condition of the animals (e.g., Fryxell 1987). Assessment of the negative effects on each other requires measurement of a reduction in fecundity, growth and/or survivorship.

Finally, competitive interactions can be highly asymmetrical, with different consequences for each interacting species (e.g., Sinclair 1977). This is particularly relevant when there is a large numerical disparity between competing species. The effect on the less abundant species is expected to be pronounced, with little or no effect on the more abundant species. (The more abundant species' population may, however, be regulated by food limitation and, therefore, intraspecific competition within the species may be important.) Such asymmetry is clearly seen in the interaction between buffalo and wildebeest in the Serengeti, with the smaller populations of buffalo being significantly affected by the larger populations of wildebeest, but not vice versa (Sinclair 1977).

General biology of Grevy's zebra

To provide the foundation on which this study was based, I briefly describe the present distribution, numbers and basic ecology of Grevy's zebra. In particular, I focus on those aspects of the nutritional and reproductive ecology that may be important to demonstrate competition.

Distribution

The ancestral form of Grevy's zebra was once widespread - ranging from central Asia to southern Africa. However, in the past few thousand years, Grevy's zebra have been confined to arid areas in the Horn of Africa (Kingdon 1979). Their historical distribution ranges from the Danakil desert in Eritrea, through the Awash Valley, the Ogaden region, and north-east of Lake Turkana in Ethiopia. They were found in northern Kenya, east of the Rift Valley into western Somalia (Figure 1). There were also reported sightings of Grevy's zebra west of the Rift Valley in Kenya (Stewart & Stewart 1963; Stigand 1913).

Grevy's zebra are considered extirpated from their former range in Eritrea and Somalia (Rowen & Ginsberg 1993; Williams 1998). At present, they are restricted to a few areas (including only one protected area) in Ethiopia: the Alledeghi plains, within the Alledeghi Wildlife Reserve (177 individuals);Yabello Sanctuary and surrounding areas including the Borana Controlled Hunting Area (c. 30 individuals); and in the vicinity of Chew Bahir (about 370 individuals). The total number in Ethiopia was about 1,500 in 1980. A recent aerial survey suggested a total between 500 - 600 animals (Thouless 1995a; Thouless 1995b). This indicates that there has been a serious decline in the number of Grevy's zebra since 1980 in Ethiopia.

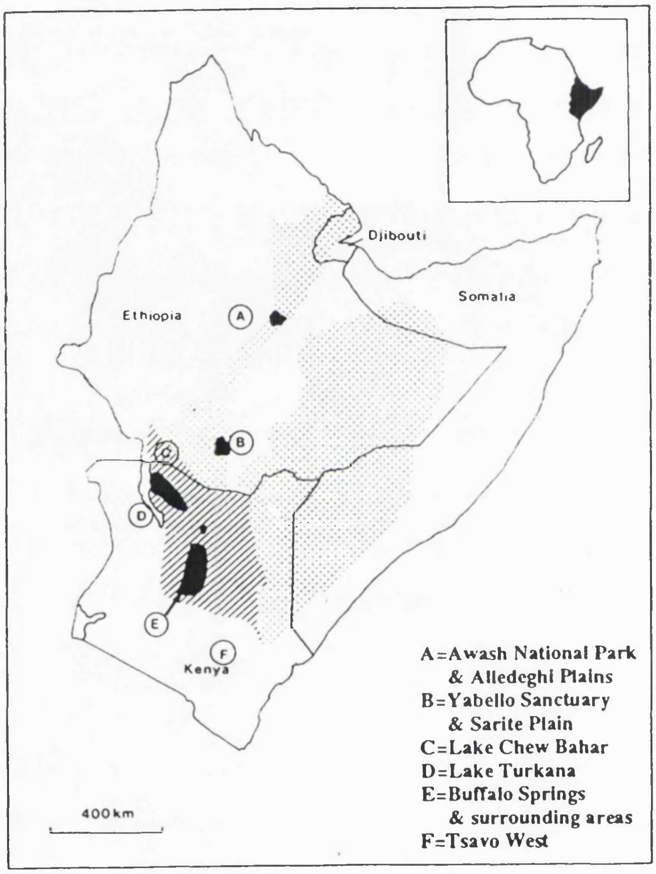

Figure 1. Map of historic (stippled, Kingdon 1979) and present day (hatched ≡ rare, shaded ≡ more abundant, Rowen & Ginsberg 1993) range of Grevy's zebra.

There has been a similar rate of decline in Kenya over the same period. Between 1977 and 1988, a 70% decline in the number of Grevy's zebra was recorded (13,700 to 4,276 animals) (Dirschl & Wetmore 1978; Grunblatt *et al.* 1989; Rowen & Ginsberg 1993).

More recent data suggest that the decline in numbers is continuing, although at a slower rate (Kenya Department of Resource Surveys and Remote Sensing, unpublished data). In contrast, there is evidence that Grevy's zebra are increasing in numbers on the Laikipia Plateau, which, historically, may have been a marginal area for Grevy's (Kingdon 1979).

The largest and most stable remaining Grevy's zebra population is in the south of their range in Kenya (Rowen & Ginsberg 1993; Williams 1998). The estimated size of this population is 1,500 individuals. This population was the focus of this study.

Conservation status

Grevy's zebra are listed on Appendix 1 of CITES. They are legally protected in Ethiopia. In Kenya, they have been protected by the hunting ban since 1977 (Rowen & Ginsberg 1993; Williams 1998).

Grevy's zebra are listed as Endangered A1a and 2c by the IUCN (1996). They are listed because of the 70% decline in numbers in Kenya between 1977 - 1988 (Grunblatt *et al.* 1989), and similar declines reported in Ethiopian populations (Thouless 1995a; Thouless 1995b), and because there is no evidence of any sort of recovery. In fact, the decline is thought to be continuing, albeit at a slower rate.

Ecology and behaviour

The ecology and behaviour of the population of Grevy's zebra that was the focus of this study have been well studied (Ginsberg 1988; Klingel 1974; Rowen 1992; Rubenstein 1989).

Grevy's zebra live in arid and semi-arid grass/shrubland where there is permanent water. They are predominantly grazers (Rowen & Ginsberg 1993). Like other caecal digestors, they have high intake rates and, consequently, when food is limiting they should be constrained to feed in the vegetation communities with the highest biomass of food, regardless of quality (Ginsberg 1988). They require free-standing water as part of their diet; adults can tolerate between 2-5 days away from water, while in lactating females this is reduced to 1-2 days (Becker & Ginsberg 1990). This is notable since lactating females are constrained to remain close to water sources, while other classes of adult female can move larger distances before requiring water.

The social organisation of Grevy's zebra has been described by Klingel (1974) and Ginsberg (1989). Breeding males defend large resource territories: their behaviour and mating success are dependent on the females that are attracted to their territories.

In contrast, a female's reproductive condition determines the priority that she places upon different resources. For example, lactating females are found predictably closer to water than other classes of females and therefore mate with only one male whose territory has access to water. The other classes of female, including those who are late-lactating and non-reproductive (classes of female are defined in chapter 2), are more promiscuous, mating with males whose territories contain resources that have attracted them. Females with young foals are also predictable in their patterns of movement and association. They are usually relatively sedentary, remaining in a single male's territory in close association with other females with whom they are in reproductive synchrony. The other classes of female are less predictable: their associations are fluid and their movements, which are determined by the availability and abundance of food, can be over relatively large distances (Ginsberg 1989).

Approaches of this study

In order to test the hypothesis that Grevy's zebra compete for critical resources with domestic livestock, three study area were chosen in an attempt to approximate a manipulative experiment. The study areas are fully described in chapter 2. The principal difference among the areas was their land use, particularly the density of pastoral people and their domestic livestock. This did not mean that the study was a 'natural experiment', as defined by Diamond (1983). Because the differences among the study areas in livestock densities are maintained by human management (see chapter 2), the study conformed to a manipulative experiment (Bender *et al.* 1984). Therefore, the principle that interspecific competition is best demonstrated by using manipulative experiments was adhered to in this study.

I reiterate that in order to deduce competition, the following should be demonstrated: 1) that the interacting species influence each other's use of, or access to resources; 2) that the resources are limiting; and 3) that the interaction has a negative effect, such as a reduction in abundance or recruitment, on one or both the species. It is essential to point out that in a semi-arid environment like northern Kenya, the resources which may be potentially limiting are food and water (Ginsberg 1988).

Forage

Once the study areas are described and the general methods are explained, in chapter 3, I examine the temporal and spatial availability of forage within habitats in the three study areas. I focus on the extent it appears to be affected by the density of domestic livestock species. To do this, I measured the abundance of forage in the three study areas, relating it to the different densities of domestic livestock. In this way, I assessed the influence of the domestic livestock on the availability of forage for consumption by Grevy's zebra.

In chapter 3, I also examine the responses of Grevy's zebra to the availability of forage and other parameters that may influence their foraging decisions. Their different responses to the availability of forage in the three areas gave indications to the extent to which they were limited by forage. Theory predicts that equids such as Grevy's zebra should be constrained to vegetation communities with high forage availability, regardless of quality, especially when forage is limiting. By spending time on high biomass communities, they maintain high intake rates (Duncan 1983; Duncan 1992; Foose 1982). Therefore, by measuring habitat use by Grevy's zebra in relation to forage abundance, I could assess the extent to which they were differentially constrained in the three study areas.

The extent to which resources are limiting will also affect the dispersal of animals (which for the purposes of this study is simply defined as their large-scale movement). Theory predicts that ungulates in unpredictable environments respond to depletion in the resources by dispersal. Dispersal, as an adaptive strategy, should therefore enhance the access of ungulates to patches of higher forage abundance

(Fryxell *et al.* 1988; Fryxell & Sinclair 1988a; Fryxell & Sinclair 1988b). Here, I examine the dispersal rates of individually identified Grevy's zebra within and among study areas, relating this to the availability of resources (chapter 3).

Following on from this, I examine the aggregative behaviour of Grevy's zebra in relation to key explanatory factors (chapter 4). In particular, I relate the degree of aggregation to the patchiness of resources and predator densities in the three study areas. This further extends the assessment of whether resources, and particularly forage, were limiting in relation to domestic livestock density in the three study areas.

Water

In chapter 5, I study the patterns of water use by Grevy's zebra. Water may often be the ultimate limiting factor in arid environments (Western 1975), since its absence would exclude water-dependent ungulates. Water was not thought to be limiting in this study. Instead, what I predicted to be limiting were the number of accessible water points and the number of hours in a day during which they could be used. I use spatial theory of aggregation of animals (e.g., Hanski & Gilpin 1991) as the basis for predictions and go on to examine the temporal use of water by Grevy's zebra. By doing this, I assess whether domestic livestock affect the use of, or access to, water by Grevy's zebra.

Costs of competition

Finally, in chapter 6, I investigate the relative costs incurred by individuals in the three study areas. The focus of this was two-fold. First, I examine the different energetic costs incurred by individuals among the areas. This was done by comparing the distances that the animals moved to and from water among the three areas (chapters 3 and 5). Since dispersal is also costly, the predictability of dispersal out of study areas was also examined (chapters 3 and 6).

Second, the effect that area has on recruitment was examined by studying the patterns of reproduction and juvenile survival among the study areas (chapter 6). This was based on the fact that theory and empirical studies of Grevy's zebra have shown that mares with young foals remain relatively sedentary, usually within a single male's territory (Becker & Ginsberg 1990; Ginsberg 1989). Therefore, these females and territorial males were predicted to be the only truly 'resident' animals within each of the study areas. Consequently, I compared the ecology and relative costs of lactating females among the three study areas.

The concluding chapter (chapter 7) draws together these chapters, and re-evaluates the evidence for and against interspecific competition between Grevy's zebra and domestic livestock for critical resources. I also consider the management implications for Grevy's zebra from the results of the study.

References

Becker, C. D. & Ginsberg, J. R. 1990 Mother infant behavior of wild Grevy's zebra: adaptations for survival in semi-desert east Africa. *Animal Behaviour* **40**, 1111-1118.

Bell, R. H. V. 1970 The use of the herb layer by grazing ungulates in the Serengeti. In *Animal populations in relation to their food resources* (ed. A. Watson). Oxford: Blackwell Scientific Publictions.

Bender, E. A., Case, T. J. & Gilpin, M. E. 1984 Perturbation experiments in community ecology: theory and practice. *Ecology* **65**, 1-13.

Cody, M. L. 1975 Towards a theory of continental species diversity. In *Ecology and Evolution of Communities* (ed. M. L. Cody & J. M. Diamond). Cambridge, MA: Belknap.

Connell, J. H. 1980 Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* **35**, 131-138.

Connor, E. & Simberloff, D. 1979 The assembly of species: chance or competition. *Ecology* **60**, 1132-1140.

Diamond, J. M. 1975 Assembly of species communities. In *Ecology and Evolution of Communities* (ed. M. L. Cody & J. M. Diamond). Cambridge, MA: Belknap.

Diamond, J. M. 1983 Ecology Laboratory, Field and Natural Experiments. *Nature* **304**, 586-587.

Diamond, J. M. & Case, T. J. 1986 *Community Ecology.* New York: Harper & Row.

Diamond, J. M. & Gilpin, M. E. 1982 Examination of the null model of Connor and Simberloff for species co-occurrences on islands. *Oecologia* **52**, 64-74.

Dirschl, H. J. & Wetmore, S. P. 1978 Grevy's zebra abundance and distribution in Kenya, 1977. Nairobi, Kenya: Kenya Rangeland Ecological Monitoring Unit.

Duncan, P. 1983 Determinants of the use of habitats by horses in a Mediterranean wetland. *Journal of Animal Ecology* **52**, 93-109.

Duncan, P. 1992 *Horses and grasses: the nutritional ecology of equids and their impact on the Camargue*. Ecological Studies. New York: Springer-Verlag.

Ferrar, A. A. & Walker, B. H. 1974 An analysis of herbivore/habitat relationships in Kyle National Park, Rhodesia. *Journal of the South African Management Association* **4**, 137-147.

Field, C. R. 1968 The food habits of some wild ungulates in Uganda. Cambridge: University of Cambridge.

Field, C. R. 1972 Food habits of some wild ungulates in Uganda by analysis of stomach contents. *East African Wildlife Journal* **10**, 17.

Foose, T. J. 1982 Trophic strategies of ruminant versus nonruminant ungulates. Chicago: University of Chicago.

Fryxell, J. M. 1987 Food limitation and demography of a migratory antelope, the white-eared kob. *Oecologia* **72**, 83-91.

Fryxell, J. M., Greever, J. & Sinclair, A. R. E. 1988 Why are migratory ungulates so abundant. *American Naturalist* **131**, 781-798.

Fryxell, J. M. & Sinclair, A. R. E. 1988a Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution* **3**, 237-241.

Fryxell, J. M. & Sinclair, A. R. E. 1988b Seasonal migration by white eared kob in relation to resources. *African Journal of Ecology* **26**, 17-31.

Gause, G. F. 1934 *The struggle for existence*. New York: Hafner.

Gause, G. F. 1935 Experimental demonstration of Volterra's periodic oscillation in the number of animals. *Journal of Experimental Biology* **12**, 44-48.

Gee, J. H. R. & Giller, P. S. 1987 *Organisation of Communities: Past and Present.* Oxford: Blackwell Scientific Publications.

Gilpin, M. E. & Diamond, J. M. 1982 Factors contributing to non randomness in species co-occurrences on islands. *Oecologia* **52**, 75-84.

Ginsberg, J. R. 1988 Social organization and mating strategies of an arid-adapted equid: the Grevy's zebra. Princeton, New Jersey: Princeton University.

Ginsberg, J. R. 1989 The ecology of female behaviour and male reproductive success in Grevy's zebra, *Equus grevyi*. *Symposia of the Zoological Society (London)* **61**, 89-110.

Grunblatt, J., Said, M. Y. & Nutira, J. K. 1989 Livestock and wildlife summary 1987 - 1988 for Kenya Rangelands. Nairobi, Kenya: Department of Resource Surveys and Remote Sensing, Ministry of Planning and National Development.

Gwynne, M. D. & Bell, R. H. V. 1968 Selection of vegetation components by grazing ungulates in the Serengeti National Park. *Nature* **220**, 390-393.

Hanski, I. & Gilpin, M. 1991 Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**, 3-16.

Herlocker, D. J. 1992 Vegetation types. In *Range Management Handbook of Kenya, Volume II, 2: Samburu District* (ed. S. B. Shaabani, M. Walsh, D. J. Herlocker & D. Walther). Nairobi, Kenya: Republic of Kenya, Ministry of Livestock Development (MOLD).

IUCN. 1996 *1996 IUCN Red List of Threatened Animals*. The IUCN Species Survival Commission. Gland, Switzerland: IUCN.

Jarman, P. J. 1971 Diets of large mammals in the woodlands around Lake Kariba, Rhodesia. *Oecologia* **8**, 157-178.

Jarman, P. J. 1972 Seasonal distribution of large mammal populations in the unflooded middle Zambezi valley. *Journal of Applied Ecology* **9**, 283-299.

Keddy, P. A. 1989 *Competition*. London: Chapman.

Kingdon, J. 1979 *East African Mammals: An Atlas of Evolution in Africa*. Chicago: Chicago University Press.

Klingel, H. 1974 Social organisation and behaviour of the Grevy's zebra. *Zeitscrift für Tierpsychologie* **36**, 36-70.

Krebs, J. R. & Davies, N. B. 1987 *An Introduction to Behavioural Ecology*. Oxford: Blackwells Scientific Publications.

Lack, D. 1971 *Ecological isolation in birds*. Oxford: Blackwell Scientific Publications.

Lamprey, H. K. 1963 Ecological separation of large mammal species in Tarangire Game Reserve, Tanzania. *East African Wildlife Journal* **1**, 1-20.

Law, R. & Watkinson, A. R. 1989 Competition. In *Ecological Concepts* (ed. J. M. Cherret & R. Law). Oxford: Blackwell Scientific Publications.

Levins, R. 1968 *Evolution in changing environments.* Princeton: Princeton University Press.

Lotka, A. J. 1932 The growth of mixed populations: two species competing for a common food supply. *Journal of the Washinton Academy of Sciences* **22**, 461-469.

MacArthur, J. W. 1975 Environmental fluctuations and species diversity. In *Ecology and Evolution of Communities* (ed. M. L. Cody & J. M. Diamond). Cambridge, MA: Belknap.

MacArthur, R. H. 1958 Population ecology of some warblers of north-eastern coniferous forests. *Ecology* **39**, 599-619.

Mayes, E. & Duncan, P. 1986 Temporal patterns of feeding behavior in free ranging horses. *Behaviour* **96**, 105-129.

Milne, A. 1961 Definition of competition among animals. *Symposia of the Society of Experimental Biology* **15**, 40-61.

Reynoldson, T. B. & Bellamy, L. S. 1971 The establishment of interspecific competition in field populations, with an example of competition in action between *Polcelis nigra* (Mull.) and *P. tenuis* (Ijima) (Turbellaria, Tricladida). *Proceedings of the Advanced Studies Institute in Dynamics, Numbers and Populations, Oosterbeck, 1970* .

Rowen, M. 1992 Mother-infant behavior and ecology of Grevy's zebra, *Equus grevyi.* Yale: Yale University.

Rowen, M. & Ginsberg, J. R. 1993 Grevy's zebra (*Equus grevyi* Oustalet). In *Equid Action Plan* (ed. P. Duncan). Gland, Switzerland: IUCN.

Rubenstein, D. I. 1986 Life history and social organisation in arid adapted ungulates. In *Ecological aspects of social evolution.* (ed. D. I. Rubenstein & R. W. Wrangham). Princeton: Princeton University Press.

Rubenstein, D. I. 1989 Life History and Social Organization In Arid Adapted Ungulates. *Journal Of Arid Environments* **17**, 145-156.

Simberloff, D. 1983 Competition theory, hypothesis testing, and other community ecological buzzwords. *American Naturalist* **122**, 626-635.

Simberloff, D. S. 1984 Properties of coexisting bird species in two archipelagoes. In *Ecological Communities: Conceptual issues and evidence* (ed. D. R. Strong, D. S. Simberloff, L. G. Abele & A. B. Thistle). Princeton, New Jersey: Princeton University Press.

Sinclair, A. R. E. 1977 *The African Buffalo.* Chicago: Chicago University Press.

Sinclair, A. R. E. 1979 Dynamics of the Serengeti ecosystem: process and pattern. In *Serengeti: Dynamics of an Ecosystem* (ed. A. R. E. Sinclair & M. Norton-Griffiths). Chicago: Chicago University Press.

Sinclair, A. R. E. & Arcese, P. 1995 *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem.* Chicago: The University of Chicago Press.

Sinclair, A. R. E., Dublin, H. & Borner, M. 1985 Population regulation of Serengeti wildebeest - a test of the food hypothesis. *Oecologia* **65**, 266-268.

Sinclair, A. R. E. & Norton-Griffiths, M. 1979 *Serengeti: Dynamics of an Ecosystem.* Chicago: Chicago University Press.

Sinclair, A. R. E. & Norton-Griffiths, M. 1982 Does competition or facilitation regulate migrant ungulate populations in the Serengeti? A test of hypotheses. *Oecologia* **53**, 364-369.

Stewart, D. R. M. & Stewart, J. 1963 The distribution of some large mammals in Kenya. *Journal of the East African Natural History Society and Coryndon Museum* **24**, 1-52.

Stigand, C. H. 1913 *The Game of British East Africa.* London: McMillan & Co., Ltd.

Thouless, C. R. 1995a Aerial Surveys for Wildlife in Eastern Ethiopia. London: Ecosystem Consultants.

Thouless, C. R. 1995b Aerial Surveys for Wildlife in Omo Valley, Chew Bahir and Borana Areas of Southern Ethiopia. London: Ecosystem Consultants.

Tilman, D. 1982 *Resource competition and community structure.* Princeton: Princeton University Press.

Volterra, V. 1926 Variations and fluctuations in the numbers of individuals in animal species living together. In *Animal Ecology* (ed. R. N. Chapman). New York: McGraw Hill.

Western, D. 1975 Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East African Wildlife Journal* **13**, 265-286.

Williams, S. D. 1998 Grevy's zebra. In *Zebras, Asses, and Horses: An Action Plan for the Conservation of Wild Equids* (ed. P. Moehlman). Gland, Switzerland: IUCN.

2. General methods

In this chapter, I describe the general methodology used during this study. The detailed methods that are pertinent for the data analyses in each of the subsequent chapters are therein described.

Study areas

As described in chapter 1, three study areas were chosen to approximate a manipulative experiment. The areas, each approximately 200 km^2, were in the western extension of Isiolo District, Kenya (between 37 - 38°E and 0 - 1°N; Figure 1). The study areas were matched as closely as possible for their climate, topography, geology, soil types, altitude, and general vegetation classification (Herlocker 1993; Jätzold & Bake 1995; Pratt *et al.* 1971; Pratt & Gwynne 1977; Schwartz & Walsh 1993; Touber 1993).

The three areas, Barsalinga, Ngare Ndare and Buffalo Springs National Reserve (hereafter referred to as Buffalo Springs), were chosen because they were areas known to be used by Grevy's zebra, and because they were thought to be important birthing areas (P. Jenkins, personal communication; Rowen & Ginsberg, 1993). The principal difference among the three study areas was the level of use by pastoralist people (Table 1). Barsalinga was an area heavily used by pastoralists. Ngare Ndare was used less intensively by pastoralists. Finally, pastoralists and their domestic livestock were excluded from the third study area, Buffalo Springs. The exclusion of pastoral people from Buffalo Springs is historic, and has been the case since the area was gazetted as a Game Reserve in the 1962.

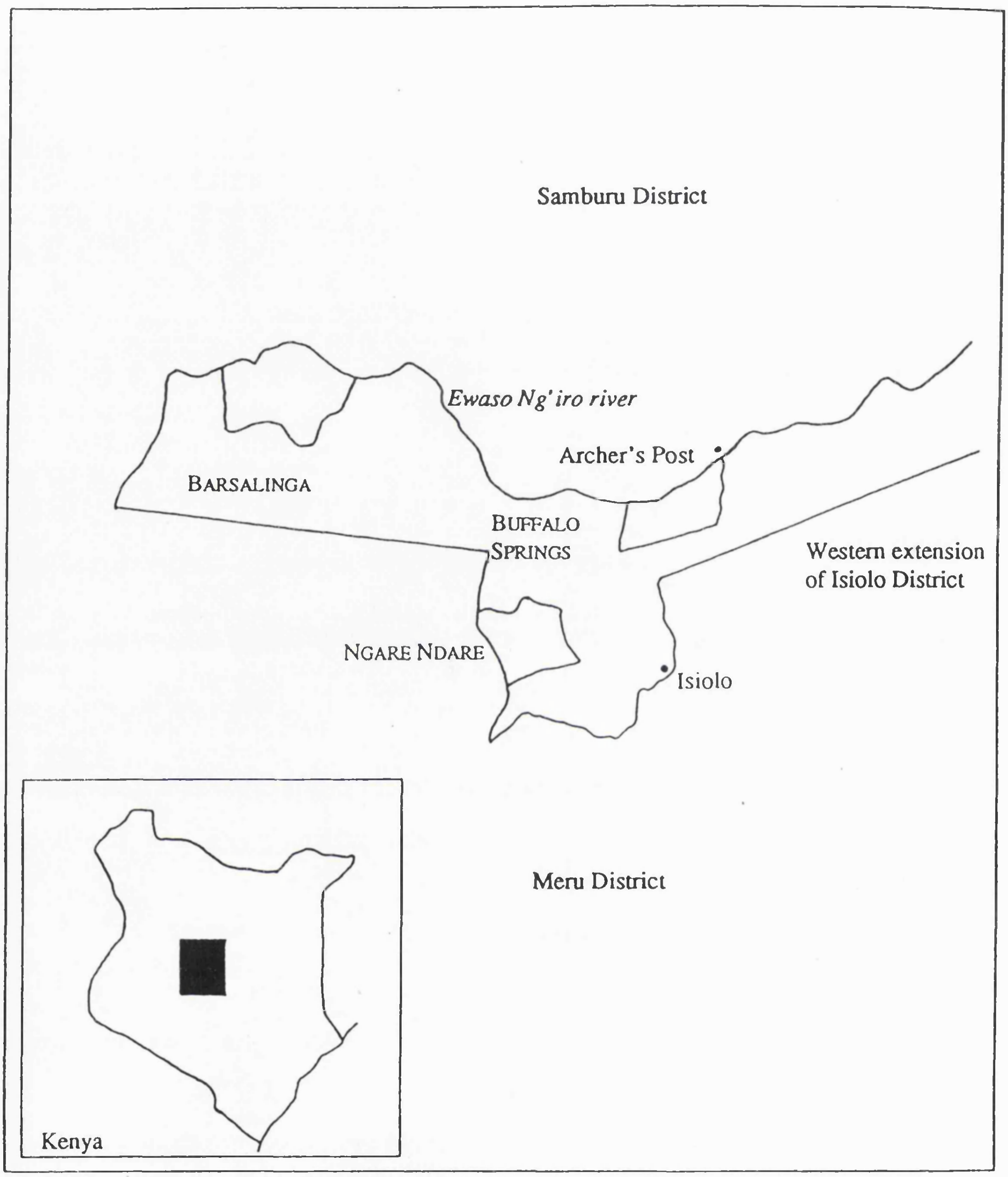

Figure 1. The location of the three study areas, Barsalinga, Ngare Ndare and Buffalo Springs in the western extension of Isiolo District, Kenya.

The study was obviously limited by having only three study areas. However, I shall argue in this thesis that the study areas were used by a large proportion of the southern population of Grevy's zebra. For example, a total of 300 births were recorded over this study. In a population of approximately 1,500 animals (see chapter 1), and assuming an equal sex ratio, this probably represents a sample of up to 50% of the reproductively viable and mature females. Hence, although the data on the Grevy's zebra may be representative, I will be limited in the extent to which I will be able to generalise the results of the effects of the study areas on the zebra. The study was also limited to three study areas by practical and time constraints.

Table 1. The differences in the density indices of humans and their domestic livestock species in Barsalinga and Ngare Ndare. The density of pastoral people and domestic livestock in Buffalo Springs was zero. For the livestock species, the standard error about the mean over 5 surveys is given in parentheses, while the standard deviation is given for humans.

	Barsalinga	Ngare Ndare
Cattle	2131 (± 732.7)[§]	1380 (± 277.2)
Smallstock[*]	4323 (± 998.2)	3126 (± 920.1)
Donkeys	272 (± 49.6)	159 (± 44.7)
Camels	177 (± 92.1)	278 (± 96.3)
Humans	0.39 (± 0.24)[‡]	0.15 (± 0.29)

[*] Smallstock refers to mixed groups of sheep and goats, which were managed by the pastoral people as a single, broad trophic unit. They are therefore referred to as 'smallstock' throughout this thesis.

[§] The mean density indices of the domestic livestock species were calculated from data over five surveys of the study areas. The indices for each survey were calculated from the number of each species recorded during the survey and the effort (time spent) surveying.

[‡] The density indices for the human were calculated from the mean number of people from a sample of 13 *manyattas* (pastoralist family unit villages) and the total number of permanent *manyattas* in each area.

The communities of both wild and domestic ungulates, and therefore potential competitors, were markedly different in each of the study areas. In Buffalo Springs, the ungulate community was comprised only of wild ungulates. These included: elephants (*Loxodonta africana*), buffalo (*Synercus caffer*), eland (*Taurotragus oryx*), plains zebra (*Equus burchelli*), beisa oryx (*Oryx b. beisa*), Grant's gazelle (*Gazella granti*), warthog (*Phacochoerus aethiopicus*), giraffe (*Giraffa camelopardalis reticulata*), impala (*Aepyceros melampus*) and gerenuk (*Litocranius walleri*). In contrast, in Barsalinga the ungulate community was dominated by domestic livestock species (cattle, smallstock, donkeys and camels), although the same wild ungulate species were present at lower densities than in Buffalo Springs (S. D. Williams, unpublished data; Grunblatt *et al.* 1989).

The densities of predators, in particular lions and hyaenas, were different in the three study areas, with Buffalo Springs having higher overall densities (see chapter 3, 4 & 5).

Those wild ungulates that could potentially act as competitors to Grevy's zebra, and, therefore, confound the study, were Beisa oryx (*Oryx b. beisa*) and plains zebra (*Equus burchelli*). However, these species have coevolved with Grevy's zebra in this environment, and their coexistence should have been facilitated by niche differentiation. Therefore, competition among these species should be minimised. In contrast, domestic livestock are, in ecological time, exotics: evidence suggests the earliest they were introduced into the region was 8,000 BP (Phillipson 1976; Sobania 1979). However, it was not until the 1940s and the introduction of development aid (Brown & Wolf 1984; Sinclair & Fryxell 1985) that the number of domestic livestock substantially increased (Bronner 1990, data from the Kenya National Archives). Therefore, interspecific competition between the wild ungulates and Grevy's zebra is likely to have become highly attenuated through coevolution (Connell 1980). Moreover, numerically, in an area such as Barsalinga, the domestic livestock outnumber the wild ungulates by 70:1 (this study; Grunblatt *et al.* 1989). Therefore, the relative impact of interspecific competition between Grevy's zebra and wild ungulates is likely to be far outweighed by the effect of domestic livestock.

Climate and seasonality

The climate in the region including the study areas is described as hot and dry (Pratt *et al.* 1971). There is a clear annual bimodality of rainfall, and therefore the area is generally described as having two dry and two rainy seasons (Pratt & Gwynne 1977). However, rainfall is highly variable, with a mean of 357mm, with a coefficient of variation of 43mm (long-term data taken from 1957 - 1994 for Archer's Post; data from the Kenya Meteorological Department). There is a low predictability of an area receiving rain even during the 'rainy' season (Jätzold & Bake 1995).

In this study, the seasons were defined by the amount of available water in the study areas, and categorised into rains, early dry, dry, or late dry seasons (after Ginsberg 1988). During the rainy season, water was generally ubiquitous. Water availability declined towards the late dry season as ephemeral water dried up, leaving only permanent water sources in the late dry season (Ginsberg 1988). There were no drought conditions over the period of the study, where drought was defined as one wet season being missed (Ginsberg 1988). The cycle of the seasons was re-started as soon as any rain fell. Therefore, the seasons were clearly defined but highly variable.

Soils and landforms

The geology of the region in which the study areas are found is comprised of a diversity of soil and rock types associated with a long history of erosion of Pre-Cambrian basement rocks, fluvial accumulation of sediments and soils deriving from recent volcanic activity (Jennings 1966). The most detailed study of the landforms and soils of the region is published by Touber (1993).

The topography of the three areas was very similar. In general, the topography consisted of flat or gently undulating erosion plains, volcanic plains or footslopes, all either flat or gently to very gently undulating topography with long slopes of up to a maximum of 5%. The geology was also similar, dominated by colluvia or complexes derived from Basement System rocks (mainly undifferentiated), lavaflows of Pleistocene to Recent age, and more rarely Pleistocene calcareous lake bed deposits. Finally, the soils were equivalent, with three soil types dominating all three study areas: 1) well drained, moderate to very deep, dark reddish brown to dusky red, friable to firm, coarse sandy loams to sandy clay (sometimes stony and sometimes with a coarse sandy topsoil), often with local rock outcrops in upslope positions; 2) imperfectly drained, very deep, dark greyish brown to black, cracking clays, in places saline in the deeper subsoil, with a stony surface; and 3) well-drained, shallow to moderately deep, dark brown to dark reddish-brown, friable, gravelly, coarse sandy clay loam, with local rock outcrops in upslope positions. (Touber 1993).

Study area differences in soil attributes arising from both gully and sheet erosion may be attributed to the long-term effects of heavy grazing regimes maintained by pastoral people over the past 50 years (Bronner 1990; Herlocker 1993; Mäckel & Walther 1994; Touber 1993).

Vegetation communities

The study areas conformed to Pratt *et al.*'s (1971) ecological Zone V, semi-arid wooded and bush-covered grasslands. In a more detailed vegetation classification for Isiolo District (Herlocker 1993), the region which included the study areas is comprised of: *Oropetium - Indigofera - Acacia tortilis* deciduous wooded grassland, *Leptothrium - Aristida - Cordia - A. tortilis* deciduous bush grassland, *Panicum - A. tortilis - A. mellifera* deciduous bush grassland, and *Tetrapogon - Aristida - A. tortilis - A. senegal* deciduous bush annual grassland.

For the purposes of this study, the vegetation communities were described in more detail than in either Pratt *et al.*'s (1971) or Herlocker's (1993) classifications. Here, I described vegetation communities by their dominant plant species at each of the tree, shrub and dwarf shrub, and herbaceous levels. At the beginning of the fieldwork, the vegetation community boundaries were determined subjectively during driven surveys of the study areas (see below) using tree, dwarf shrub, succulent and some grass species, and soil colour and texture as indicators. The boundaries were later confirmed and the vegetation communities described quantitatively when the proportional species composition was estimated by step-point measurements (see below). The species of each hit was recorded as well as those data required for quantification of the food availability.

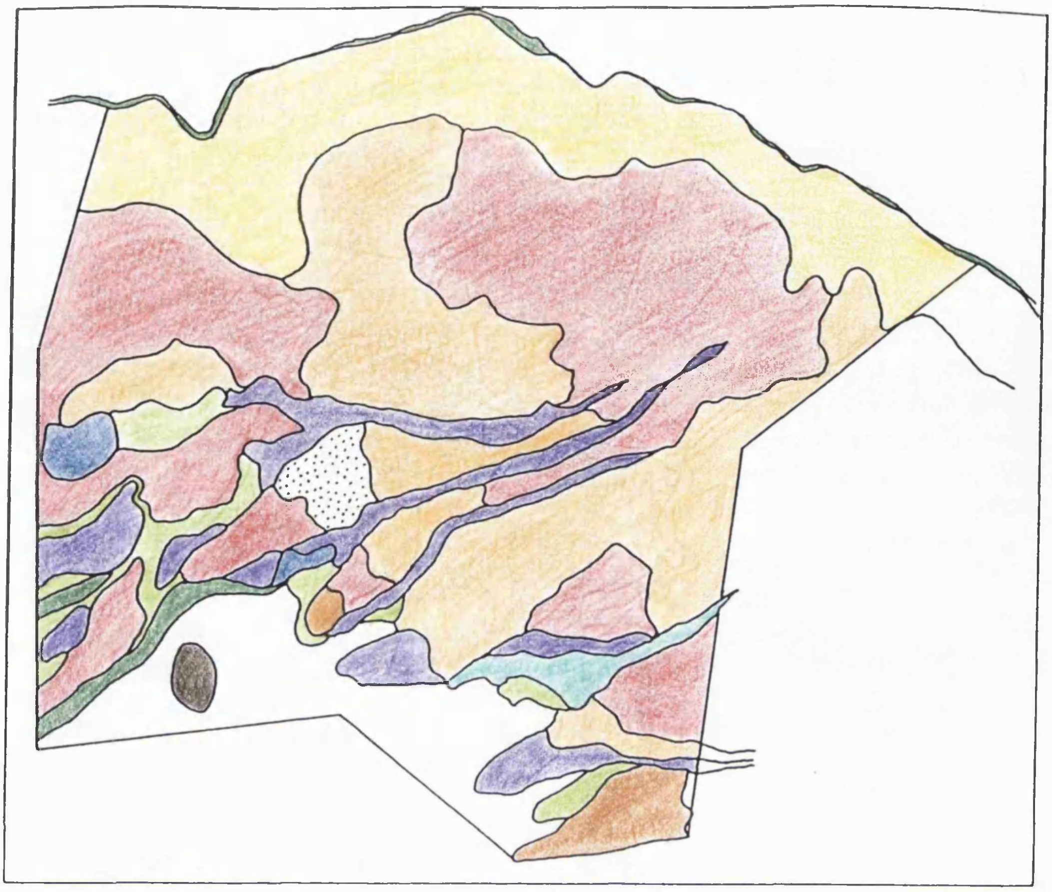

Figure 2a. The vegetation communities in Barsalinga. Key:

🟪 Alluvial *Pennisetum* sp/*Setaria* sp grassland

☐ *A. tortilis* shrub grassland

🟦 *A. tortilis* dwarf shrubland

🟧 *A. tortilis/Commiphora* sp woodland

🟨 *A. senegal/Commiphora* sp woodland

🟩 Mixed *A. tortilis/A. reficiens* woodland

🟧 *A. reficiens* woodland

⬚ *A. reficiens* dwarf shrubland

☐ *A. reficiens/A. nubica/A. horrida* woodland

🟩 Dry river bed/riverine

🟦 Mixed *A, tortilis/A. reficiens* woodland

🟫 Granite outcrop

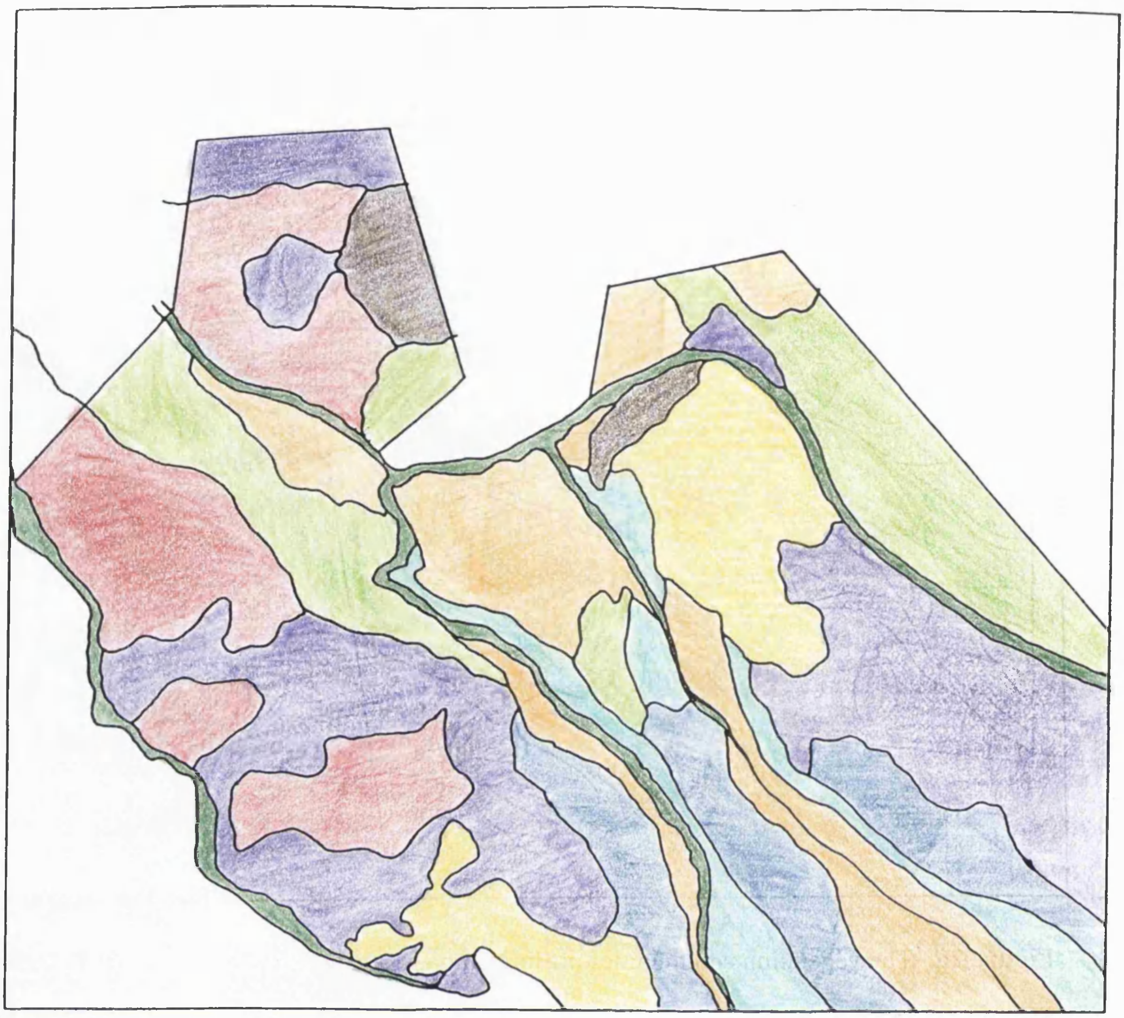

Figure 2b. The vegetation communities in Ngare Ndare. Key:

🟪 Alluvial *Pennisetum* sp/*Setaria* sp grassland

🟥 *tortilis* shrub grassland

🟨 *tortilis* dwarf shrubland

🟦 *tortilis*/*Commiphora* sp woodland

▨ Mixed *A. tortilis*/*A. reficiens* woodland

🟩 *reficiens* woodland

🟧 *tortilis*/*A. mellifera*/*A. horrida* riverine woodland

▩ Dry river bed/riverine

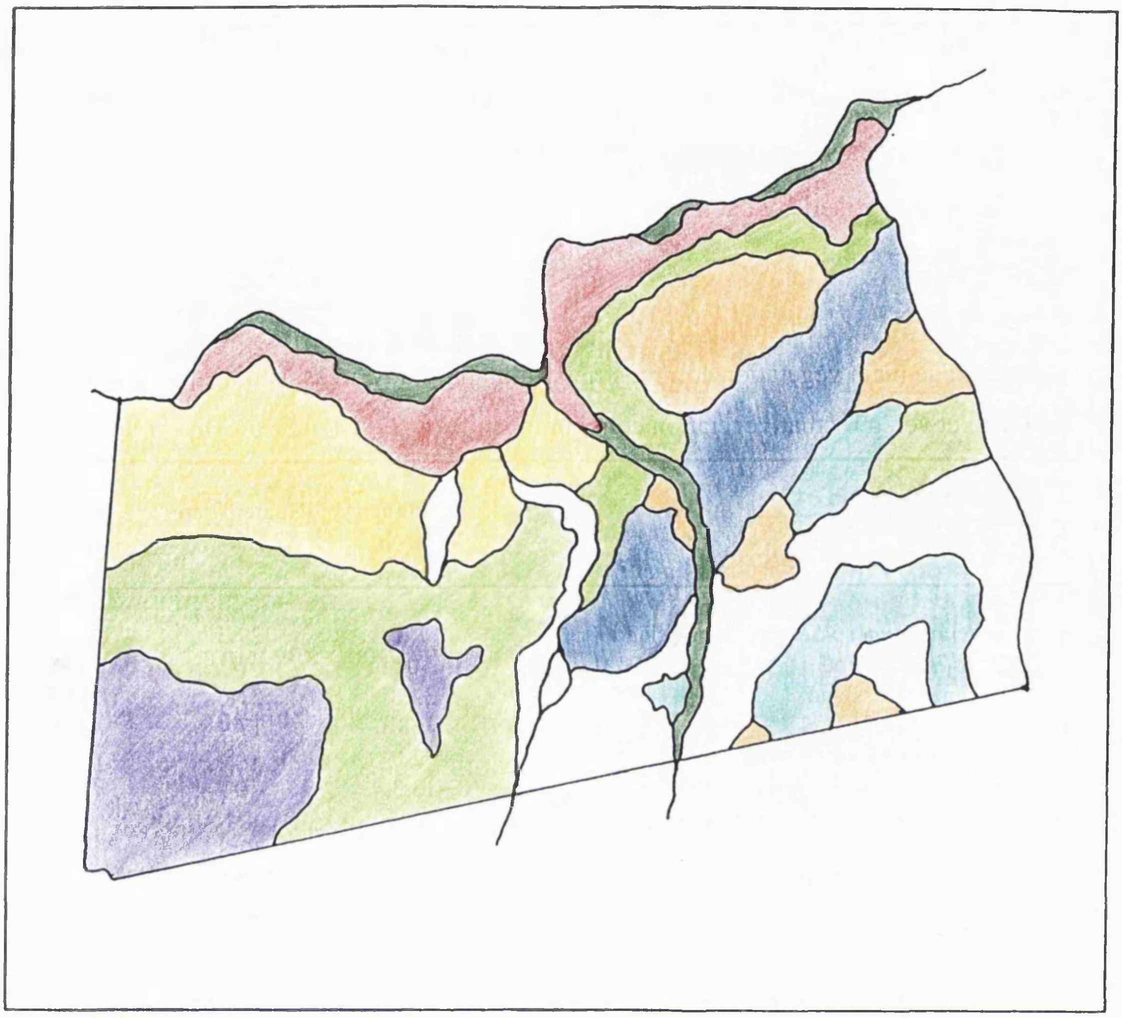

Figure 2c. The vegetation communities in Buffalo Springs. Key:

🟪 Alluvial *Pennisetum* sp/*Setaria* sp grassland

🟨 *Acacia tortilis* grassland

⬜ *A. tortilis* shrub grassland

🟩 *A. tortilis* dwarf shrubland

🟦 Mixed *A. tortilis*/*A. reficiens* woodland

🟧 *A. reficiens* woodland

🟦 *A. reficiens* dwarf shrubland

🟩 Dry river bed/riverine

🟥 *Salsola dendroides*/*Sporobolus spicatus* shrubland

Once the vegetation communities were described, maps of each of the study areas were drawn (Figure 2a-c). In order to estimate the proportion of each study area comprised by each vegetation community, a grid, representing 300 x 300m on the ground, was layered over the maps. The number of corners (where the grid lines intersected) in each vegetation community was counted. The percentage of each study area comprised by each vegetation community could then be calculated (Table 2).

Table 2. The main vegetation communities within the study areas, and the percentage of each area covered by that vegetation community.

	Barsalinga	Ngare Ndare	Buffalo Springs
Alluvial *Pennisetum* sp/*Setaria* sp grassland	7.0	29.3	7.7
Acacia tortilis grassland	0	0	2.7
A. tortilis shrub grassland	32.8	21.6	14.3
A. tortilis dwarf shrubland	0.8	17.4	33.5
A. tortilis/Commiphora sp woodland	32.0	6.5	0.3
A. senegal/Commiphora sp woodland	13.3	0	0
Mixed *A. tortilis/A. reficiens* woodland	1.1	4.4	11.9
A. reficiens woodland	6.7	13.8	6.7
A. reficiens dwarf shrubland	0	0	6.4
A. reficiens/A. nubica/A. horrida woodland	5.4	0	0
A. tortilis/A. mellifera/A. horrida riverine woodland	0	4.8	0
Dry river bed/riverine	1.1	2.2	3.3
Salsola dendroides/Sporobolus spicatus shrubland	0	0	13.3

As with the differences in soils, fine scale differences in the vegetation communities of the areas may also be attributed to the long-term effects of heavy grazing regimes maintained by pastoral people over the past 50 years (Bronner 1990; Herlocker 1990; Herlocker 1992; Herlocker 1993)[1].

Water sources

All three study areas had permanent water sources for use by grazing ungulates. Therefore, water *per se* was not a limiting resource for grazing ungulates.

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[1] For alternative explanations see references in Behnke (1992), although in contrast to the work of Bronner and Herlocker, studies published in Behnke (1992) were not conducted in northern Kenya and therefore may not be applicable.

The different distribution of water sources in each of the areas did have important implications on the distribution of both the Grevy's zebra and the domestic livestock species. In Ngare Ndare, there were water sources that were accessible to domestic livestock, but not by Grevy's zebra. This was because of: 1) the depth of human-dug wells[2]; and 2) their proximity to human habitation. The consequence was that the distribution of water sources in Ngare Ndare allowed domestic livestock access to the whole study area. In contrast, the distribution of water for use by Grevy's zebra was the same in both Barsalinga and Ngare Ndare, with a single linear source being usable only at specific, accessible points.

In this study, I defined water sources by their accessibility for use by ungulates, and therefore as 'usable'. Three categories were used to define a water source as usable: 1) the steepness of the approach to water; 2) the thickness of the surrounding vegetation and therefore the visibility it allowed ungulates on their approach to water; and 3) its proximity to human habitation. This was a modification of Ginsberg's (1988) definition of water sources in Buffalo Springs. He defined 'safe' water by the visibility and accessibility. Thus using criteria determined by Ginsberg (1988), safe water required a visibility of greater than 20m in all directions. In this study, water in the vicinity of human habitation may have been 'safe' but may have been unusable for Grevy's zebra. Visibility was considered to be important since lion predation occurs mostly near water (see chapter 5; Packer 1986; Schaller 1972). Lions are the only major predator in northern Kenya know to take adult Grevy's zebra (pers. obs.; Rowen & Ginsberg 1993).

Data collection

The study was conducted between September 1993 and August 1995. During this period, the study areas were visited in rotation, with each rotation starting in Barsalinga and ending in Buffalo Springs. Because of the unpredictable nature of the

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[2] The water from deep human-dug wells was made accessible to domestic livestock species by their human herders, who carried the water in buckets from the depths of the well to fill troughs (personal observation; Spencer 1965)

seasons, it was impossible to schedule surveys of the study areas by season. The surveys were, therefore, conducted successively and while in each study area the season was recorded (Table 3). Over the duration of the study, six complete rotations of the study areas were conducted. In addition, in June 1995, a seventh survey of Buffalo Springs and the two adjacent national reserves - Samburu and Shaba - was conducted as part of a larger survey for Grevy's zebra in northern Kenya (Wisbey 1995). This final survey was used only in the capture-mark-recapture analyses of survival (see chapter 6).

Within each rotation of the study areas, and, hence, during all surveys, the availability of forage in vegetation communities was measured (with the exception of the first rotation and the final survey), the distribution of water mapped, and the area censused for animals.

Forage availability

The quantitative analysis of forage focused primarily on the amount of grass available for consumption by grazing herbivores. Previous studies have shown that forage closest to the water sources is most rapidly depleted through the dry season (Herlocker 1992; Western 1975). Therefore, in theory, vegetation communities that have the same species composition, but occur at different distances from permanent water, could have different forage availability. Therefore, measurements were taken within each 'habitat', defined here as being vegetation communities at different distances from water. The following intervals, in kilometres from water, for the measurements were chosen: 0.25km; 2km; 4.5km; 7.5km; and 12km. A finer interval was chosen closer to water to quantify the greater rate of forage depletion in the vicinity of water reported by Herlocker (1992) and Western (1975).

Because of time constraints, the abundance of forage was not quantified in all possible habitats. However, all the main habitats were sampled (Table 2). In order to measure the availability of forage, four independent 50 step-point samples were taken in each habitat at each distance from water, each starting from a random point and taken in a random direction (after Ginsberg 1988). At each pace, the class of plant (graminoid or forb) hit by a point directly in front of the big toe was recorded at the

Table 3. The timing of the surveys in each study area (Barsalinga: Bar; Ngare Ndare: NN; Buffalo Springs: BS) in relation to the seasons. The first survey 'A' was conducted without vegetation measurements, but is included here as the areas were surveyed for animals.

Year	1993			1994												1995			
Month	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4
Season	**Rains**	**Early dry**		Dry	Late dry		**Rains**	**Early dry**		Dry			**Rains**	**Early dry**		Dry		**Rains**	
Study area	Bar	NN	BS	Bar	NN	BS	Bar	NN	BS		Bar	NN	BS	Bar	NN	BS	Bar	NN	BS
Survey		A			1			2				3			4			5	

herbaceous level. This step-point sampling provided data on the vegetation cover at this level. If grass was 'hit', then its height was also recorded. In addition, later in the study, the species of grass was also recorded, if hit, so as to estimate the compositions of the vegetation communities.

These crude measures of forage abundance were related to the biomass of vegetation available for consumption by clipping an area of $0.2m^2$ to the ground, during seasons of high, medium and low forage availability. The clipping was taken at the fiftieth pace of each of the 50 step-points, and therefore four times per habitat. The clippings were weighed and allowed to dry. The clipped grass was weighed every two months until the weight reached a constant: this was taken as the dry weight of the clipping. The regression between the log of the dry grass weight (log biomass) from the clippings and the percentage cover of grass was highly significant ($r^2=0.33$, $F_{1,136}=65.8$, $P<0.001$, Figure 3). The percentage cover of grass was, therefore, taken as the general measure of availability of forage throughout this thesis.

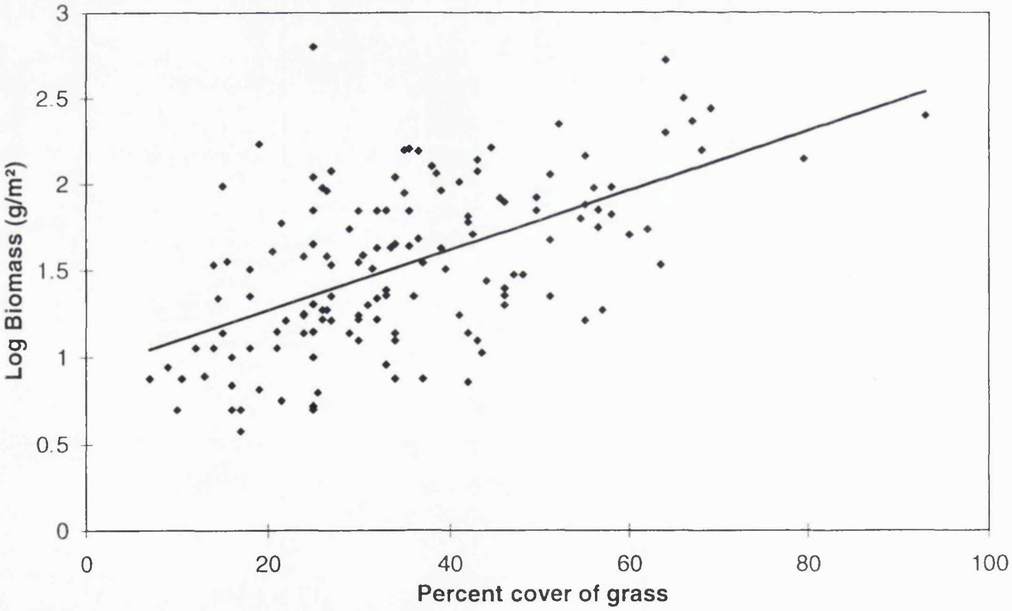


Figure 3. The regression between the log of dry grass weight from clippings (log biomass) and the percent cover of grass.

In addition, the density of tre~~s~~es was quantified while measuring the forage abundance: at the fiftieth step of each step-point sample, the distance in metres to the nearest tree in each of four sectors about the observer was estimated. The mean distance to the nearest tree, over the entire study, for each vegetation community was calculated, from which the density of trees per hectare was calculated.

Each vegetation community was categorised with an index of visibility or 'sightability' of zebras, ranging from 1 (for bushy and wooded communities with relatively low visibility, e.g., *Acacia reficiens/A. nubica/A. mellifera* woodland) to 4 (for open grasslands, e.g., alluvial *Pennisetum* sp. grassland). The index was relative and was dependent on the density of trees in each vegetation community. Hence, the regression between the visibility index and the density of trees in each vegetation community was highly significant ($F_{1,207} = 66.3$, $P < 0.001$). When considering the habitat use of zebra (chapter 3), the visibility index allowed the number of Grevy's zebra sighted during a survey, by habitat, to be corrected for the differential 'sightability'.

Mapping water distribution

Throughout the surveys of the areas, the locations of water points were recorded to a minimum accuracy of 100m using a Garmin 45™ Global Positioning System (GPS). The water points were then checked through time and seasons, to assess whether they were ephemeral or permanent.

Animal Surveys

Surveys for animals were conducted from a slow moving vehicle during daylight hours. For the surveys, the study area were divided into three areas of approximately equal size. Each third was surveyed in a north-south direction, with the surveys starting at the northernmost point, with one day was then spent surveying each third. The study areas were, therefore, surveyed for a total of six days (divided into two three-day periods) per study area per rotation. While surveying for animals, every effort was made to cover the entire area within so the counts of animals approximate a total count. Total counts were favoured over sample counts because of practical considerations: a truly random survey would have been impracticable, both in terms of the time required and fuel expended; straight line transects were equally impossible because of the nature of the terrain (e.g., erosion gullies, lava plains or swamps). If problems were to arise from this, it would be in the calculation of the habitat use of Grevy's zebra. The methods to control for biases in my movements are described in chapter 3.

Sightings of Grevy's zebra and domestic livestock species (cattle, smallstock, donkeys and camels) were recorded concurrently during the surveys. Data were also collected on predators: lions (*Panthera leo*), cheetah (*Acinonyx jubatus*) and hyaenas (*Crocuta crocuta*). For each group of animals encountered, where groups were defined as all animals occurring within 50 metres of another individual (after Ginsberg 1988; cf. Jarman 1987), the position was recorded using a Garmin 45™ GPS. The habitat on which the animals were situated, the animals' activity and the total number of individuals in the group were also recorded.

In addition, for Grevy's zebra, group composition was recorded by sex, age and, within the sexes, reproductive class. The sexes were easily distinguished. A female's reproductive class was assessed visually and using the ages of foals up to 1 year, which was estimated from their body size and coat colour (after Rowen 1992). Females were thus classified into 5 classes (Ginsberg 1989; Rowen 1992):

1. Late pregnancy (final trimester of pregnancy - within 4 months of parturition);
2. Early lactation (3 months post-partum, and included post-partum oestrus females, defined as females that have an oestrus two and six weeks post-partum. Oestrus was determined visually (enlarged labia, vaginal 'winking' of the labia, tail position (after Waring 1983)), and behaviourally (mountings by territorial males));
3. Mid-lactation (3 - 6 months);
4. Late lactation (6 months - 1 year; to the weaning of foal);
5. Non-reproductive. Within this class were cycling oestrus (defined as all oestrus females other than the post-partum females) and anoestrus females, and females in the early- to mid-pregnancy.

Individuals were also identified using their natural markings, using a technique developed by Rubenstein (1986), but modified by Ginsberg (1988). The rear right thigh was used for the individual identification of Grevy's zebra. The shapes of the stripes were drawn on to a prepared data sheet, starting from below the level of the anus, where the strips begin to thicken. The stripes were classified into six shapes: Y, Bar, Vee, Chromosome, Eye and Dash. These were treated like an 'alphabet', in the order shown. The code for a particular female always began with the first clearly visible Y, and the subsequent stripes formed the basis for identification. The identities were catalogued in 'alphabetical' order into 'stripe books' by sex. Stripe books were used in the field and therefore identification of individuals was almost immediate. The technique has been successfully used in four previous studies (Ginsberg 1988; Rowen 1992; Rubenstein 1986; Wisbey 1995).

In addition, a female's body condition was recorded when she was identified. Body conditions were visually assessed using techniques developed by Pollock (1980), adapting the methods of Riney (1960), and which have been used successfully in two previous studies of Grevy's zebra (Ginsberg 1988; Rowen 1992). This technique uses assessment of the body fat deposits on the loins and hips of an individual, and involves a scoring system between 0 (worst) and 5 (best).

The number and location of pastoralist *manyatta*s (pastoralist villages) in Barsalinga and Ngare Ndare were also recorded during each rotation.

Patterns of dispersal

The study areas were not closed. There was no barrier, except distance, impeding the movement of animals among the study areas. In this study, dispersal was defined as the movement of animals out of a given study area. The movement of individuals within and among study areas was assessed using the repeated sightings of individually identified females. Any individual could repeatedly disperse between any two study area throughout the course of the study.

Data analyses

The distances of the groups of animals from permanent, usable water were calculated, *post hoc*, using the latitude and longitude readings of the group sightings and the position of the water sources.

The analyses in this thesis, unless otherwise indicated in each chapter, were primarily done using generalised linear models (McCullagh & Nelder 1987) using Genstat 5 Release 3.2 (Payne *et al.* 1993) or GLIM 4.0 (Francis *et al.* 1993). Generalised linear models were used to analyse the data since they 1) retain the error structure in the data; 2) allow exploration of the data and have no fixed rules or absolutes; and 3) are powerful (Crawley 1993).

Models were fitted to the data, with the object of determining a minimum adequate model to describe the data set (Crawley 1993). A full model was first fitted to the data using a parameter for each observation. A step-wise progression from the full model to the minimum adequate model was made through a series of simplifications on the basis of deletion tests. Therefore explanatory variates or factors were dropped from the model. *F*-tests or χ^2 tests assessed the significance of the change in deviance when a given term is removed from the model.

In the following chapters, the response variates will be described, including, where necessary, their error structures. If the data were normally distributed, no error structure was necessary and a linear regression was used. The error structures that are generally found in this thesis are of the following kinds: 1) binomial errors for proportional data, where the response variate is constrained - and hence cannot be greater than some total. The total of which the response variate is a proportion of is the binomial denominator in the model; 2) binomial errors for binary response variates, usually 1 and 0. These data are analysed using binomial errors, with 1 as the binomial denominator and an appropriate link function; and 3) Poisson errors for count data. In order for the fitted values to be positive, a log link was used. The response variate was the number of animals, say, using a habitat. Since count data were often clumped or overdispersed, the dispersion parameter was estimated. The change in deviance was then divided by the dispersion parameter to get a chi-squared value with which to test the effect of a particular parameter (Crawley 1993). The explanatory variables to be tested in the models will also be listed.

References

Behnke, R. H. & Scoones, I. 1992 Rethinking Range Ecology: Implications for Rangeland Management in Africa. In *Range Ecology at Disequilibrium.*

Bronner, G. 1990 *Vegetation and land use in the Matthews Range area, Samburu District.* Dissertationes Botanicae. Berlin: J. Cramer.

Brown, L. R. & Wolf, E. 1984 Food crisis in Africa. *Natural History* **93**, 16-26.

Connell, J. H. 1980 Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* **35**, 131-138.

Crawley, M. J. 1993 *GLIM for Ecologists.* Methods in Ecology. Oxford: Blackwell Science.

Francis, B. *et al.* 1993 *The GLIM System: Release 4 Manual.* Oxford: Clarendon Press.

Ginsberg, J. R. 1988 Social organization and mating strategies of an arid-adapted equid: the Grevy's zebra. Princeton, New Jersey: Princeton University.

Ginsberg, J. R. 1989 The ecology of female behaviour and male reproductive success in Grevy's zebra, *Equus grevyi. Symposia of the Zoological Society (London)* **61**, 89-110.

Grunblatt, J., Said, M. Y. & Nutira, J. K. 1989 Livestock and wildlife summary 1987 - 1988 for Kenya Rangelands. Nairobi, Kenya: Department of Resource Surveys and Remote Sensing, Ministry of Planning and National Development.

Herlocker, D. J. 1990 Rangeland Vegetation of Isiolo District. Nairobi, Kenya: Ministry of Livestock.

Herlocker, D. J. 1992 Vegetation types. In *Range Management Handbook of Kenya, Volume II, 2: Samburu District* (ed. S. B. Shaabani, M. Walsh, D. J. Herlocker & D. Walther). Nairobi, Kenya: Republic of Kenya, Ministry of Livestock Development (MOLD).

Herlocker, D. J. 1993 Vegetation types. In *Range Management Handbook of Kenya, Volume II, 5: Isiolo District* (ed. D. J. Herlocker, S. B. Shaabani & S. Wilkes). Nairobi, Kenya: Republic of Kenya, Ministry of Agriculture, Livestock Development and Marketing.

Jarman, P. J. 1987 Group Size and Activity In Eastern Grey Kangaroos. *Animal Behaviour* **35**, 1044-1050.

Jätzold, R. & Bake, G. 1995 The climatology of northern and north-eastern Kenya. In *Range Management Handbook of Kenya, Vol. II.* (ed. D. Herlocker, M. Nicholson & S. Allanson). Nairobi, Kenya.: Ministry of Agriculture, Livestock Development and Marketing (MALDM).

Jennings, D. J. 1966 Geology of the Archer's Post Area. Nairobi: Geological Survey of Kenya.

Mäckel, R. & Walther, D. 1994 *A field guide to soil erosion & its management implications in northern Kenya (Range Monitoring Series No. 2).* Nairobi, Kenya: Republic of Kenya, Ministry of Agriculture, Livestock Development and Marketing (MALDM).

McCullagh, P. & Nelder, J. A. 1987 *Generalised Linear Models.* Monographs on Statistics and Applied Probability. London: Chapman and Hall.

Packer, C. 1986 The ecology of socality in felids. In *Ecological aspects of social evolution* (ed. D. I. Rubenstein & R. W. Wrangham). Princeton: Princeton University Press.

Payne, R. W., Lane, P. W., Digby, P. G. N., Harding, S. A., Leech, P. K., Morgan, G. W., Todd, A. D., Thompson, R., Tunnicliffe Wilson, G., J., W. S. & White, R. P. 1993 *Genstat 5 Release 3 Reference Manual.* Oxford: Clarendon Press.

Phillipson, D. W. 1976 Fisherman and the beginnings of East African farming: new light from northern Kenya. In *Historical Association of Kenya, Annual Conference.* Nairobi, Kenya.

Pollock, J. 1980 *Behavioural Ecology and body condition changes in New Forest Ponies.* The Causeway, Horesham, Great Britain: The Farm Livestock Advisory Committee RSPCA (Scientific Publications).

Pratt, D. J., Greenway, P. J. & Gwynne, M. D. 1971 A classification of East African rangeland, with an appendix on terminology. *Journal of Applied Ecology* **3**, 369-382.

Pratt, D. J. & Gwynne, M. D. 1977 *Rangeland management and ecology in East Africa.* Kent: Hodder and Stoughton.

Riney, T. 1960 A field technique for assessing physicl condition of some ungulates. *Journal of Wildlife Management* **24**, 92-94.

Rowen, M. 1992 Mother-infant behavior and ecology of Grevy's zebra, *Equus grevyi.* Yale: Yale University.

Rowen, M. & Ginsberg, J. R. 1993 Grevy's zebra (*Equus grevyi* Oustalet). In *Equid Action Plan* (ed. P. Duncan). Gland, Switzerland: IUCN.

Rubenstein, D. I. 1986 Life history and social organisation in arid adapted ungulates. In *Ecological aspects of social evolution.* (ed. D. I. Rubenstein & R. W. Wrangham). Princeton: Princeton University Press.

Schaller, G. B. 1972 *The Serengeti Lion: A Study of Predator-Prey Relations.* Chicago: Chicago University Press.

Schwartz, H. J. & Walsh, M. 1993 Range unit inventory. In *Range Management Handbook of Kenya, Volume II, 5: Isiolo District* (ed. D. J. Herlocker, S. Shaabani & S. Wilkes). Nairobi, Kenya: Republic of Kenya, Ministry of Agriculture, Livestock Development and Marketing (MALDM).

Sinclair, A. R. E. & Fryxell, J. M. 1985 The Sahel of Africa - ecology of a disaster. *Canadian Journal of Zoology-Journal Canadien de zoologie* **63**, 987-994.

Sobania, N. W. 1979 Background History of the Mt Kenya region of Kenya. Nairobi, Kenya: UNEP - MAB Integrated Project in Arid Lands.

Spencer, P. 1965 *The Samburu.* London: Routledge & Kegan Paul.

Touber, L. 1993 Landforms and soils. In *Range Management Handbook of Kenya, Volume II, 5: Isiolo District* (ed. D. J. Herlocker, S. Shaabani & S. Wilkes). Nairobi, Kenya: Republic of Kenya, Ministry of Agriculture, Livestock Development and Marketing (MALDM).

Waring, G. H. 1983 *Horse Behavior.* New Jersey: Noyes Publications.

Western, D. 1975 Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East African Wildlife Journal* **13**, 265-286.

Wisbey, J. 1995 The population status of Grevy's zebra (*Equus grevyi*) in selected areas of northern Kenya. London: University College London.

3. Use of space by Grevy's zebra: the effects of food, predators, competitors and water

Summary

1. The behavioural responses of Grevy's zebra (*Equus grevyi* Oustalet), as measured by spatial distribution and use of habitats, were studied in relation to the spatial and temporal availability of both food and water resources, the distribution of potential interspecific competitors and the distribution of humans.
2. Although no single factor determined the space use of Grevy's zebra, the distribution of food was an important determining factor. Zebras were probably maximising their grass intake.
3. When the availability of forage dropped below a certain threshold, Grevy's zebra responded by dispersal, which was defined as the movement of zebra out of a study area. Different reproductive classes of female appeared to exhibit different thresholds for dispersal.
4. Use of space by Grevy's zebra was constrained by their dependence on water.
5. There was evidence of interspecific competition between Grevy's zebra and pastoral people and their livestock. In one of the study areas, Grevy's zebra avoided the areas used by people. Furthermore, there was evidence that food was a limiting resource for Grevy's zebra in study areas used by domestic livestock, but not in the area from which livestock were excluded.

Introduction

The use of space by animals is an important aspect of their behavioural ecology since it underpins optimisation of resource use. It is often assumed that patterns of movement and habitat selection are such that ~~they~~ animals maximise nutrient capture rates relative to time and energy costs (Charnov 1976; Krebs 1978). These models of space use predict that, other things being equal, ungulates should feed selectively in those parts of the range in which their preferred food items are most abundant, thereby maintaining high intake rates (Arnold & Dudzinski 1978; Stephens & Krebs 1986). However, all things are rarely equal, and the use of space is, therefore, unlikely to be determined simply by the distribution of a single resource. Similarly, departures from the 'ideal free distribution' (Fretwell 1972; Fretwell & Lucas 1970) are often linked with the assumption the animals can move between resource sites or patches without encountering aggressive interference from predators or competitors (e.g., Lima & Dill 1990). Hence, ungulates, who are selecting their foraging areas over longer periods, will also have to meet requirements for water (Becker & Ginsberg 1990; Western 1975), refuge from predators (Fryxell 1991), interspecific competitors (Sinclair 1985), and social factors (Ginsberg 1989) that may complicate optimality principles.

There have been relatively few attempts to measure and distinguish resource availability and other variables affecting habitat selection (Barton *et al.* 1992), especially in large species where manipulation of the resource variables is impracticable. In this chapter, I quantified key variables likely to influence foraging decisions in Grevy's zebra (*Equus grevyi* Oustalet). I focused on the spatial distribution of females. Since their reproductive success is more strongly determined by their ability to acquire nutrients than it is in males (Clutton-Brock 1989; Gosling 1986). In addition, by focusing on females, I eliminated the effects of territorial constraints. Ginsberg (1988; 1989) showed that there are significant differences in the spatial distributions of male and female Grevy's zebras which is, in part, due to the constraint of territoriality in males.

Methods

For this study, three areas were chosen in Isiolo District, Kenya (as described in chapter 2). The study areas were surveyed in rotation over the duration of the research. During each rotation, while in each study area, the season was recorded and the availability of forage in habitats - defined as habitats at different distances from water - was quantified using standard methods (chapter 2). The study areas were also surveyed for animals, including Grevy's zebra and domestic livestock species (see chapter 2).

Between rotations the same routes were driven: these were determined in advance. However, all routes were not random: a truly random survey would have been impracticable, both in terms of the time required and fuel expended. This lack of random sampling could have resulted in unequal representation of certain parts of the study areas. The inequalities may have been the result of geography (e.g., erosion gullies, lava plains or swamps), or a conscious decision to focus my work on collecting data on a sub-set of animals (females). Hence, my inability to drive either random or fixed surveys meant that the searching effort in each habitat had to be standardised across all habitats. Therefore, the route, distance travelled and time spent within each habitat was recorded using a Garmin 45™ Global Positioning System (GPS), the vehicle odometer and a clock. To distinguish patterns of zebra habitat use from the biases in my movement, all discussion of zebra habitat use have been corrected for biases in search effort (see below for correction indicies).

For each group of animals encountered, the location and the habitat on which they were sighted and their activity, their group size, the sex and reproductive class composition, the individual identity of Grevy's zebra were all recorded using standard methods (chapter 2). The locations of each group were used, *post hoc*, to calculate the distance to other groups of animals, to usable water and to the human villages, or *manyatta*s.

Although groups of animals were rarely feeding in more than one habitat, the data on habitat use were collected at the individual rather than the group level. The decision to analyse the data at the individual, rather than the group level stemmed from the previous work on Grevy's zebra by Klingel (1974) and Ginsberg (1988; 1989). In his study, Klingel found that group composition was very unstable and changed on a daily basis. This implied that decisions about space use were being made at the level of the individual. With the exception of early lactation females, Ginsberg's work supported this: "the requirements of individual females and ecological conditions produces a range of behavioural responses" (Ginsberg 1989). A female's reproductive condition determines the priority that she places upon different resources. For example, lactating females are found predictably closer to water than other classes of females. Females with young foals are usually relatively sedentary, remaining in a single male's territory, and form close associations with other females with whom they are in reproductive synchrony. Other females are less predictable: their associations are fluid and their movements, which are determined by the availability and abundance of food, can be over relatively large distances (Ginsberg 1989). Therefore, it is likely that although Grevy's zebra choose to associate in groups (see chapter 4), their responses to distributions of resources are made at the individual rather than group level. The choices each individual makes is likely to be independent of other members of the group with which it is seen. Therefore, all analyses were conducted at the individual rather than group level.

Data analyses

Forage availability

Initially, forage availability was related to the rainfall. Thereafter, multiple regressions were used for the detailed analysis of forage availability, with percentage cover of grass (see chapter 2) as the response variate. Percentage cover of grass was a continuous variate and distributed normally (goodness of fit test: $\chi^2=14.84$, d.f. = 12, P = NS).

Percentage cover was analysed in two models: first, among the study areas and, second, within the study areas. For the among-study-area analyses, a full model, using season (dry vs. rains), distance from usable water, study area, and the interaction between season and distance to water as explanatory variables, was fitted to the data. For these analyses, season was limited to "rains" and "dry" seasons since not all the study areas were surveyed in equivalent dry season conditions. Models were constructed, first, including all the parameters and then dropping each in a step-wise deletion until all variables were significant. This was the minimum adequate model.

For the within study area analyses, the effects of season, rotation (which, for the purposes of these analyses, was defined as each time a study area was surveyed for availability of forage, regardless of season. Rotation had no biological significance but was included to assess temporal variation of grass cover over the duration of the study), habitat, distance to usable water on the availability of forage were analysed. Not all the terms could be fully included in a full model since some of the parameters were aliased (e.g., season and rotation). When this was the case, the full model was re-run with the aliased terms being tested alternately. Again, percentage cover was the response variate and each of the explanatory variates or factors tested in a step-wise deletion. Where appropriate, comparisons between the forage availability between specified habitats were conducted by testing the effect that a factor that distinguished them on the percentage cover of grass. For example, in Barsalinga, the effect of the alluvial *Pennisetum* sp. grassland was compared to all other habitats.

Habitat selection by Grevy's zebra

The analyses of habitat use were purely descriptive. However, they give an indication of the different patterns of habitat use in each study area. The statistical analysis of factors affecting the space use of Grevy's zebra is described below.

To describe the habitat selection by Grevy's zebra, first, the number of animals in each habitat was first corrected for the visibility or "sightability" of zebras, using the visibility index (chapter 2). Second, the proportional use of a habitat by Grevy's zebra was calculated specifically to correct for biases of time spent in habitats. Finally, the relative feeding densities of zebra on habitats was calculated to correct for the compensate for the compositional differences of habitats among the study areas. In the results, I present the final part of these analyses to describe the habitat use of Grevy's zebra.

The proportional use (Ui, adapted after Ginsberg 1988) of a habitat by Grevy's zebra was:

$$U_i = \frac{\frac{n_i}{t_i}}{\sum_{a=1}^{N} \frac{n_a}{t_a}} \qquad \text{(where } \sum U_i = 1\text{)} \qquad (1)$$

and where n_i was the total number of animals seen during a rotation in habitat *i*; t_i was the standardised time spent searching for animals in habitat *i*; and *N* was the total number of habitats surveyed.

In order to compensate for the compositional differences of habitats among the study areas (chapter 2, Table 2), the index of selection (*E*) by animals of Jacobs (1974) was calculated for each habitat. E_i was defined as the relative difference between the use and the availability (i.e., area) of a given habitat, and gives an indication of the relative feeding densities of animals on each habitat. Therefore,

$$E_i = \frac{(U_i - A_i)}{[(U_i + A_i) - \{2(U_i \times A_i)\}]} \qquad (2)$$

where A_i was the proportion of the study area occupied by habitat *i*. E_i varied between +1 and -1, with values between -1 and 0 indicating that the species or sex classes avoided the habitat, and values between 0 and +1 indicating selection of that habitat. Here, the selective index, *E*, was simply used as a descriptive tool of habitat use by Grevy's zebra.

Distribution of Grevy's zebra relative to water

It was not possible to do a comparison of the distribution of Grevy's zebra relative to usable water among study areas because of differences in the water distribution. The distribution of water in Buffalo Springs meant zebra could not be greater than 6km from water (see Figure 2c, Chapter 2). In comparison, the maximum distance that the zebras could be from water was 12km and 10km in Barsalinga and Ngare Ndare respectively.

However, to analyse the differential effects of water within each of the study areas, the distribution of different reproductive classes of Grevy's zebra female (see chapter 2 for definitions) relative to water was analysed. These data were analysed by the proportion of each group comprised by early- or mid-lactation females, since previous work on Grevy's zebra has found these female classes to be the most dependent on water (Becker & Ginsberg 1990; Ginsberg 1989). Hence the data were analysed with binomial errors, with the number of lactating females (the sum of early- and mid-lactation females) in each group as the response variate, with the total number of females per group as the binomial denominator. Distance to usable water, in kilometres, was the explanatory variate for the model.

Space use of Grevy's zebra

Generalised linear models were used to assess the relative influence of water, availability of food, distribution of predators, distribution of potential competitors and distribution of people on the overall patterns of distribution of zebra. For these analyses only the domestic livestock were considered as the potential competitors; the ratio of domestic ungulates to potential wild competitors was heavily skewed towards the domestics (e.g., approximately 70:1, this study; Grunblatt *et al.* 1989). Therefore, the effect of wild ungulates was considered negligible in comparison. Furthermore, the distribution of *manyatta*s - the small, kin-based villages in which the pastoral people of East Africa live (Spencer 1965) - was taken as an index of human distribution. Although each group of livestock was accompanied by a herder, it was impossible to distinguish the effects of the livestock and/or the human herder on zebra distribution. None of the pastoral people would allow their livestock to wander untended.

Two models were used to assess the relative influence of all explanatory variables, each using different response variates: 1) those using the presence/absence of zebra; and 2) those using the number of zebra. This was to distinguish effects that may have been masked by clumping or aggregation of the zebra (cf., chapter 4) when using numbers alone. These analyses differed from those described above to describe the habitat use of Grevy's zebra. Because the analyses of space use of Grevy's zebra assessed the effects of a number of measured or calculated variables, zebra numbers and presence/absence could be used as the response variate without being corrected.

In the first, the presence/absence of zebras, with a 1 or 0 response to indicate presence or absence, respectively, was used as the response variate fitted to a generalised linear model with binomial errors and a binomial denominator of 1 (Crawley 1993).

In the second, the number of females in each sighted group (sample size = 438 groups over three study areas; mean = 3.46; variance = 49.63) of Grevy's zebra was used as the response variate of a generalised linear model with Poisson errors corrected for overdispersion (McCullagh & Nelder 1987).

Distance to the nearest usable water (water), distance to the nearest *manyatta* (manyatta), distance to the nearest group of livestock (livestock), percentage cover of grass in the habitat (cover) in which each group of zebra were sighted, and the interaction terms between distance to the nearest group of livestock and the distance to the nearest *manyatta* (livestock.manyatta), the distance to the nearest usable water (livestock.water), and the percentage cover of grass on the habitat on which the zebra were sighted (livestock.cover) were included in the models as explanatory variables.

Initially, models were fitted to the complete data set - thus including all three areas - to assess the relative effects of rotation, the distribution of forage, and the distribution of water on the distribution of zebras over the three areas. Distance to livestock and *manyatta*s could not be fitted in these models since neither livestock nor *manyatta*s were not present in Buffalo Springs. The models were then fitted to the data from each study area.

Dispersal

Finally, data on the dispersal of Grevy's zebra females were described. In this study, dispersal was defined as the movement of animals out of a given study area. Given that individuals were identified, their movements could be tracked over time from area to area. I use the term 'dispersal' rather than 'migration' because although the movements were often related to the availability of resources (see below) and hence season, there was no predictability to the movements or, more importantly, whether the animals would return. The predictability of departure and return are implied by the term 'migration'.

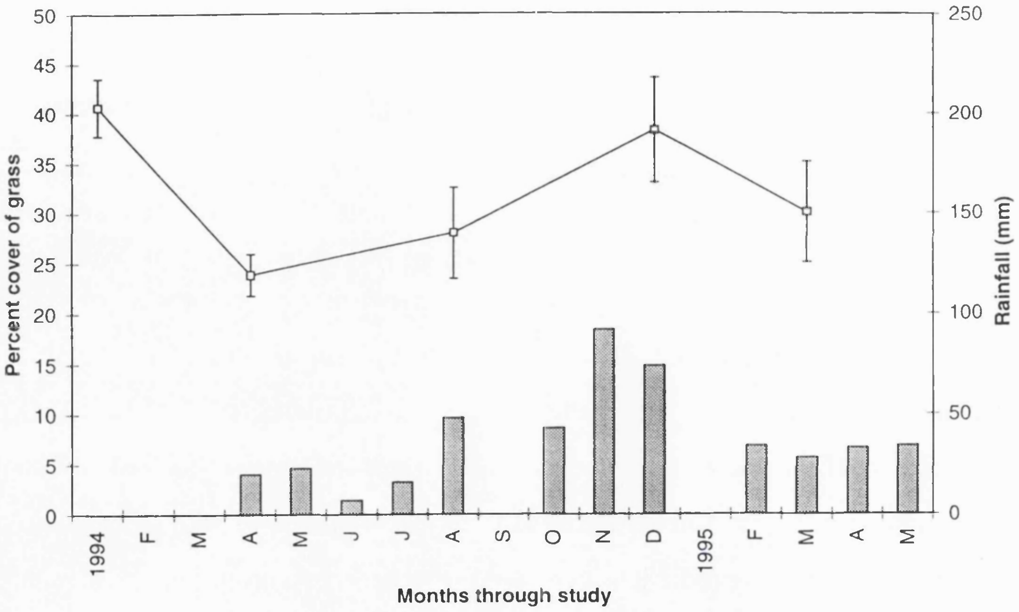
The analysis of the dispersal of Grevy's zebra focused on the number of identified animals from each reproductive class sighted in each study area and then subsequently resighted in another study area. Changes in the number of a particular reproductive class could occur if 1) they changed reproductive class, 2) there was immigration or emigration of animals to or from an area, or 3) they died. Since only 3 fresh adult carcasses were found over the course of the study, death was disregarded as an explanation for large changes in the numbers of animals. These analyses are descriptive, but they do indicate the degree of dispersal.

Results

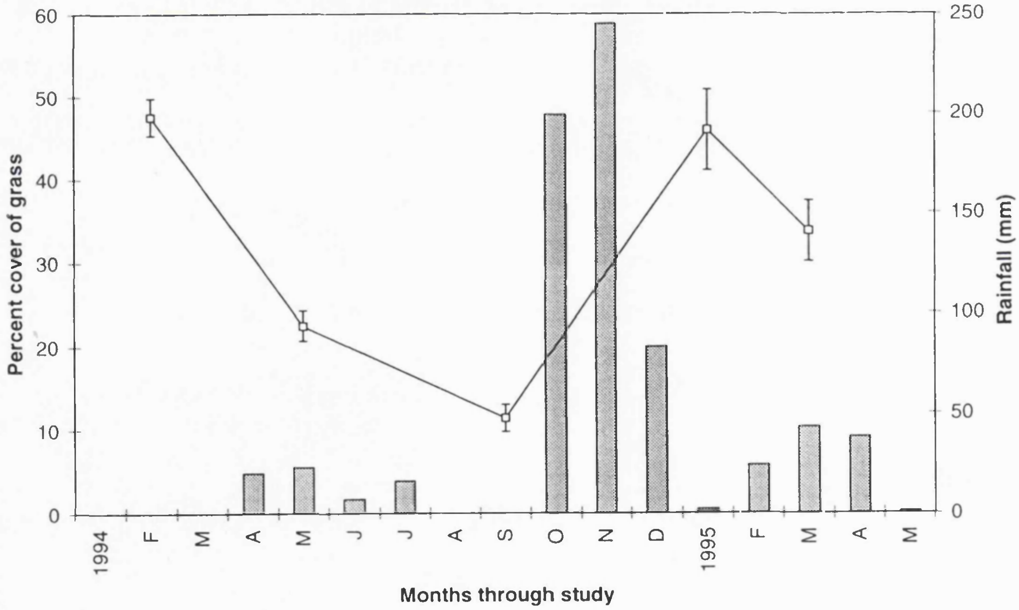
Availability of forage

In general, in the three study areas, the availability of forage increased with the flush of growth following the rains. Peak grass availability tended to be in the early dry season, following which there was a general decline through the dry season (Figure 1).

a) Barsalinga (full title on following page, see below)



b) Ngare Ndare



c) Buffalo Springs

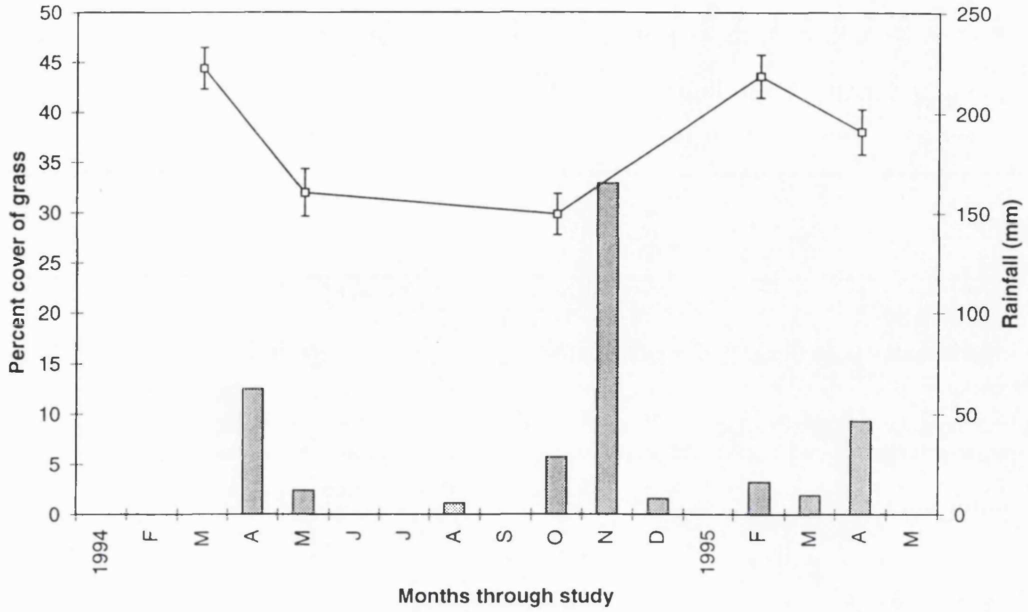


Figure 1. The seasonal changes in the availability of forage, as measured by the percentage cover of grass, across all habitats (mean, with standard errors, across all habitats shown as joined points), in relation to the rainfall (bars) in each study area.

In the study areas there was, however, little or no plant growth following the rains of April 1994. This was probably because the rains were only 42% of the long-term average for this period (using data for Archer's Post Meteorological Station, data from the Kenya Meteorological Department). In contrast, growth was good following the October/November 1994 rains, which were 32% above the long-term average.

In the analysis of the effect of season, distance from water, study area, and the interaction term between season and distance to water on the availability of forage, over the three study areas, season distance to usable water and study area were found to have significant effects (Table 1). Hence, the final model contained these parameters.

Table 1. Impact of water, season and study area on grass cover. Grass cover was fitted to a multiple regression model, with these as explanatory variables. The change in deviance and their significance following step-wise deletion of parameters (where "water" is distance to usable water and "area" is study area) from the full model is reported. The sum of squares for the model was 5092. The total sum of squares was 62272.

	F-tests	P
Full model	$F_{5,220} = 3.92$	0.002
season.water	$F_{1,221} = 0.36$	NS
water	$F_{1,222} = 5.23$	0.023
season	$F_{1,225} = 4.99$	0.027
area	$F_{2,224} = 4.11$	0.018

Overall, there was significantly greater abundance of grass in Buffalo Springs and Ngare Ndare than in Barsalinga (coefficient estimates: Barsalinga = 0; Ngare Ndare = +0.62; Buffalo Springs = +8.02). For the analysis of the effect of season, there was an overall higher availability of forage during the dry season (coefficient estimates: rains = 0; dry = +4.83). Finally, the availability of food increased with distance from usable water (coefficient estimate: + 0.29).

Vegetation analysis by study area

When the study areas were considered separately, there were differences in the factors and variates influencing the availability of forage (Table 2).

In Barsalinga, there was significant temporal variation in the availability of forage: the parameter "rotation" had a significant effect on the model of percentage cover of grass (Table 2a). However, season, defined as rains and dry, had no effect.

Habitat type also had a significant effect on the availability of forage in Barsalinga (Table 2a). In the detailed analysis of the comparisons between certain habitat types, there was significantly higher grass cover in the alluvial *Pennisetum* grassland (see effect of "bcm" habitats on Table 2a; coefficient estimates: alluvial *Pennisetum* grassland = 0; other habitats = -21.66). In contrast, there was no significant difference between *Acacia senegal*/*Commiphora* sp. woodland and *Acacia tortilis*/*Commiphora* sp. woodland.

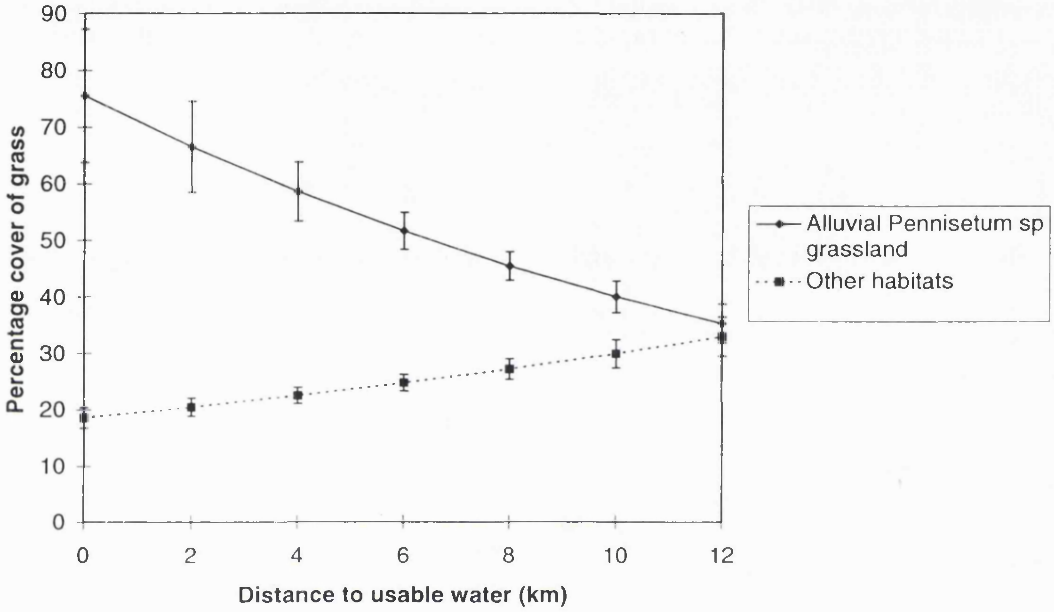


Figure 2. A comparison of forage availability and distance to water between the alluvial *Pennisetum* sp. grassland and other habitats. The values were predicted from the models in Table 2a.

Over all habitats, distance from usable water had no effect on the availability of forage. However, the interaction term between the comparison between the alluvial *Pennisetum* grassland and other habitats and the distance from usable water (bcm.water; Table 2a) had a significant effect. When the values were predicted from the model, the cover of grass in the alluvial *Pennisetum* grassland decreased with distance from water, while the percentage cover of grass in all other habitats increased with distance from usable water (Figure 2).

As with Barsalinga, in Ngare Ndare, there was no effect of season but there was significant temporal variation in the availability of forage through rotations (Table 2b). Distance from usable water did not have a significant effect on the grass cover in Ngare Ndare.

The parameter "habitat" had a significant effect on the availability of forage. Again as with Barsalinga, the *Pennisetum/Setaria* sp. grassland had significantly higher availability of forage than the other, grouped, habitats (coefficient estimates: the *Pennisetum/ Setaria* sp. grassland = 0; other habitats = -7.85).

In contrast to both Barsalinga and Ngare Ndare, in Buffalo Springs, not only was there significant temporal variation of the availability of forage, but there was also a significant effect of season. The dry season had significantly higher availability of forage than in the rains (Table 2c; coefficient estimates: rains = 0; dry season = 10.93).

There was a significant effect of "habitat" on the availability of forage in Buffalo Springs. In the detailed comparisons among the habitats, the *Acacia reficiens* habitats had significantly higher availability of forage than the other habitats (Table 2c; coefficient estimates: *Acacia reficiens* habitats = 0; other habitats = -12.14). In contrast, the *A.tortilis* dwarf shrubland had significantly lower availability of forage than other habitats (Table 2c; coefficient estimates: *A.tortilis* dwarf shrubland = 0; all other habitats = +19.64).

Finally, there was a significant effect of distance from usable water on the availability of forage in the *Acacia tortilis* dwarf shrubland habitats, with the availability of forage decreasing with increasing distance (Table 2c; coefficient: water = -2.16).

Table 2. Results of the analyses of variates and factors affecting availability of forage in each study area as measured by the percentage cover of grass in habitats. The following effects were tested: 1) rotation; 2) habitat; 3) the comparison between "bcm" habitats and all others (see text for details); 4) the comparison between "rt" habitats and other habitats (see text for details); 5) the interaction terms between "bcm" habitats and distance from usable water (bcm.water); and 6) the interaction term between the comparison between "rt" habitats and the distance from water (rt.water); 7) season (divided into dry and rains) and 8) distance to usable water (water).

a) Barsalinga. "bcm" habitats represents the comparison between the alluvial *Pennisetum* grassland and other habitats; "rt" represents the comparison between the comparison between *Acacia senegal/Commiphora* sp woodland and *Acacia tortilis/ Commiphora* sp. woodland. Three models were fitted to differentially assess the effects of aliased terms (habitat type, bcm - the alluvial *Pennisetum* sp. grassland and other habitats, and rt - the two *Acacia* habitats).

	F-tests	*P*
Initial testing of significance of parameters with a full model		
rotation	$F_{4,34} = 5.57$	0.001
season	$F_{1,74} = 0.13$	NS
bcm	$F_{1,75} = 26.66$	< 0.001
rt	$F_{1,30} = 3.09$	< 0.1
habitat	$F_{14,53} = 3.59$	< 0.001
water	$F_{1,29} = 0.01$	NS
Testing using minimum adequate models		
Model: + rotation + water + bcm + bcm.water (model explains 59.6% of the total variance)		
bcm.water	$F_{1,69} = 18.78$	< 0.001
water	$F_{1,70} = 0.29$	NS
rotation	$F_{4,74} = 3.98$	0.006
bcm	$F_{1,75} = 26.66$	< 0.001
Model: + rotation + habitat (model explains 61.3% of the total variance)		
habitat	$F_{14,63} = 2.89$	0.002

b) Ngare Ndare. "bcm" represents the comparison between the *Pennisetum/Setaria* sp. grassland and all other habitats.

	F-tests	*P*
Initial testing of parameters with a full model: only non-significant parameters shown		
season	$F_{1,70} = 1.09$	NS
Testing using minimum adequate models		
Model: + rotation + water + bcm + bcm.water (model explains 65.1% of the total variance)		
bcm.water	$F_{1,66} = 0.0$	NS
water	$F_{1,67} = 3.82$	NS
bcm	$F_{1,68} = 8.83$	0.004
rotation	$F_{4,72} = 11.10$	< 0.001
Model: + rotation + habitat (model explains 81.7% of total variance in the model)		
habitat	$F_{15,68} = 2.94$	0.001

c) Buffalo Springs. "bcm" represents the comparison between *Acacia reficiens* habitats with all other habitats; "rt" represents the comparison between *A.tortilis* dwarf shrubland and all other habitats.

	F-tests	*P*
Testing using minimum adequate models (there were no non-significant parameters)		
Model: + rotation + habitat (model explains 67.1% of total variance)		
habitat	$F_{17,72} = 3.01$	< 0.001
rotation	$F_{4,76} = 3.33$	0.014
Model: + rotation + water + bcm + bcm.water (model explains 23.5% of total variance)		
bcm.water	$F_{1,70} = 0.15$	NS
water	$F_{1,71} = 0.22$	NS
bcm	$F_{1,76} = 10.12$	0.002
Model: + season + water + rt + rt.water (model explains 47.5% of total variance)		
rt.water	$F_{1,73} = 1.49$	NS
water	$F_{1,74} = 8.71$	0.004
rt	$F_{1,76} = 20.94$	< 0.001
season	$F_{1,75} = 15.38$	< 0.001

Distribution of domestic livestock groups and manyattas

The distribution of sighted groups of domestic livestock species, relative to usable water and by rotation, in both Barsalinga and Ngare Ndare are presented in Table 3.

It is interesting to note that in Barsalinga, in rotation 2, there was a large decline in the number of cattle, which coincided with the low forage abundance at this time (Figure 1a).

Table 3. The mean distance to water that groups of domestic livestock species were sighted in Barsalinga and Ngare Ndare. The sample sizes used for analysis in this chapter are also shown.

		Rotation				
a) Barsalinga		1	2	3	4	5
Cattle	Mean distance to water	5.6	7.4	4.9	4.0	4.7
	s.e.	0.39	1.80	0.35	0.37	0.29
	No of groups	48	3	35	46	32
	Total number of individuals	4093	222	1896	2452	934
Small stock	Mean distance to water	4.5	2.9	4.5	3.5	3.4
	s.e.	0.66	0.29	0.29	0.26	0.19
	No of groups	22	31	55	41	37
	Total number of individuals	2262	3585	5739	4214	3038
Donkeys	Mean distance to water	2.8	3.0	3.5	4.0	3.8
	s.e.	0.38	0.38	0.41	0.37	0.29
	No of groups	14	13	22	30	22
	Total number of individuals	196	155	263	565	145
Camels	Mean distance to water	3.9	3.1	5.1	4.3	3.7
	s.e.	0.42	0.62	0.53	1.77	0.42
	No of groups	11	5	17	4	9
	Total number of individuals	115	73	381	30	84

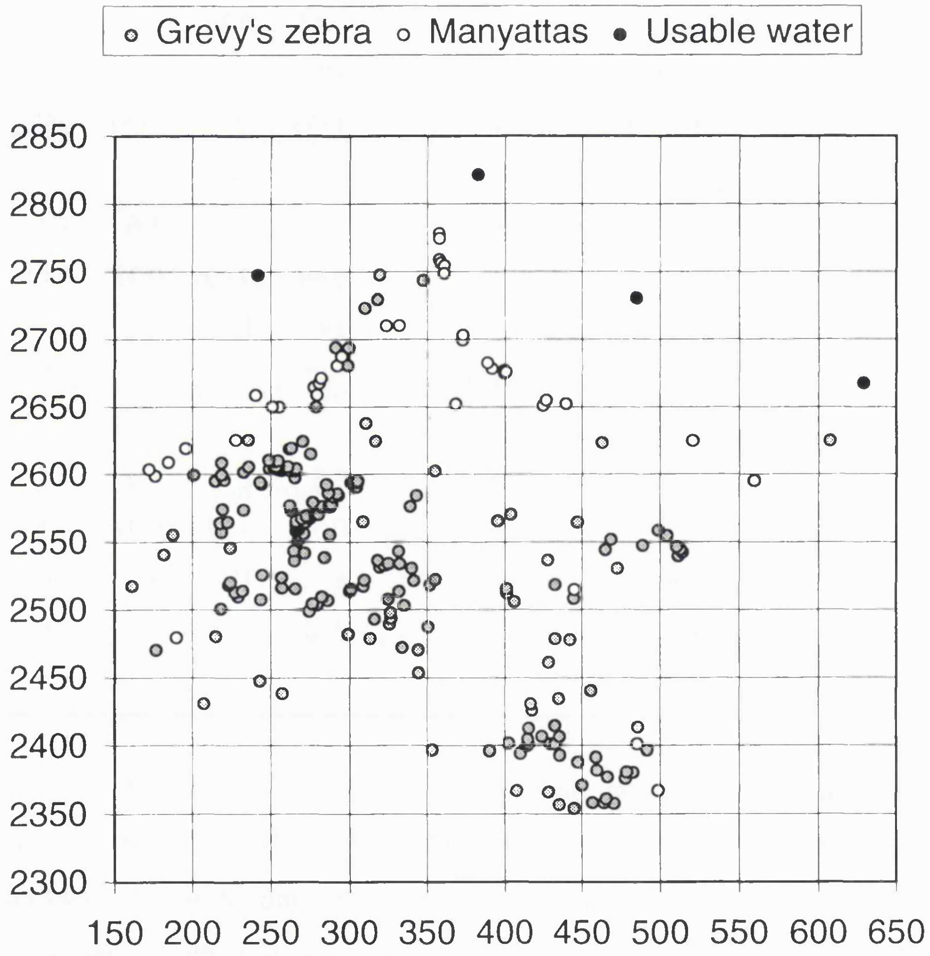
b) Ngare Ndare		1	2	3	4	5
Cattle	Mean distance to water	2.0	2.3	1.0	1.5	1.8
	s.e.	0.28	0.39	0.17	0.40	0.42
	No of groups	26	19	7	11	16
	Total number of individuals	1250	757	319	691	556
Small stock	Mean distance to water	2.4	2.2	1.4	2.6	1.6
	s.e.	0.44	0.36	0.16	0.84	0.51
	No of groups	18	17	18	9	12
	Total number of individuals	1378	1955	2651	950	709
Donkeys	Mean distance to water	2.2	2.4	1.6	1.4	1.1
	s.e.	0.44	0.40	0.33	0.65	0.31
	No of groups	19	13	4	5	15
	Total number of individuals	147	121	13	67	78
Camels	Mean distance to water	2.3	2.8	1.0	3.1	2.7
	s.e.	0.57	0.37	0.37	0.54	0
	No of groups	8	13	5	11	1
	Total number of individuals	216	245	43	232	11

The *manyattas* in Barsalinga were found at a mean distance of 3.6km from usable water (with a standard error of 0.3 about the mean; N = 40). Those in Ngare Ndare were found at a mean distance of 2.0km from usable water (with a standard error of 0.49 about the mean; N = 10). One reason for the disparity in the distances that the *manyattas* were found may have been the differences in the ethnic groups found in the two study areas. Barsalinga was dominated by Samburu people, while Ngare Ndare had Somali, Turkana and Samburu peoples. Since the Somali and Turkana people are pastoral people who favour camels, as opposed to the cattle based pastoralism favoured by the Samburu, they were more likely to be found further away from water.

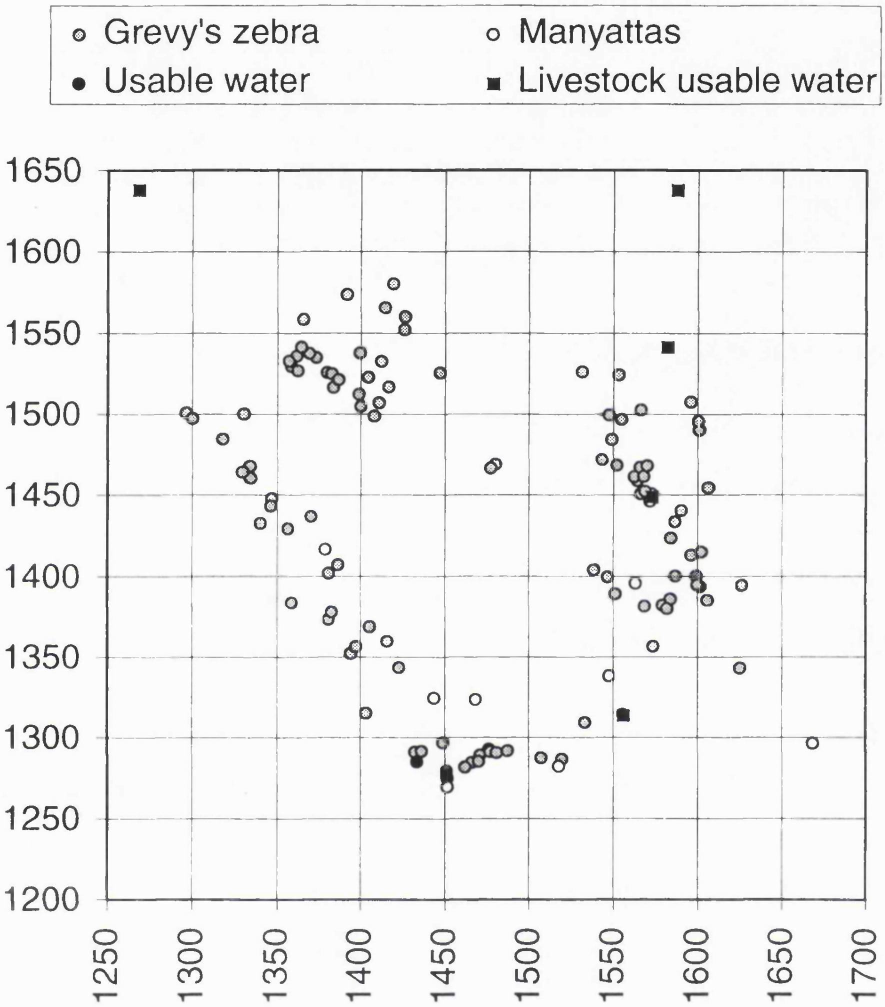
Distribution of Grevy's zebra

The distribution of groups of Grevy's zebra, recorded over the duration of the study, relative to usable water and *manyattas*, are shown in Figures 3a-c.

a) Barsalinga



b) Ngare Ndare



c) Buffalo Springs

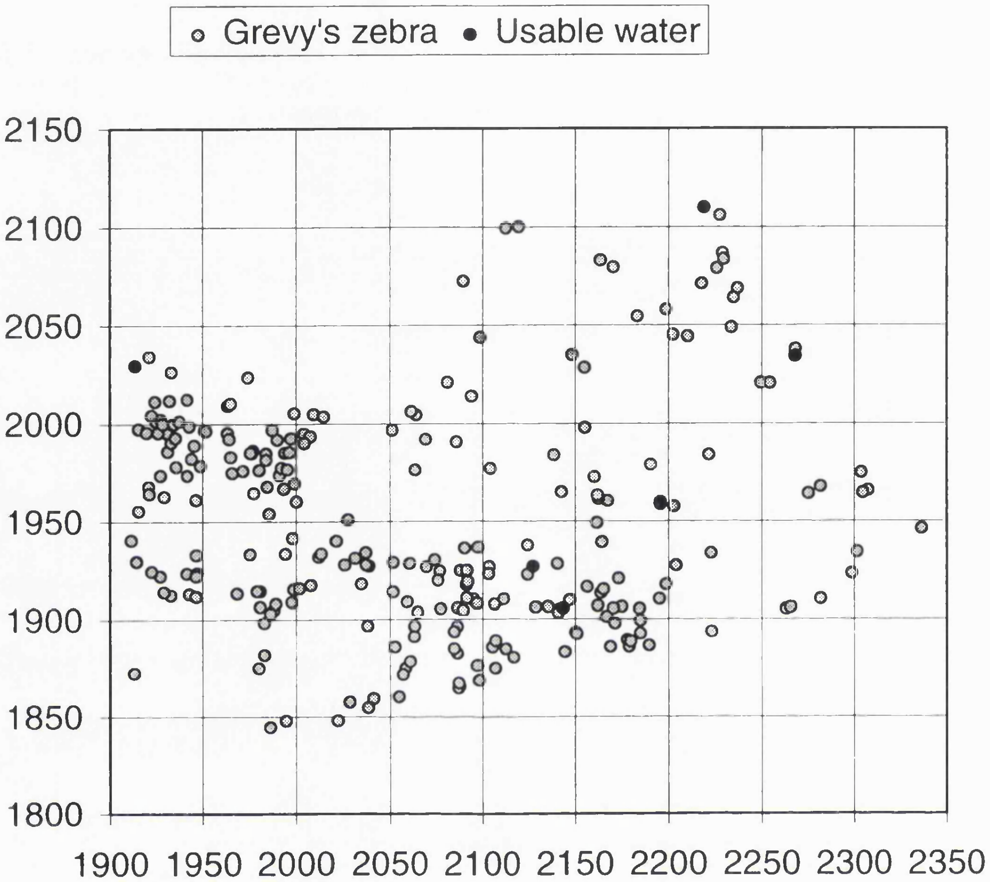


Figure 3. Scatterplots of the distribution of groups of Grevy's zebra over the duration of the study, shown relative to usable water points and the human habitations or *manyattas*. The *x*- and *y*-axes are longitude and latitude displayed in seconds.

The sample sizes of number of groups of Grevy's zebra, total number of individuals, and total number of females sighted during each rotation used in the analysis in this chapter are shown in Table 4.

Table 4. The number of groups, total number of individuals, and total number of adult females sighted during each rotation in the three study areas. These data were used throughout the analysis in this and subsequent chapters.

	Rotation				
	1	2	3	4	5
Barsalinga					
Number of groups	15	36	22	10	2
Total number of individuals	246	279	472	108	5
Total number of adult females	171	137	236	75	2
Ngare Ndare					
Number of groups	20	24	5	10	13
Total number of individuals	247	243	20	97	233
Total number of adult females	109	101	12	67	86
Buffalo Springs					
Number of groups	22	27	23	6	12
Total number of individuals	222	349	363	28	184
Total number of adult females	82	154	201	12	81

Responses of Grevy's zebra to food resources

The selectivity index, *E*, was used to describe the habitat use by Grevy's zebra. Where possible, this was kept at the level of patches. Hence, where zebras were observed on patches of known, i.e., measured, availability of grass, they were kept separate from other patches of the same habitat. The selection of habitats indicated that, in general, but particularly in Barsalinga, Grevy's zebra selected to feed in the habitats with the greatest forage availability (Table 5).

Table 5. The proportion of feeding sightings and the selection index (given in parentheses) of Grevy's zebra on different patches of the habitats in Barsalinga during different seasons throughout the study. Distance to water is given in the second column. For clarity, the habitats with significantly higher availability of forage (from the above analyses) are shown in bold and darkly shaded cells, and the patches that were strongly selected by the Grevy's zebra are shown in shaded cells.

a) Barsalinga

Habitat or patch		Late dry	Rains	Dry	Early dry	Dry
A. reficiens woodland	all					
A. reficiens/ A.nubica/ A. horrida woodland	7.5					
A. senegal/ Commiphora sp. woodland	2				0.011 (-)	
A. tortilis dwarf shrubland	7.5					
A. tortilis shrub grassland	4.5		0.62 (++)			
	7.5			0.19 (-)		
	7.5	0.07(-)			0.258 (++)	0.2 (++)
	12	0.04 (-)				
A. tortilis/ Commiphora sp. woodland	4.5		0.15 (-)		0.161 (--)	
	7.5		0.13 (++)		0.172 (+)	0.6 (++)
Alluvial Pennisetum sp. grassland	**4.5**	0.07 (-)	0.08 (++)	0.31 (++)	0.366 (++)	
	7.5	0.41 (+)	0.02 (+)	0.37(+)		0.2 (++)
	7.5	0.26 (++)			0.032 (++)	
	7.5	0.05 (++)				
	12	0.08 (++)				
Dry river bed	7.5					
Mixed A. tortilis/ A. reficiens woodland	4.5			0.12 (++)		
Sample size (n)		276	107	266	93	5

-- indicates strong avoidance (- 0.5 to - 1); - weak avoidance (- 0.1 to - 0.49), 0 neutral (0.09 to - 0.09), + weak selection (0.1 to 0.49), and ++ strong selection (0.5 to 1).

b) Ngare Ndare

habitat		Late dry	Early dry	Rains	Dry	Rains
A. reficiens woodland	4.5					0.028 (++)
	7.5				0.038 (+)	
A. tortilis dwarf shrubland	0.25					
	2		0.073 (++)	0.048 (+)		
	4.5				0.038 (-)	
	7.5	0.469 (++)	0.056 (-)		0.628 (++)	0.88 (++)
A. tortilis shrub grassland	0.25				0.205 (++)	
	2	0.315 (-)	0.068 (0)			0.024 (--)
	4.5	0.007 (--)	0.424 (++)	0.19 (+)	0.09 (+)	0.016 (--)
	7.5		0.288 (++)			
A. tortilis/ A. mellifera/ A. reficiens riverine woodland	4.5			0.524 (++)		
A. tortilis/ Commiphora sp. woodland	all					
Alluvial *Setaria* sp. grassland	**0.25**	0.049 (++)				
	2	0.028 (0)				
	4.5	0.014 (-)	0.085 (++)			
	7.5	0.119 (--)	0.006 (--)	0.238 (+)		0.052 (--)
Dry river bed	all					
Mixed A. tortilis/ A. reficiens woodland	4.5					
Riverine	0.25					
Sample size (*n*)		143	177	21	78	251

-- indicates strong avoidance (- 0.5 to - 1); - weak avoidance (- 0.1 to - 0.49), 0 neutral (0.09 to - 0.09), + weak selection (0.1 to 0.49), and ++ strong selection (0.5 to 1).

c) Buffalo Springs

habitat		Late dry	Early dry	Rains	Dry	Rains
A. reficiens dwarf shrubland	**0.25**					
	2					0.044 (++)
A. reficiens woodland	**0.25**			0.039 (++)	0.027 (0)	
	2		0.206 (++)			
A. tortilis dwarf shrubland	0.25					
	0.25	0.126 (--)		0.574 (++)		0.063 (-)
	2	0.37 (0)	0.11 (--)	0.106 (-)	0.243 (+)	
	4.5		0.006 (--)	0.199 (+)	0.378 (0)	0.308 (+)
	6		0.052 (++)			
A. tortilis grassland	0.25					
	2	0.101 (++)			0.054 (++)	
	4.5					
A. tortilis shrub grassland	0.25	0.176 (+)	0.065 (+)		0.135 (++)	
	2	0.067 (--)	0.006 (--)	0.007 (--)	0.108 (-)	0.038 (--)
	4.5				0.054 (++)	0.547 (++)
A. tortilis/ Commiphora sp. woodland	2					
Alluvial Setaria sp. grassland	0.25					
	2					
	4.5		0.394 (+)			
	6	0.16 (++)				
Mixed A. tortilis/ A. reficiens woodland	**0.25**			0.007 (--)		
	2		0.161 (++)	0.067 (++)		
Riverine	0.25					
Salsola denroides/ Sporobolus spicatus shrubland	0.25					
Sample size (n)		119	155	282	37	159

-- indicates strong avoidance (- 0.5 to - 1); - weak avoidance (- 0.1 to - 0.49), 0 neutral (0.09 to - 0.09), + weak selection (0.1 to 0.49), and ++ strong selection (0.5 to 1).

Responses of Grevy's zebra to water resources

Groups of Grevy's zebra in Barsalinga and Ngare Ndare were rarely found less than 5km from usable water (Figure 4).

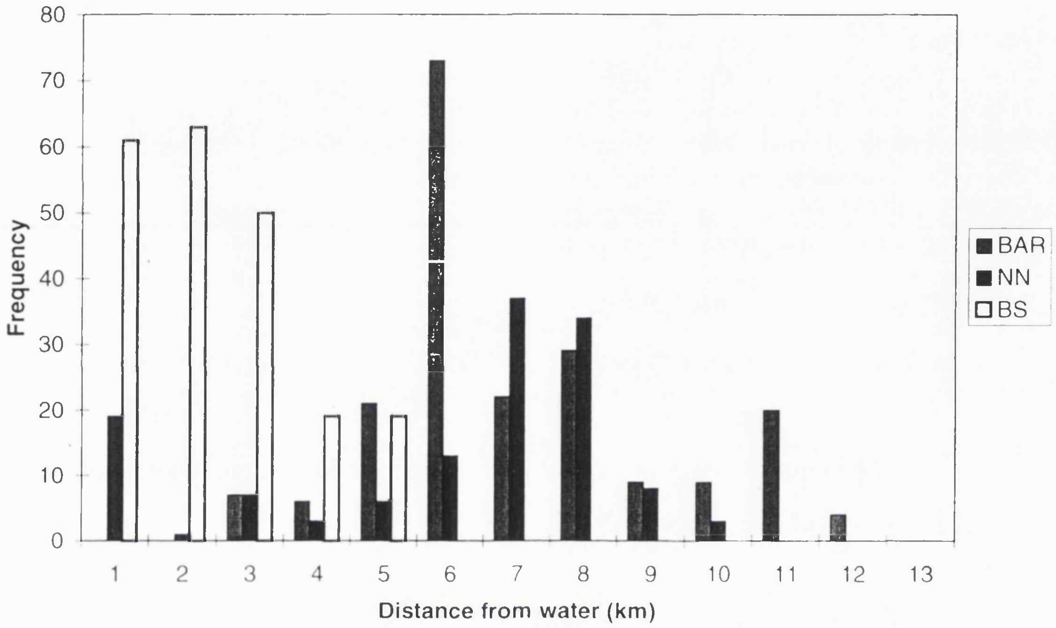


Figure 4. The distribution of the distance from usable water that groups of female Grevy's zebra were sighted in the three study areas. In the legend, BAR ≡ Barsalinga; NN ≡ Ngare Ndare; and BS ≡ Buffalo Springs.

The analysis of the distribution of lactating females compared with other classes of female, relative to water was conducted to assess whether there was a trade-off between the requirements for water and the distribution of food. The analyses showed that in Barsalinga, the lactating females were closer to water sources than other classes of female (Table 6). Here, the proportion of lactating females in the groups of Grevy's zebra decreased with distance from usable water (see coefficient estimate, Table 6). There was no effect of female class in the other two study areas (Table 6).

Table 6. The effect of class of female on the distribution of Grevy's zebra relative to usable water, as measured by how the proportion of early- and mid-lactation females in each group changes with distance from water.

Study areas	Deviance (χ^2)	*d.f.*	*P*	Coefficient estimates
Barsalinga	80.1	1	< 0.001	- 0.41
Ngare Ndare	3.6	1	NS	
Buffalo Springs	1.5	1	NS	

Responses of Grevy's zebra to predators

There was an insufficient number of sightings of predators in any of the study areas over the duration of the study for analysis of their effects on the distribution of zebra (Table 7). However, more lions, the only predator known to take adult Grevy's zebra, were seen in Buffalo Springs.

Table 7. The number of predators sighted in each of the three study areas over all surveys.

	Lions	Cheetahs	Hyaenas
Barsalinga	0	13	0
Ngare Ndare	1	3	0
Buffalo Springs	19	1	0

Overall distribution of Grevy's zebra

The analysis of the space use of Grevy's zebra was conducted using both zebra presence/absence and not just the numbers of zebra because it was expected that numbers may mask some of the effects that would be detected by the presence/absence analyses.

When presence/absence of Grevy's zebra, and the number of females recorded in all sighted groups of Grevy's zebra were fitted as response variates, over all study areas, rotation, the percentage cover of grass and the distance to usable water had significant effects (Table 8 in which the results for only the model of zebra presence/absence are presented: the results in both models were equivalent).

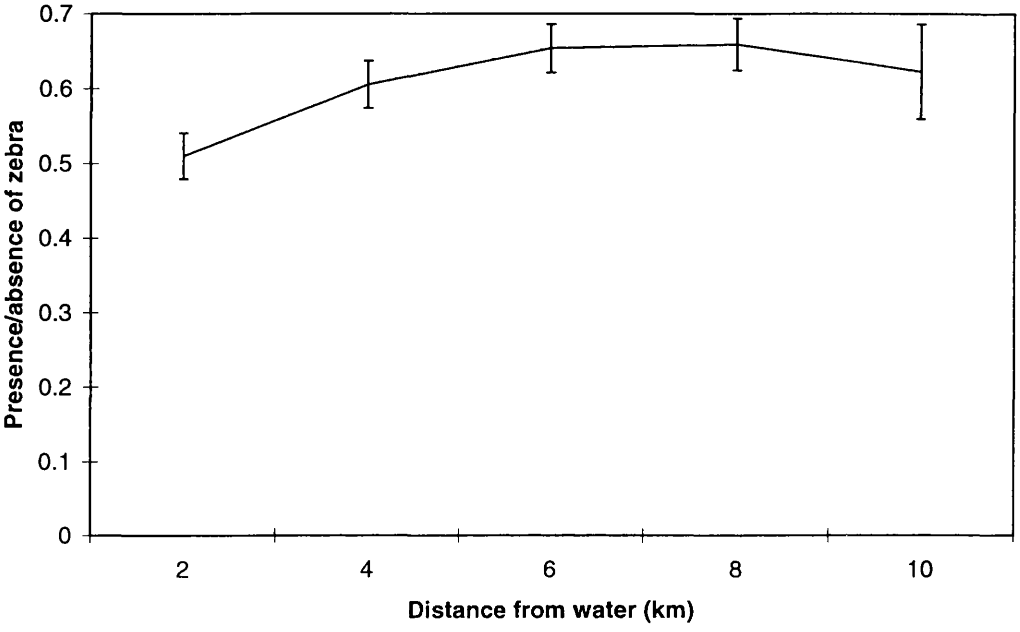


Figure 5. The peaked distribution of Grevy's zebra relative to distance to water. The values (±s.e.) were predicted from the model using the quadratic of distance to water (water + water^2) as the explanatory variate, and the presence/absence of zebra as the response variate.

To test whether the distribution relative to water was peaked, the distance to water was squared and the quadratic, water+water^2, was fitted to the model. This was significant ($\chi^2 = 15.5$, *d.f.* = 2, $P < 0.001$), therefore, indicating a peaked distribution of zebra from water (Figure 5).

Table 8. The results of the analysis of the effect of rotation (rotation), the availability of forage as measured by the percentage cover of grass (cover), and the distance of groups from the nearest usable water (water) on the distribution of Grevy's zebra, as measured by their presence/absence in habitats. The full model had a deviance of 55.7, with 6 degrees of freedom, and a total deviance of 561.8).

Parameters	Deviance	*d.f.*	*P*	Coefficient estimates
Cover	18.4	1	< 0.001	+ 0.04
Water	10.9	1	< 0.001	+ 0.12
Rotation	40.4	4	< 0.001	

In the models for the data from Barsalinga, there was no difference between the models of zebra presence/absence or zebra female numbers. The distance to water, the distance from the nearest group of livestock, the availability of forage and rotation had significant effects on the distribution of Grevy's zebra. Here, I present the model using the numbers of female Grevy's zebra as the response variate, showing that the availability of food has the most important effect on their distribution (Table 9). The number of Grevy's zebra females increased with the grass cover (Table 9). As with the distribution of Grevy's zebra relative to water discussed above, in Barsalinga the number of Grevy's zebra increased with increasing distance to water (Table 9). Again, the distribution of zebra relative to water was tested for a peak by fitting the quadratic, water+water^2. This was significant (deviance = 138.9, dispersion parameter = 4.99, $\chi^2 = 27.8$, *d.f.* = 2, $P < 0.001$). When the values were predicted from the model, the peak in distribution of zebras relative to water was between 7 - 8km.

Table 9. The minimum adequate model for the analysis of the effect of explanatory variates and factors on the distribution of Grevy's zebra in Barsalinga, using the number of females in each sighted group as the response variate in the model. The explanatory variables included distance to livestock (livestock), percentage cover of grass (cover), distance to usable water (water) and the temporal scale of rotation (rotation). The deviance for the full model was 487, with a dispersion parameter of 7.23 and 7 degree of freedom, from a total deviance of 1551.

Parameters	Deviance	Dispersion	*d.f.*	χ^2	*P*	Coefficient estimates
Livestock	57	7.57	1	7.53	< 0.01	- 0.02
Cover	115	7.96	1	14.45	< 0.001	0.04
Water	42	7.47	1	5.62	< 0.025	0.12
Rotation	104	7.73	4	13.45	< 0.01	

Finally, there was a negative relationship with the distance to groups of livestock in Barsalinga. Hence, as the distance to livestock decreased, the number of Grevy's zebra increased. This may have been attributable to the livestock being constrained to feeding in the same habitats. Although the quadratic of distance to livestock (livestock + livestock^2) was significant (deviance = 63.0, dispersion = 7.57, χ^2 = 8.32, *d.f.* = 2, *P* <0.025), distance to livestock (as opposed to the quadratic) had a greater effect. Hence, the distribution of zebra was not peaked relative to livestock.

In contrast to Barsalinga, in Ngare Ndare there were differences in the models using presence/absence and the numbers of females in sighted groups of Grevy's zebra as the response variates. The parameters that were significant in both models were distance to the nearest *manyatta* and the interaction term between the distance to the nearest group of livestock and the percentage cover of grass (livestock.cover) (model using zebra presence/absence: manyatta: χ^2=16.4, *d.f.*=1, *P*<0.001, livestock.cover: χ^2=4.4, *d.f.*=1, *P*<0.05; model using zebra numbers: manyatta: change in deviance=27.2, dispersion parameter=5.78, χ^2=4.71, *d.f.*=1, *P*<0.05, livestock.cover:

change in deviance=29.8, dispersion parameter=5.26, $\chi^2=5.67$, *d.f.*=1, $P<0.025$). However, there were differences in the models. In the model fitted with the numbers of female Grevy's zebra, rotation had a significant effect (rotation: change in deviance=71.1, dispersion parameter=5.60, $\chi^2=12.7$, *d.f.*=4, $P<0.025$), while in the model of the zebra presence/absence, the percentage cover of grass had a significant effect ($\chi^2=15.5$, *d.f.*=1, $P<0.001$). Both parameters were included in the minimum adequate models (Table 10).

Table 10a. The minimum adequate model for the analysis of the effect of explanatory variates and factors on the distribution of Grevy's zebra in Ngare Ndare, using the number of females in each sighted group as the response variate. The parameters that were included in the model were the interaction term between distance to livestock and percentage cover of grass (livestock.cover), the distance to livestock (livestock), the percentage cover of grass (cover), the distance to *manyattas* (manyatta), and rotation (rotation) The model had a deviance of 129.5, with a dispersion parameter of 5.03 and 8 degrees of freedom, while the total deviance was 693.4.

Parameters	Deviance	Dispersion	*d.f.*	χ^2	*P*	Coefficient estimates
cover.livestock	26.9	5.23	1	5.14	< 0.025	- 0.03
livestock	2.1	5.20	1	0.4	NS	
cover	3.2	5.21	1	0.61	NS	
manyatta	26.2	5.22	1	5.02	< 0.05	0.01
rotation	41.4	5.22	4	7.93	< 0.005	

Table 10b. The minimum adequate model for the analysis of the effect of explanatory variates and factors on the distribution of Grevy's zebra in Ngare Ndare, using zebra presence/absence as the response variate. The parameters included in the model were the same as the above model. The model had a deviance of 42.6 with 8 degrees of freedom, while there was a total deviance of 163.3.

Parameters	Deviance (χ^2)	*d.f.*	*P*	Coefficient estimates
cover.livestock	3.0	1	NS	
livestock	3.5	1	NS	
cover	9.5	1	< 0.005	0.06
manyatta	17.5	1	< 0.001	0.03
rotation	4.2	4	NS	

There were also differences in the results from the minimum adequate models for Ngare Ndare (Table 10). The distance to *manyatta*s was significant in both models, but it was the most important for determining the zebra presence/absence (Table 10b). With increasing distance from *manyatta*s, the zebra presence increased. Hence, the zebra were avoiding people. The percentage cover of grass also had an effect on zebra presence - with zebra presence increasing with increasing abundance of grass (Table 10b). Percentage cover of grass had no effect on zebra numbers (Table 10a).

The most important effect on zebra numbers in Ngare Ndare was rotation. Zebra presence/absence was less likely to be influenced by rotation if the number of groups that were seen in each rotation were approximately the same. The interaction term between cover of grass and the distance to livestock also had a strong effect on the zebra numbers (Table 10a). To explore the effect of the interaction term between the cover of grass and the distance to livestock further, values were predicted from the model (Figure 6). This indicated that as the distance from the nearest group of livestock and the percentage cover of grass increased, there was an increase in the number of Grevy's zebra females. At low grass abundance and in close proximity to livestock, the numbers of zebra were low.

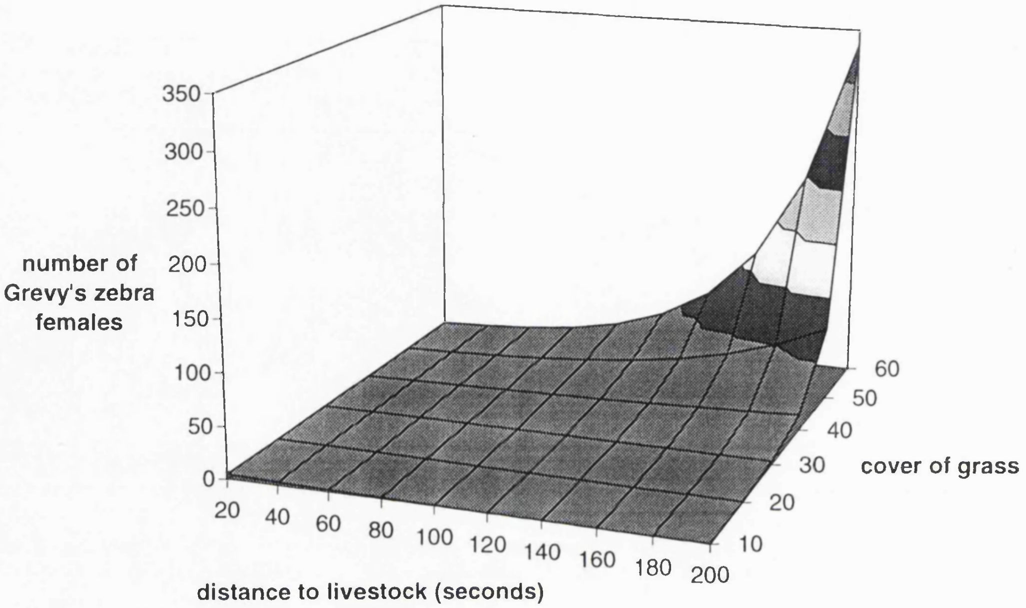


Figure 6. The predicted effect of distance of the nearest group of livestock and the cover of grass on the number of Grevy's zebra females.

In the analysis of the factors affecting the distribution of Grevy's zebra in Buffalo Springs, there were also differences in the models fitted to zebra presence/absence and numbers of Grevy's zebra females (Table 11).

These results (Table 11a) show that rotation has a strong effect on the numbers of Grevy's zebra (as with Ngare Ndare) since this was the only parameter to have a significant effect on the number of zebra. In contrast, both cover of grass and distance to water had significant effects on zebra presence. These effects indicated that zebra presence declines with increasing distance from water (coefficient of relationship = - 0.26) and with increasing cover of grass (coefficient = - 0.04).

Table 11a. The minimum adequate model for the analysis of the effect of explanatory variates and factors on the distribution of Grevy's zebra in Buffalo Springs, using the number of females in each sighted group as the response variate in the model. The parameters fitted to the model were distance to usable water (water), percentage cover of grass (cover) and rotation (rotation). The model had a deviance of 154.7 with a dispersion parameter of 7.44 and 6 degrees of freedom. The total deviance was 1107.2.

Parameters	Deviance	Dispersion	*d.f.*	χ^2	*P*
water	0.9	7.39	1	0.12	NS
cover	2.0	7.35	1	0.27	NS
rotation	152	8.26	4	18.4	< 0.005

Table 11b. The minimum adequate model for the analysis of the effect of explanatory variates and factors on the distribution of Grevy's zebra in Buffalo Springs, using zebra presence/absence as the response variate in the model. The fitted parameters were the same for the above model. The model deviance was 31.5 with 6 degrees of freedom. The total deviance was 182.5.

Parameters	Deviance (χ^2)	*d.f.*	*P*	Coefficient estimates
rotation	11.5	4	< 0.025	
cover	9.8	1	< 0.005	- 0.04
water	8.4	1	< 0.005	- 0.26

Dispersal

The number of adult females recorded in each of the study gives an indication to the flux of movement of individuals in and out of the study areas (Table 12).

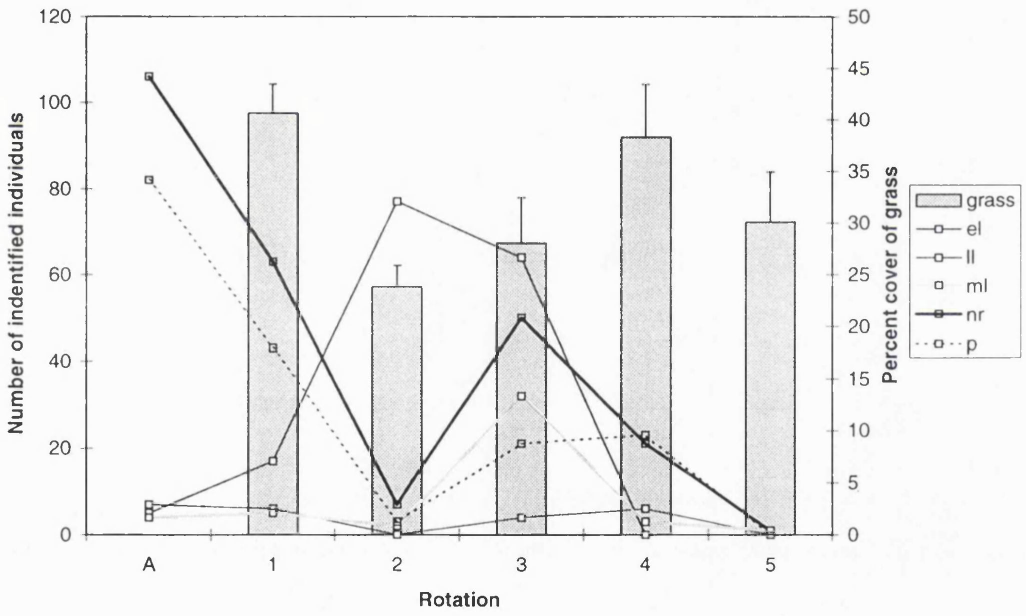
Table 12. The number of adult females individually identified in each of the study areas through the study. The total number of females per rotation is the sum of those seen in each of the study areas, and is also displayed. During the first rotation shown here, 'A', the vegetation was not measured.

	Rotation					
	A	1	2	3	4	5
Barsalinga	205	134	89	168	53	2
Ngare Ndare	85	62	56	8	51	77
Buffalo Springs	35	67	91	170	34	68
Total	322	259	233	329	138	142

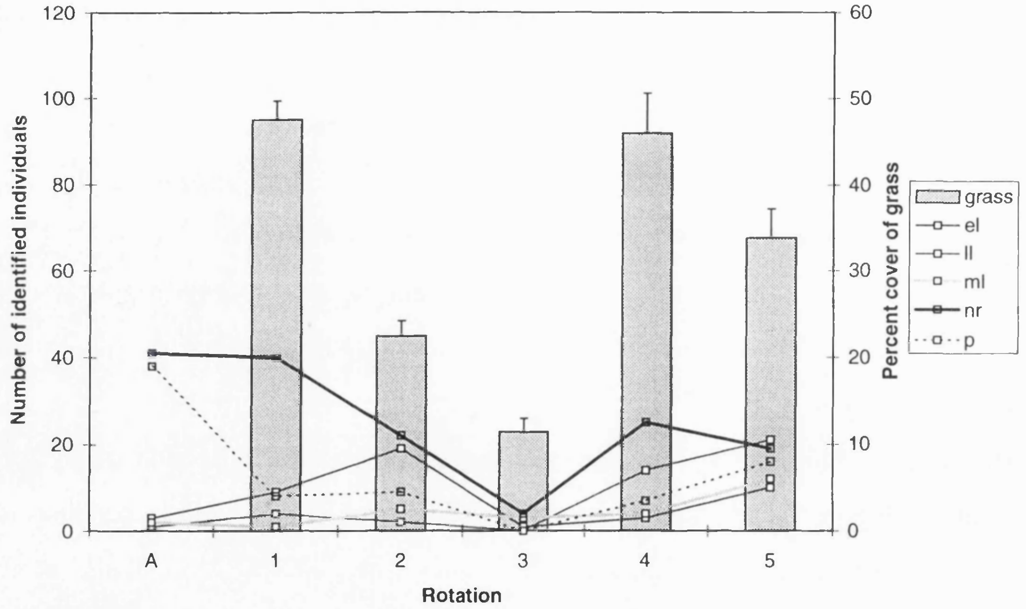
Analysis of the individually identified zebra indicated that a total of 284 adult females were sighted on two or more rotations of the study areas. Of these, just 104 were seen to spend time in just one area, 151 were seen in two areas, and 29 were sighted in all three areas. When those females that were sighted in two or three areas were studied in more detail, the following pattern emerged: of a total of 185 individuals that were seen to use more than one study area, 110 changed area twice, 55 changed area three times, 15 changed area four times, 4 changed area five times, and one individual was seen to change study area six times. The small disparity in the number of animals sighted in two or more study areas on a rotational basis (i.e., 180 individuals), and those seen to use two or more study areas (i.e., 185 individuals) arose since 5 individuals were sighted in different study areas within the same rotation.

In Barsalinga, the emigration of non-reproductive females corresponded with a decline in the availability of forage. There was a 93% (*N*=99) decline in the number of non-reproductive females in Barsalinga during the first two surveys (surveys 'A' and 1 on Table 3, chapter 2), but no corresponding increase in the number of sighted pregnant females (Figure 7). Unlike the non-reproductive females, early lactation females did not emigrate until after the third rotation (rotation 2 on Table 3, chapter 2) in Barsalinga, although part of their decline in numbers can be attributed to change in reproductive class - hence to mid-lactation females. However, by the fourth rotation, only 4 of the 104 females with foals from the third rotation remained in Barsalinga. Although there was recovery in the vegetation in Barsalinga by the fifth rotation (Figure 7), the number of all females sighted in Barsalinga declined to two adult females during the final rotation - representing a 99% (*N*=202) decline in the numbers of females over the course of the study.

a) Barsalinga (see next page for title)



b) Ngare Ndare



c) Buffalo Springs

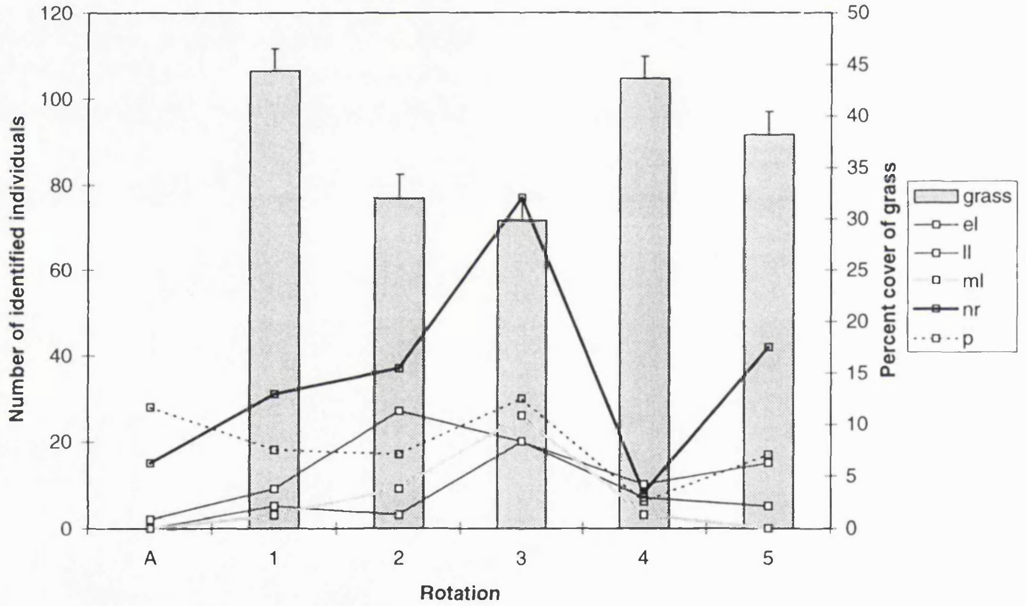


Figure 7. The number of identified females of each reproductive class sighted in the three study areas over the duration of the study. This is shown relative to the availability of forage as measured by the mean percentage cover of grass over all habitats (shown with error bars of the standard error about the mean). In the legend, the symbols for the reproductive classes are: el - early lactation; ll - late lactation; ml - mid lactation; nr - non reproductive; and p - pregnant females. During the first shown rotation, 'A', the vegetation was not measured, but the areas were surveyed for animals.

There was a similar decline in the number of non-reproductive females (90.2% *N*=37) in Ngare Ndare from the second to the fourth rotation (Figure 7). However, their emigration was accompanied by a 78.9% decrease in the number of early lactation females (*N*=14, having accounted for individuals that changed in reproductive class to mid-lactation). Hence, in Ngare Ndare and unlike Barsalinga, the early lactation females dispersed at the same time as the non-reproductive females. Alternatively, the rotations around the study areas were not frequent enough to pick up the different times of dispersal between these classes of female. A total of 86% (*N*=77) of all females had emigrated by the fourth rotation, when the availability of forage was at its lowest. Unlike Barsalinga, with the recovery of the vegetation by the fifth rotation, the numbers of adult females also recovered.

In contrast to Barsalinga and Ngare Ndare, in Buffalo Springs there was no apparent relationship between the movement of animals and the availability of forage (Figure 7). Instead, increases in the numbers coincided with periods when the forage availability was lowest in the domestic livestock areas (Barsalinga and Ngare Ndare) and, therefore, when animals were emigrating from those areas.

Discussion

Although it was evident from the results that no single factor determined the use of space by Grevy's zebra, the abundance of forage was an important determining factor, especially in the areas used by pastoral people. Even though the measure of forage was crude, the relationship between space use of Grevy's zebra and abundance of forage emerged. By feeding selectively in those parts of the range in which forage was most abundant, it is likely the zebra were trying to maintain high intake rates. This is consistent both with previous studies and with theory (Arnold & Dudzinski 1978; Duncan 1992; Duncan *et al.* 1990; Ginsberg 1988; Gordon 1989a; 1989b; Mayes & Duncan 1986).

However, by feeding in the habitats with the highest abundance of forage - specifically the alluvial *Pennisetum/Setaria* sp. grassland (Table 5) - there may have been a trade-off between quality and high biomass. By feeding in these habitats, the zebra were probably feeding on *Pennisetum mazianum* and *Setaria* sp. - although their use of plant species or plant part was not measured in this study. The measures of forage abundance were also crude: forage quality was not measured. However, other workers have found these species of grass to be fibrous and of low palatability, particularly during the dry season (Bronner 1990; Herlocker 1993). Such a trade-off would be consistent on theoretical grounds for equids (Belovsky 1986; Chacon & Stobbs 1976; Illius & Gordon 1987; 1990). Equids have rarely been found to use forage quality as a determinant for their habitat use. Instead, absolute forage biomass is a more important determinant (Bell 1971; Casebeer & Koss 1970; Duncan 1992; Duncan *et al.* 1990; Gordon 1989a; Gordon 1989b; Janis 1976).

There appeared to be thresholds of forage availability in Ngare Ndare and Barsalinga since when the forage availability dropped below this level, Grevy's zebra dispersed from an area (Figure 7). At these thresholds, presumably the zebra were not able to sustain their high intake requirements. When food is limiting, forage biomass has been found to be a critical determinant in the habitat use of equids (Duncan 1983; Ginsberg 1988; Moehlman 1974; Rubenstein 1981; 1986). Dispersal provides an adaptive strategy by which animals can move away from areas of low forage availability, and should enhance the access of the migrant to patches of high forage quality or quantity (Fryxell *et al.* 1988; Fryxell & Sinclair 1988; Western 1975). Previous studies have also shown that Grevy's zebra respond to decreases in the abundance of forage by dispersal, particularly in drought periods when food was limiting (Ginsberg 1988). This implied that food was seasonally limited, particularly in Barsalinga and Ngare Ndare.

The results also suggest that different reproductive classes of female have different thresholds before dispersal (Table 12; Figure 7). In Barsalinga, the non-reproductive females dispersed earlier than lactating females. This did not imply that lactating females had higher tolerances to lower biomass of forage. Instead, it implied they were more constrained by their need for water. That they were was supported by the results that lactating females were found closer to water in Barsalinga (Table 6) - which was consistent with previous studies (Becker & Ginsberg 1990). In comparison, in Ngare Ndare, where the forage availability dropped to below levels recorded in Barsalinga, all the female Grevy's zebra, including those lactating, dispersed (Figure 7). Therefore, this suggested that lactating and non-reproductive females have different thresholds of dispersal, which although mediated by the availability of forage, are determined by their differential dependence on water.

These results are in direct contrast to Klingel's (1974) findings. In his study he found one threshold for all classes of female. However, in his study, water ceased to be available, when all classes of Grevy's zebra would be forced to disperse simultaneously.

In contrast to Ngare Ndare and Barsalinga, in Buffalo Springs, even though there were significant differences in the forage availability among the habitats, there was no pattern of selection of habitat by Grevy's zebra on the basis of the abundance of forage (Table 5c and 11a,b). Indeed, they seemed to avoid habitats with the highest forage abundance (Table 11b). However, Buffalo Springs, from which pastoral people were excluded, was the study area with the highest overall availability of forage. Hence, there may have been sufficient biomass of forage across all habitats. This was supported by the dispersal of Grevy's zebra: the dispersal from Ngare Ndare and Barsalinga coincided with an increase in the number of zebra in Buffalo Springs. Hence, Buffalo Springs may act as a refuge for zebra when forage availability in the surrounding areas used by pastoral people drops below the apparent thresholds.

The above effects of forage abundance on space use and dispersal of zebra would seem to suggest that zebra may be distributed themselves in an ideal free manner (Fretwell & Lucas; Fretwell 1972). However, other factors did have an effect. Theory predicts that the space use of water dependent ungulates such as Grevy's zebra should be constrained by the distribution of water sources (Vesey-Fitzgerald 1965; Western 1975). There appears to be a physiological barrier to the heavy utilisation of low water forage such as grasses in arid areas (Schmidt-Nielsen 1964) which limits the distance that grazing herbivores can move away from permanent water sources (Vesey-Fitzgerald 1965; Western 1975). The results are consistent with this. Although over all study areas and within Barsalinga, there was a positive relationship with the distance to water and both the zebra presence/absence and the numbers of female Grevy's zebra, when the quadratic was fitted to the model, the significant result indicated a peaked distribution of zebras relative to water (Figure 5). Such a peak in the distribution suggested they were limited in the distance they could move away from water. That the zebras were constrained by water was further exemplified by the distributions of the different classes of female in Barsalinga. Here, lactating females, with high water requirements, were found closer to the water sources (Table 6).

Few zebra were found in the vicinity of the water sources in the areas used by pastoral people, particularly in Barsalinga. Unlike in Buffalo Springs, where the zebra presence increased closer to water, there was a peaked distribution between 7 - 8km from water. This was probably an artefact of the distribution of food resources. Indeed, the abundance of forage in all habitats but the alluvial *Pennisetum* sp. grassland increased with distance from usable water in Barsalinga. This was probably due to sustained, heavy grazing pressure by domestic livestock in the vicinity of water. The habitat that showed a decrease in the food availability with distance from water, the alluvial *Pennisetum* sp. grassland, was distributed such that the nearest habitat was 4.5km to water (Figure 2c, chapter 2).

Similarly, the effect of distance to livestock on the distribution of Grevy's zebra in Barsalinga was also probably an artefact of the effect of abundance of forage (Table 9). Although these analyses have not considered the selection of habitats by domestic livestock, that the number of zebras increased with decreasing distance to domestic livestock provides indirect evidence that the livestock were selecting to feed in the same areas as the zebra. Like the zebras, they, too, may be constrained to feed in these areas simply because there is insufficient forage in other habitats. This was supported by the dispersal of cattle in the second rotation (Table 3a), which coincided with the low abundance of forage in April 1994 (Figure 1a).

In contrast to Barsalinga, in Ngare Ndare, the pastoral people and their livestock had a negative effect on the distribution of Grevy's zebra (Table 10a,b). The zebra avoided people, measured by the distribution of *manyattas*. This provides indirect evidence of interference between pastoralists and zebra (Bunderson 1981; Pierpont 1986). Similarly, the distribution of zebras in Barsalinga relative to water also provides indirect evidence that they were avoiding the water sources during the diurnal surveys (cf, chapter 5).

What was more important and evident from this study was that forage abundance was significantly lower in the two areas used by pastoral people and their domestic livestock than in Buffalo Springs, the area from which pastoralists were excluded. It was apparent that food was seasonally limited in the pastoralist areas, in which the conditions and responses of Grevy's zebra mimic those recorded by (Ginsberg 1988) during a drought. The consequences of this on the aggregative behaviour of Grevy's zebra will be explored in the next chapter, while the effect on recruitment will be examined later in the thesis.

References

Arnold, G. W. & Dudzinski, M. L. 1978 *Ethology of free living domestic animals*. Amsterdam: Elsevier.

Barton, R. A., Whiten, A., Strum, S. C., Byrne, R. W. & Simpson, A. J. 1992 Habitat use and resource availability in baboons. *Animal Behaviour* **43**, 831-844.

Becker, C. D. & Ginsberg, J. R. 1990 Mother infant behavior of wild Grevy's zebra: adaptations for survival in semi-desert east Africa. *Animal Behaviour* **40**, 1111-1118.

Bell, R. H. V. 1971 A grazing ecosystem in the Serengeti. *Scientific American* **224**, 86-93.

Belovsky, G. E. 1986 Optimal foraging and community structure implications for a guild of generalist grassland herbivores. *Oecologia* **70**, 35-52.

Bronner, G. 1990 *Vegetation and land use in the Matthews Range area, Samburu District.* Dissertationes Botanicae. Berlin: J. Cramer.

Bunderson, W. T. 1981 Ecological Separation of wild and domestic mammals in an East African ecosystem. Logan, Utah: Utah State University.

Casebeer, R. L. & Koss, G. G. 1970 Food habits of wildebeest, zebra, hartebeest and cattle in Kenya Maasailand. *East African Wildlife Journal* **8**, 25-36.

Chacon, E. & Stobbs, T. H. 1976 Influence of progressive defoliation of a grass sward on the eating behaviour of cattle. *Australian Journal of Agricultural Research* **27**, 709-727.

Charnov, E. L. 1976 Optimal foraging: the marginal value theorem. *Theoretical Population Biology* **9**, 129-136.

Clutton-Brock, T. H. 1989 Mammalian mating systems. *Proceedings of the Royal Society, London, Series B* **236**, 339-372.

Crawley, M. J. 1993 *GLIM for Ecologists.* Methods in Ecology. Oxford: Blackwell Science.

Duncan, P. 1983 Determinants of the use of habitats by horses in a Mediterranean wetland. *Journal of Animal Ecology* **52**, 93-109.

Duncan, P. 1992 *Horses and grasses: the nutritional ecology of equids and their impact on the Camargue.* Ecological Studies. New York: Springer-Verlag.

Duncan, P., Foose, T. J., Gordon, I. J., Gakahu, C. G. & Lloyd, M. 1990 Comparative nutrient extraction from forages by grazing bovids and equids a test of the nutritional model of equid bovid competition and coexistence. *Oecologia* **84**, 411-418.

Fretwell, S. D. & Lucas, H. J. J. 1970 On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretika* **19**, 16-36.

Fretwell, S. D. 1972 *Populations in a seasonal environment.* Princeton: Princeton University Press.

Fryxell, J. M. & Sinclair, A. R. E. 1988 Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution* **3**, 237-241.

Fryxell, J. M. 1991 Forage quality and aggregation by large herbivores. *American Naturalist* **138**, 478-498.

Fryxell, J. M., Greever, J. & Sinclair, A. R. E. 1988 Why are migratory ungulates so abundant. *American Naturalist* **131**, 781-798.

Ginsberg, J. R. 1988 Social organization and mating strategies of an arid-adapted equid: the Grevy's zebra. Princeton, New Jersey: Princeton University.

Ginsberg, J. R. 1989 The ecology of female behaviour and male reproductive success in Grevy's zebra, *Equus grevyi. Symposia of the Zoological Society (London)* **61**, 89-110.

Gordon, I. J. 1989a Vegetation community selection by ungulates on the Isle of Rhum: 2. vegetation community selection. *Journal of Applied Ecology* **26**, 53-64.

Gordon, I. J. 1989b Vegetation community selection by ungulates on the Isle of Rhum: 3. determinants of vegetation community selection. *Journal of Applied Ecology* **26**, 65-79.

Gosling, L. M. 1986 The evolution of mating strategies in male antelopes. In *Ecological Aspects of Social Evolution* (ed. D. I. Rubenstein & R. W. Wrangham). Princeton: Princeton University Press.

Grunblatt, J., Said, M. Y. & Nutira, J. K. 1989 Livestock and wildlife summary 1987 - 1988 for Kenya Rangelands. Nairobi, Kenya: Department of Resource Surveys and Remote Sensing, Ministry of Planning and National Development.

Herlocker, D. J. 1993 Vegetation types. In *Range Management Handbook of Kenya, Volume II, 5: Isiolo District* (ed. D. J. Herlocker, S. B. Shaabani & S. Wilkes). Nairobi, Kenya: Republic of Kenya, Ministry of Agriculture, Livestock Development and Marketing.

Illius, A. W. & Gordon, I. J. 1987 The allometry of food intake in grazing ruminants. *Journal of Animal Ecology* **56**, 989-999.

Illius, A. W. & Gordon, I. J. 1990 Constraints on diet selection and foraging behaviour in mammalian herbivores. In *Behavioural mechanisms of food selection* (ed. R. N. Hughes). Berlin: Springer-Verlag.

Jacobs, J. 1974 Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's electivity index. *Oecologia* **14**, 413-417.

Janis, C. 1976 The evolutionary strategy of equidae and the origins of rumen and cecal digestion. *Evolution* **30**, 757-774.

Klingel, H. 1974 Social organisation and behaviour of the Grevy's zebra. *Zeitscrift für Tierpsychologie* **36**, 36-70.

Krebs, J. R. 1978 Optimal foraging: decision rules for predators. In *Behavioural Ecology* (ed. J. R. Krebs & N. B. Davies). Oxford: Blackwell Scientific Publications.

Lima, S. L. & Dill, L. M. 1990 Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**, 619-640.

Mayes, E. & Duncan, P. 1986 Temporal patterns of feeding behavior in free ranging horses. *Behaviour* **96**, 105-129.

McCullagh, P. & Nelder, J. A. 1987 *Generalised Linear Models.* Monographs on Statistics and Applied Probability. London: Chapman and Hall.

Moehlman, P. D. 1974 Behaviour and Ecology of Feral Asses. Wisconsin: University of Wisconsin.

Pierpont, N. 1986 Interspecific aggression and the ecology of woodcreepers (Aves: Dendrocolaptidae). Princeton: Princeton University.

Rubenstein, D. I. 1981 Behavioural ecology of island feral horses. *Equine Veterinary Journal* **13**, 27-34.

Rubenstein, D. I. 1986 Life history and social organisation in arid adapted ungulates. In *Ecological aspects of social evolution.* (ed. D. I. Rubenstein & R. W. Wrangham). Princeton: Princeton University Press.

Schmidt-Nielsen, K. 1964 *Desert Animals: Physiological Problems of Heat and Water.* Oxford: The Clarendon Press.

Sinclair, A. R. E. 1985 Does interspecific competition or predation shape the African ungulate community. *Journal of Animal Ecology* **54**, 899-918.

Spencer, P. 1965 *The Samburu.* London: Routledge & Kegan Paul.

Stephens, D. W. & Krebs, J. R. 1986 *Foraging theory.* Princeton: Princeton University Press.

Vesey-Fitzgerald, D. F. 1965 The utilization of natural pastures by wild animals in the Rukwa Valley, Tanganyika. *East African Wildlife Journal* **3**, 38-48.

Western, D. 1975 Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East African Wildlife Journal* **13**, 265-286.

4. Grevy's zebra aggregations: patches, fear or food?

Summary

1. Aggregative behaviour in ungulates is generally explained in three ways: 1) as a result of spatial variation in resource availability; 2) decreasing the risk of predation through dilution or satiation; and/or 3) as a means of maintaining forage in an immature but highly nutritious state.
2. These hypotheses were tested using two methods of measuring aggregation. The first used nearest neighbour distances between groups of Grevy's zebra (*Equus grevyi* Oustalet), while the second used the size of individual groups. The measures of aggregation were examined for Grevy's zebra in relation to key explanatory variables.
3. Barsalinga had the greatest degree of aggregation, with Ngare Ndare the least. This was consistent using both measures of zebra aggregation.
4. The results suggest that the aggregation of Grevy's zebra was not explicitly explained by any one hypothesis. Overall, the effect of predators, including humans, were important. However, within each study area different factors were important dependent on conditions in each. When food is limiting, the spatial distribution of resources may have the most important role. Where food is not limiting both predators and the forage-maturation were important.

Introduction

The aggregative behaviour of large herbivores is generally explained in three ways. First, aggregation results from spatial variation in nutrient quality and/or productivity of vegetation (Fryxell 1991; Fryxell & Sinclair 1988; McNaughton 1988; Sinclair 1977; Western 1975). This is based on the principles of optimality (Charnov 1976; Krebs 1978) which predicts that animals should feed selectively in those parts of the range where their preferred food items are most abundant. If food resources are patchily distributed, then aggregation should result. An extension of this, though more rarely evoked, is that aggregations result from the animals' use of a rare, locally distributed resource such as water in arid or semi-arid ecosystems (e.g., Moehlman 1979).

Second, aggregation reduces the risk of predation, by increased detection of the predators, or by the dilution effect (Caro & FitzGibbon 1992; FitzGibbon & Lazarus 1995; Lipetz & Bekoff 1982). Aggregation due to predation should occur in areas where predator density is high and aggregations of females with young foals, that are vulnerable to predation, should be greater than that of other reproductive classes of female (Estes 1976). The third explanation is that aggregation maintains vegetation in a highly nutritious, immature state (Hobbs & Swift 1988; McNaughton 1984; 1986). The regrowth of plants is highly nutritious and by remaining in areas of regeneration, herbivores increase their foraging success. This predicts that herbivore aggregation will be seasonal and most pronounced during the plant-growing season.

Few studies have considered the relative importance of these hypotheses for aggregation. While the role of predation in causing animals to aggregate is the most widely accepted hypothesis, recent modelling has shown that both the forage-maturation and spatial variation hypotheses should additively tend to increase the degree of aggregation (Fryxell 1991). Moreover, previously the hypotheses have been tested primarily in ruminants. In this chapter, I quantified the key variables likely to influence the aggregative behaviour of an equid, Grevy's zebra (*Equus grevyi* Oustalet), in three different study areas in northern Kenya. I show that aggregation in Grevy's zebra results from different factors in each study area - but was dependent on the conditions in each area. Hence, in the area where predator density was highest with high forage abundance, both forage-maturation and predation were important. In contrast, in the area where forage was limiting, the spatial variation of food was important. Human densities were also important in the areas used by pastoral people. Finally, I consider whether the recorded aggregative behaviour of Grevy's zebra differs from the ideal free distribution (Fretwell 1972; Fretwell & Lucas 1970; Parker 1970).

Methods

This study was conducted in three study areas in northern Kenya (as described in chapter 2). Among the areas, there were general differences in the key variables likely to affect the aggregative behaviour of Grevy's zebra (Table 1).

Table 1. The general differences in the key variables among the study areas. Humans and wild predators are shown as relative densities of humans and wild predators. Food availability is expressed in terms of seasonal variation. All these variables were quantified in this study.

	Barsalinga	Ngare Ndare	Buffalo Springs
Wild predators	Low	Intermediate	High
Humans	High	Intermediate	Nil
Spatial variation of food		To be determined	
Seasonality of food	High	High	High

The distribution of usable water was mapped and the presence of other aggregated resources - such as salt-licks - that may have additionally affected the aggregative behaviour of Grevy's zebra, was determined.

For the duration of the study, the study areas were surveyed in rotation. While in each study area, the season was recorded (as defined in chapter 2). The plant growing season was restricted to the rains and resulted in peak food availability in the early dry season (see chapter 3), which was consistent with similar semi-arid areas (Pratt & Gwynne 1977).

During each visit to each study area, the availability of forage for grazing ungulates was quantified in each habitat (see chapter 2 for methods, definitions of habitats, and chapter 3 general results of analysis of food availability). In this chapter, the 'patchiness' of the forage availability was quantified by the coefficient of variation among the habitats within each study area. The coefficient of variation is a method of comparing the relative amounts of variation in populations with different means (Sokal & Rohlf 1995).

During each visit to each study area, the number and distribution of animals was also recorded (for animal surveying methods, see chapter 2). Data were collected on Grevy's zebra and predators: lions (*Panthera leo*), cheetah (*Acinonyx jubatus*) and hyaenas (*Crocuta crocuta*). The total number of individuals of Grevy's zebra and predator species in each group encountered was recorded. Groups were defined as all animals occurring within 50 metres of another individual (after Ginsberg 1988; cf. Jarman 1987). The groups of Grevy's zebra that were either using water, or moving to or from water were removed and analysed separately to test whether aggregations at water were different from those away from such locally distributed resources. The location of each group encountered was recorded to a minimum accuracy of 100m using a Garmin 45™ Global Positioning System (GPS). The vegetation community on which the groups of animals were encountered was also recorded.

During the surveys, the number and location of pastoralist *manyatta*s (pastoralist villages) were recorded. In order to estimate the density of people in the areas used by pastoral people, the number of people in a random sample of *manyatta*s (Barsalinga, $N = 8$; Ngare Ndare, $N = 5$) were counted. The density was calculated from the mean number of people per *manyatta*, the number of *manyatta*s and the area of that study area.

Water source monitoring

There were problems estimating the densities of lions and hyaenas, which are usually nocturnal (see chapter 5; Kruuk 1972; Schaller 1972), from diurnal surveys. Hence, a further method was used for estimating the density of predators. A water source in each area was monitored for a total of 240 hours randomly distributed through a lunar month (28 days) during the dry season (for more details on the water source monitoring see chapter 5). The observations were conducted from a hide, using binoculars by day and night vision equipment by night. All the animals visiting the water sources were recorded, including the predators. The data collected from the water source monitoring provided information on the aggregation size of Grevy's zebra at water sources; the rate of predation attempts at water; and the relative density of predators in each of the areas in which the monitoring was conducted. Logistics precluded conducting the water source monitoring in the Ngare Ndare area; therefore, water sources were only monitored in Barsalinga and Buffalo Springs (see chapter 5 for details).

Predator density

The density of predators, per kilometre^2, was calculated from the maximum number of individuals sighted during any one survey of a study area. The density index from the water source monitoring was simply calculated from the total number of sightings over a lunar month.

Data analyses

When testing the hypotheses in this chapter, the effects of territoriality were removed. Territorial males are constrained to remaining in their territory, and whether or not there were other individuals on the territory, they were more often found alone (this study; Ginsberg 1989). Therefore, analyses were restricted to those that contained adult females and/or non-territorial males.

Aggregation was measured in two ways. First, the nearest neighbour distances between groups of Grevy's zebra were calculated from their GPS locations. The mean nearest neighbour distance was then compared to the mean of 100 random distributions. The same number of observations was used for both the observed and generated distributions. Comparison of the observed and random generated (and therefore expected) means was conducted using a chi-squared (χ^2) test (Krebs 1989).

The second method of aggregation measurement was more direct, and used the sizes of individual groups of Grevy's zebra. Analyses relating group size to the explanatory variables were conducted using generalised linear models (see chapter 2; McCullagh & Nelder 1987) using Genstat 5 Release 3.2 (Payne *et al.* 1993). The response variates used throughout these analyses was the number of individuals in the groups. The models were, therefore, fitted with Poisson errors (Crawley 1993). This represents a different analysis from that done in chapter 3, where the response variate was also number of female Grevy's zebra in a group. Because the analysis in chapter 3 was the use of space, those models included the areas where no zebras were sighted. In contrast, in this chapter, the analysis focuses on the factors that affect the group size of females. These analyses did not include groups sizes of zero.

The data were overdispersed and, hence, the dispersion parameter was estimated from the models. The χ^2 used to test the statistical significance of a particular parameter was calculated by dividing the change in deviance by the dispersion parameter when that parameter was dropped from the model (Crawley 1993).

When assessing the effects across all study areas, the following parameters were fitted as explanatory variables to the models: the quadratic of the distance to water and the distance to water squared (water + water^2); study area as a factor (area); season - divided into rains - thus, the plant growing season - and dry season (season); the rotation during which the observation took place (rotation); the availability of forage in the habitat in which the groups were sighted, as recorded by the percentage cover of grass (see chapter 2 for the relationship between percentage cover and the biomass of grass) (cover); the density of predators (predators); and the density of humans (humans). Although the density of predators and humans were the same for all groups within each study area, the analysis was not the same as that for study area. Study area was fitted as a factor, whereas predators and humans were fitted as variates for the exact values of their density. The interaction terms between the availability of food and study area (area.cover) and that between the season and study area (season.area) were also assessed.

When examining the within study area effects, the models were built with the following parameters: the quadratic of distance to usable water it square (water + water^2); the availability of forage in the habitat in which the group was sighted (cover); and the season (dry vs. rains) (season). In addition, in each study area, the group size on specific habitats was compared. For example, in Barsalinga, the sizes of groups sighted on the alluvial *Pennisetum* grassland habitats (therefore, those with the highest forage availability, chapter 3) was compared with those on all other habitats. The effect of human presence was also assessed in the two study areas used by pastoral people. The distance to human habitation (manyatta) was used to assess the human effect on group size.

Results

Availability of forage: seasonal differences

In chapter 3, I demonstrated that there were study area differences in the availability of forage. Over the course of the study, Buffalo Springs had a significantly higher abundance of grass, while Barsalinga had the lowest (chapter 3, Table 1). Similarly, over the three study areas, there were seasonal differences in the availability of forage, with the highest forage abundance occurring in the early dry season (as defined by the availability and distribution of water, see chapter 2; see chapter 3, Table 1), once the growing season was complete (see chapter 3, Figure 1).

A further indication of the effect of the growing season on plant growth was the difference in the availability of forage measured in the different rotations of each study area. "Rotation" had a significant effect on the availability of forage, with the greatest effect in Ngare Ndare, and the least in Buffalo Springs (see chapter 3, Table 2). (Note: this was different from the effect of "season" although it reflected the seasonal growth of grass in each study area. The analysis by season was conducted by the season recorded during each rotation. However, because the definition of season was dependent on the availability and distribution of water, it masked the effect of the unpredictable rain patterns on the growth of grass.)

Availability of forage: food patchiness

When the coefficients of variation were compared among the study areas, those in Barsalinga were generally the highest, with those in Buffalo Springs generally the lowest, particularly in the latter part of the study (Figure 1).

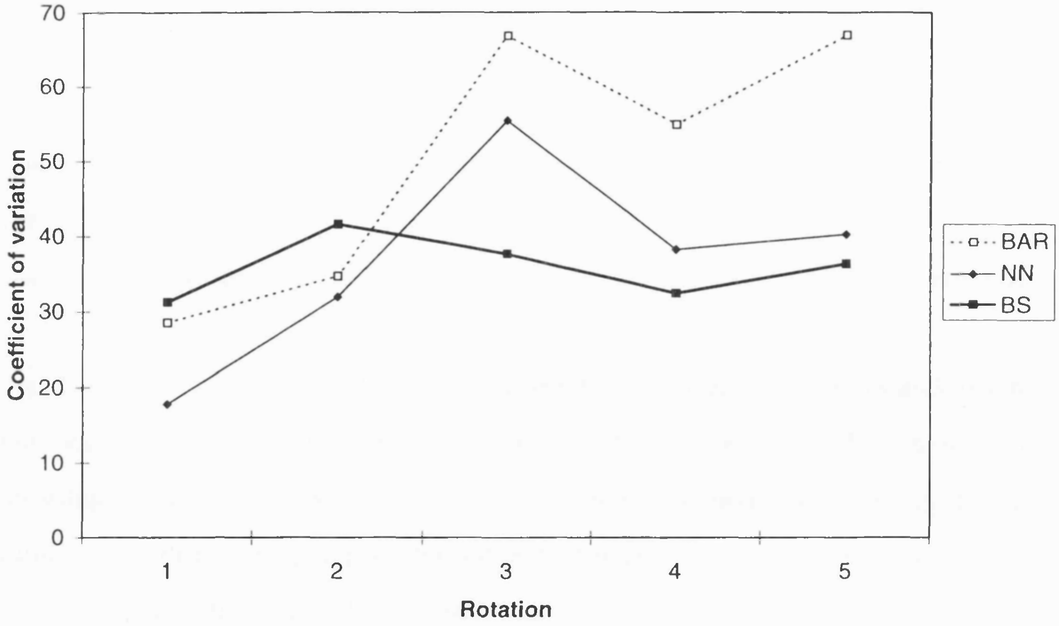


Figure 1. Temporal variation in the coefficient of variation among the habitats in the three study areas, Barsalinga (BAR), Ngare Ndare (NN) and Buffalo Springs (BS).

In chapter 3 (Table 2), I presented results that showed that in Barsalinga the alluvial *Pennisetum* sp. habitats had significantly higher forage abundance than other habitats. Given that the *Pennisetum* sp grassland communities made up only 7.0% of the Barsalinga study area, in four main but similar sized patches, the food resources were highly aggregated. This was accentuated by the relatively large areas covered by vegetation communities with low forage abundance: Barsalinga was made up of 13.3% of *Acacia senegal/Commiphora* sp woodland, 32% of *Acacia tortilis/Commiphora* sp woodland and 32.8% of *Acacia tortilis* shrub grassland.

As in Barsalinga, in Ngare Ndare, the *Pennisetum/Setaria* spp. habitats had the highest forage availability (chapter 3, Table 2). However, these comprised 29.3% of Ngare Ndare. Hence, the food resources were less aggregated than in Barsalinga.

Finally, the *Acacia reficiens* habitats, with higher forage abundance (chapter 3, Table 2) covered 25% of Buffalo Springs. In contrast, the *A. tortilis* dwarf shrubland, which had significantly lower forage abundance than other habitats, covered 33.5% of Buffalo Springs. These differences may explain the variation in the coefficients of variation.

Predator presence

There were differences in the number of predators sighted in the three study areas (Table 2).

Table 2. The total number of predator sightings in the three study areas during the diurnal surveys over the whole study. Hyaenas are not shown as they were never seen during the surveys.

	Barsalinga	Ngare Ndare	Buffalo Springs
Lions	0	1	19
Cheetahs	13	3	3

The sightings of lions recorded from the surveys gave an estimated maximum density of 0.13 lions/km^2 in Buffalo Springs and 0.01 lions/km^2 in Ngare Ndare, with no sightings in Barsalinga. The estimated densities for cheetahs in the study areas were Barsalinga: 0.061 cheetah/km^2; Ngare Ndare: 0.04 cheetah/km^2; and Buffalo Springs: 0.03 cheetah/km^2. The differences among the study areas were statistically significant for lions, but not for cheetahs: area had a significant effect on the model with number of predators (lions or cheetahs) as the response variate (area effect on cheetahs: deviance = 9.73, dispersion = 2.80, $\chi^2 = 3.475$, *d.f.* = 2, P = NS; area effect on lions: deviance = 36.0, dispersion = 2.21, $\chi^2 = 16.29$, *d.f.* = 2, $P < 0.001$, coefficients: Barsalinga: 0; Ndare Ndare: 7.9; Buffalo Springs: 10.8).

The water source monitoring revealed that hyaenas were present in Barsalinga (relative density index: hyaenas=0.008, $N = 2$), but not in Buffalo Springs. However, lions were present in Buffalo Springs, at a higher relative density (lions=0.297, N = 69) than the hyaenas in Barsalinga. No lions were recorded in Barsalinga.

Pastoral people densities

There were 40 permanent *manyatta*s in Barsalinga, in comparison with 10 in Ngare Ndare. From the sample of counts of humans per *manyatta*, the mean number of humans was 12.2 (standard error ± 2.3). There was no difference in the mean number of people per *manyatta* between Ngare Ndare and Barsalinga. This gave relative density estimates for Barsalinga and Ngare Ndare of 0.39 and 0.15 density units respectively. As expected, the density of pastoral people in Buffalo Springs was zero. Primarily in Barsalinga, there was seasonal variation in the number of people using the study areas (pers. obs.). These were people with migratory herds of domestic livestock, usually cattle, who had apparently dispersed as a result of declining food resources for cattle elsewhere. The maximum number of '*fora*' (temporary) *manyatta*s in Barsalinga was 8 (with a mean of 4 people per *fora*), which compared to zero recorded in Ngare Ndare. Therefore, these seasonal migrants acted to increase the human densities in Barsalinga but not in Ngare Ndare.

Grevy's zebra aggregations

Here, I present the results of the analysis of aggregation using the nearest neighbour distances between groups of Grevy's zebra. The distribution of groups of Grevy's zebra relative to one another are presented in chapter 3, Figures 3a-c. In Barsalinga, the difference between the mean of the observed nearest neighbour distances (Table 3) and the generated random nearest neighbour distances was significant (χ^2=20.4, df=1, P<0.001; N=205 groups). The compared means were not significant in Ngare Ndare (Table 3; χ^2=2.63, df=1, NS; N=119 groups), but were in Buffalo Springs (Table 3; χ^2=7.35, df=1, P<0.01; N=281 groups). In all three study areas, the observed mean was less than the random generated means, therefore the χ^2-values give an indication of degree of aggregation in the study areas.

Table 3. The mean and standard error about the mean of the nearest neighbour distance (in metres) between groups of Grevy's zebra in each of the three study areas. The nearest neighbour distances are presented by rotation to each study area.

	Rotation				
	1	2	3	4	5
Barsalinga					
Mean nearest neighbour distance	557	422	507	437	998
s.e.	91.6	100.0	66.2	94.9	294.3
N	32	57	44	52	20
Ngare Ndare					
Mean nearest neighbour distance	402	346	974	707	640
s.e.	66.4	104.9	290.7	173.0	104.9
N	26	39	13	18	23
Buffalo Springs					
Mean nearest neighbour distance	508	330	440	578	364
s.e.	97.8	48.9	41.4	131.3	108.2
N	37	59	70	62	53

Grevy's zebra group sizes

The analyses presented here represent the effect of explanatory variables (as quantified above) on the size of groups of Grevy's zebra.

The mean (± the standard error about the mean) group sizes of adult females and non-territorial adult males, inclusive, were: Barsalinga: 8.3 ± 1.21, $N = 85$; Ngare Ndare: 5.2 ± 0.68, $N = 71$; Buffalo Springs: 5.9 ± 0.91, $N = 88$. The difference between the study areas was significant (Table 4), with Barsalinga having the largest groups and Ngare Ndare the smallest (coefficient estimates: Barsalinga = 0; Ngare Ndare = -0.457; and Buffalo Springs = -0.332).

Table 4. The analysis of the effects of rains vs. dry season (season), study area (area), and the interaction term between season and study area (season.area) on the sizes of groups of Grevy's zebra. Both adult females and non-territorial males were included in the analysis. The results of the full model testing the effects of all parameters is reported first. The minimum adequate model is reported thereafter. The minimum adequate model explained a deviance of 238 with a dispersion parameter of 6.82 and 5 degrees of freedom. Total deviance was 1861.

	Deviance	Dispersion	*d.f.*	χ^2	*P*
Full model					
water+water^2	5	6.92	2	0.72	NS
cover.area	21	6.95	2	3.02	NS
cover	21	7.01	1	2.996	NS
season.area	164	7.67	2	21.38	< 0.001
season	17	7.71	1	2.21	NS
area	58	7.89	2	7.35	< 0.05
Minimum adequate model					
season.area	166	7.45	2	22.28	< 0.001
season	11	7.47	1	1.47	NS
area	61	7.66	2	7.96	< 0.025

The effect of the interaction term, season.area, was explored in greater depth by predicting values from the model (Figure 2). Hence, in Barsalinga, the groups were larger in the dry season. In Ngare Ndare, season had no effect, but in Buffalo Springs, the groups appeared larger in the rains. This was analysed further by study area.

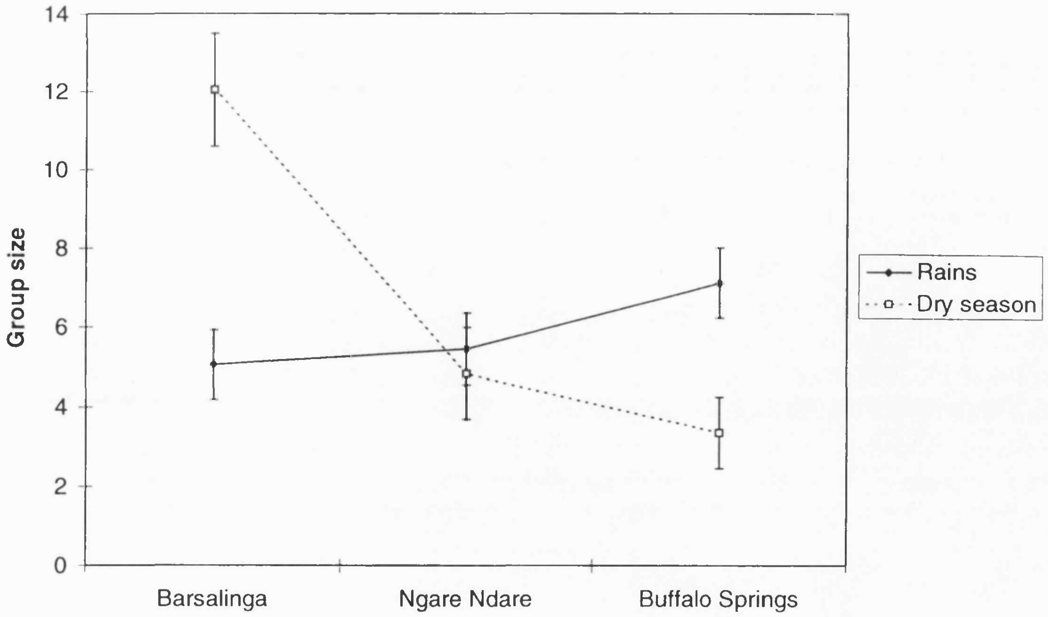


Figure 2. The predicted values from the significant interaction term between study area and season (season.area), with the season being divided into rains and dry season observations. The deviance for the interaction term was 145, with a dispersion parameter of 7.04. Hence, $\chi^2 = 20.60$, *d.f.* = 2, $P < 0.001$. Error bars represent standard errors about the mean.

Lactating females were predicted to be more sensitive to predators. Hence, if predation was important, groups containing lactating females should be larger than other groups. Across all areas, groups that contained early- and mid-lactating females were significantly larger (deviance = 84.0, dispersion = 7.66, $\chi^2 = 10.97$, *d.f.* = 1, $P < 0.001$; coefficient estimates: groups with no lactating females = 0; groups with lactating females = 0.483). The interaction term between study area and the presence of lactating females within groups was not significant. Hence, there were no differences among study areas in the size of groups with lactating females.

The density of humans in the study areas significantly affected group size (deviance = 43.0, dispersion = 7.51, $\chi^2 = 5.73$, *d.f.* = 1, $P < 0.025$) but predator density had no effect (deviance = 11.0, dispersion = 7.64, $\chi^2 = 1.44$, *d.f.* = 1, P = NS).

Within study areas, in Barsalinga, the availability of grazing and the season had significant effects on the size of groups of Grevy's zebra (Table 5). There was a significant positive relationship between the availability of grazing and group size (coefficient estimate: 0.02). Group sizes were significantly larger during the dry season than in the rains (coefficient estimates: rains = 0; dry season = 0.903).

Table 5. The analysis of the effects of explanatory variables on the group sizes in Barsalinga. The results of the full, exploratory model are presented first, and thereafter those from the minimum adequate model. The minimum adequate model explained a deviance of 175.9 with a dispersion parameter of 8.85 and 2 degrees of freedom. The total deviance was 875.3.

	Deviance	Dispersion	*d.f.*	χ^2	*P*
Full model					
manyatta	0.3	8.62	1	0.03	NS
water+water^2	35.5	8.85	2	4.01	NS
cover	42.3	9.27	1	4.563	< 0.05
season	133.6	10.8	1	12.37	< 0.001
Minimum adequate model					
cover	42.3	9.27	1	4.563	< 0.05
season	133.6	10.8	1	12.37	< 0.001

In addition, there was a significant difference between group sizes on the aggregated food of alluvial *Pennisetum* grassland habitats and all other habitats (deviance = 84.4, dispersion = 9.27, $\chi^2 = 9.10$, *d.f.* = 1, $P < 0.005$). Moreover, the interaction between presence of alluvial *Pennisetum* grassland habitats and the season (bcm.season) was significant (deviance = 35.6, dispersion = 8.17, $\chi^2 = 4.357$, *d.f.* = 1, $P < 0.05$). The effect of this interaction was explored by predicting the values from the model (Figure 3). While there were no differences between the alluvial *Pennisetum* grassland habitats and all other habitats during the rains, during the dry season, the alluvial *Pennisetum* grassland habitats had larger groups of Grevy's zebra.

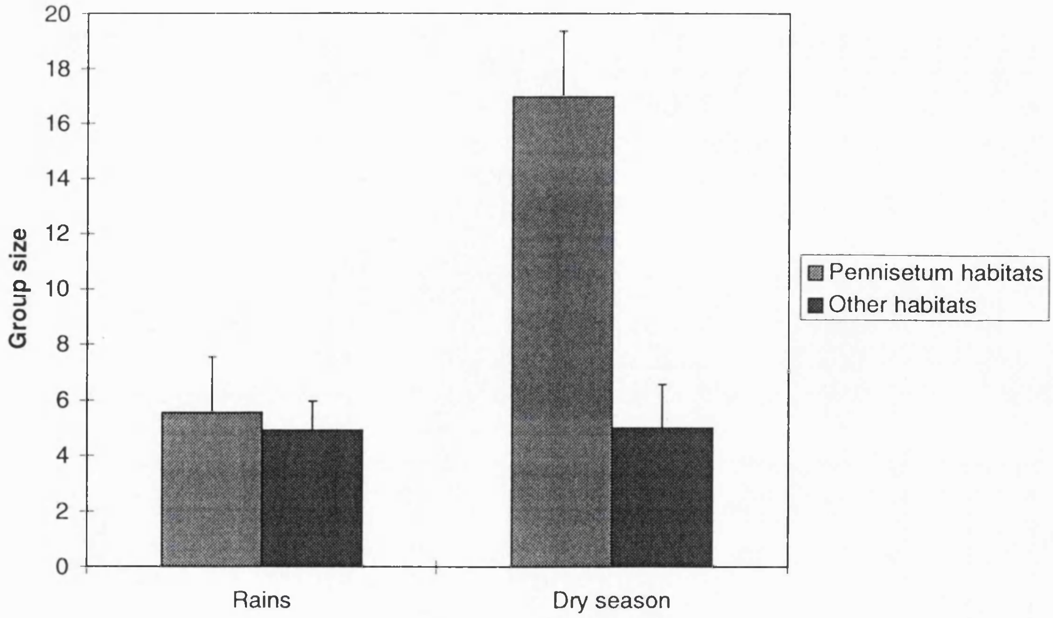


Figure 3. The effect of alluvial *Pennisetum* grassland habitat and group size with seasons (rains vs. dry season). The values are those predicted from the model. The error bars represent the standard error and are approximate.

In contrast to Barsalinga, in Ngare Ndare, none of the explanatory variables had any effect on the size of groups of Grevy's zebra. There was less variation in groups sizes in Ngare Ndare than in either Barsalinga or Buffalo Springs (coefficient of variation: Barsalinga: 135.3; Ngare Ndare: 104.6; Buffalo Springs: 143.6). The full model explanatory variables for season, distance to water, the quadratic for distance to water, the distance to *manyattas* and the availability of grazing was not significant (model deviance = 24.3, dispersion = 4.29, $\chi^2 = 5.66$, *d.f.* = 5, *P* = NS; total deviance = 302.9).

In Buffalo Springs, season was the only variable which had a significant effect on group size. The group size during the rains was significantly larger than in the dry season (deviance = 46.0, dispersion = 7.53, $\chi^2 = 6.00$, *d.f.* = 1, $P < 0.025$, coefficient estimates: rains = 0; dry season = -0.807).

Finally, the mean size (± the standard error about the mean) of the aggregations at water were: Barsalinga: 6.93 ± 2.57, *N* = 15; Buffalo Springs: 20.0 ± 3.06, *N* = 99. Therefore, aggregations of Grevy's zebra in Buffalo Springs were larger at water than away from water, whereas there was no difference in Barsalinga (Figure 4). The interaction term between study area and whether the groups were at water or away from water (area.position) was significant (deviance = 205.0, dispersion = 16.9, $\chi^2 = 12.13$, $d.f. = 1$, $P < 0.001$).

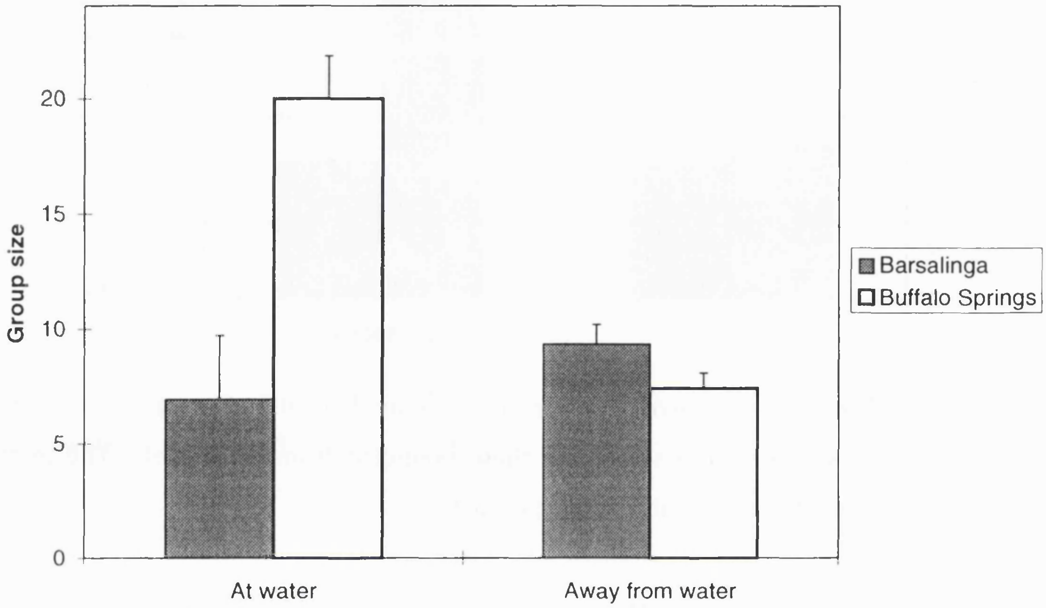


Figure 4. The comparison of the size of aggregations at water - as measured during the waterhole watches - and away from water - as counted during the surveys of the study areas - in Barsalinga and Buffalo Springs. The values are those predicted from the significant interaction term between study area and a factor indicating groups were at water or away from water (area.position) in the model analysing their effects on group size. Error bars represent approximate standard errors.

Discussion

In conclusion, the zebra were aggregated rather than having even distributions. Barsalinga had the greatest degree of aggregation, with Ngare Ndare the least. This was consistent using both measures of zebra aggregation. Over all study areas, lactating females were found in larger groups than other classes of female. This supports that predation was important in driving aggregation. Human density was also positively related to zebra aggregation. If zebra perceive humans as potential predators - which may be likely - then this also supports the predation hypothesis.

However, the positive relationship between forage availability and zebra aggregation in Barsalinga suggested that the spatial variation of food acted additively over the effect of human density. Indeed, because food was limiting in Barsalinga, the effect of forage distribution may have been more important. In contrast, the nutritive stages during regeneration of plants may have been important in Buffalo Springs where food was unlikely to be constraining. Therefore, the results suggest that the aggregation of Grevy's zebra was not explicitly explained by any one hypothesis.

Theory predicts that where predator densities are highest, aggregations should be largest (Caro & FitzGibbon 1992; FitzGibbon & Lazarus 1995). Buffalo Springs had the highest relative density of predators. Therefore, aggregations should have been most pronounced, particularly since the density of lions in Buffalo Springs (0.13 lions/km^2) was similar to those found in ecosystems where predators are thought, at least in part, to drive aggregation (e.g., Serengeti: 0.1 lions/km^2 (Hanby *et al.* 1995), although the high hyaena density - 0.44 hyaenas/km^2 - in the Serengeti may also contribute to these patterns (Hofer & East 1995)). The lack of a significant relationship between predator density and aggregation over all study areas may simply be because other, more important effects in Ngare Ndare and Barsalinga were masking the effects of predators in Buffalo Springs. However, if humans are considered as predators, then the additive effects of humans and predators explained part of the overall aggregation. Humans have been known to predate on Grevy's zebra (R. Elliott, pers. comm.; Rowen & Ginsberg 1993) and, over all study areas, there was a significant effect of human density on the group sizes of Grevy's zebra. Although there was no effect of distance to manyattas in any study areas, the results that humans were affecting the aggregation could be the factor that explains aggregation in Ngare Ndare. This was consistent with the finding that the zebras' use of space in Ngare Ndare was strongly affected by humans (chapter 3). The high human densities in Barsalinga may have also contributed, additively, to its high degree of aggregation.

That groups that contained lactating females were larger than those without supported the role of predation on aggregation. Theory and empirical evidence from other studies predicts that in order to reduce predation of juveniles, females should either give birth in an aggregated peak in time or to give birth in large spatial aggregations (Estes 1976; Fryxell 1987; Rutberg 1987). Both would reduce the risk of predation through dilution or satiation of predators. However, the grouping of lactating females may be because they have identical nutritional requirements. This hypothesis is contradicted in previous studies where lactating females are found on the poorest quality habitats (Ginsberg 1989). This, therefore, indirectly supports that predation is important.

Further support for the importance of the effect of predation on aggregation in Buffalo Springs came from the comparison of groups at and away from water. Here, there was a higher and more predictable presence of predators at water (see chapter 5) and predation attempts were recorded during the water source monitoring (N=3). The aggregations at water were also significantly larger than away from water. That aggregation reduces risk of predation, by increased detection of the predators, or by the dilution effect, is widely accepted (Caro & FitzGibbon 1992; FitzGibbon & Lazarus 1995; Lipetz & Bekoff 1982)

Aggregation may also result from the spatial distribution of resources (Fryxell 1991; Fryxell & Sinclair 1988; McNaughton 1988; Sinclair 1977; Western 1975). Hence, the large aggregations of Grevy's zebra at water in Buffalo Springs may have also been explained by the distribution of rare, locally distributed resources (Moehlman 1974; Moehlman 1979). Indeed, the spatial distribution of resources had significant effects on the aggregation of zebra, especially in Barsalinga, which had the most pronounced aggregation of Grevy's zebra among the three study areas. The spatial variation hypothesis predicts that animals will aggregate in patches of food where their preferred food items are most abundant (Fryxell 1991; Fryxell 1995; Fryxell & Sinclair 1988; McNaughton 1988; Sinclair 1977), particularly for nonruminant herbivores such as equids (Duncan *et al.* 1990; Foose 1982).

The analysis of food 'patchiness' indicated that there was high spatial variation of food in Barsalinga, particularly in the latter period of the study (Figure 1). When coupled with the comparison of spatial variation of food and the area of the habitats with the highest abundance of forage, Barsalinga had the highest degree of aggregation of food resources - particularly in the alluvial *Pennisetum* sp. communities. That the Grevy's zebra aggregations were larger on the patches of Pennisetum grassland strongly implied that the aggregation in Barsalinga was driven by the spatial variation of forage. As in chapter 3, the study was limited by the crude measure of food availability used in this thesis. Nonetheless, it was sufficiently fine to detect the relationship between food and aggregation.

However, although in Barsalinga, group size was significantly related to the availability of forage, it was the only one of the three study areas where this relationship was significant (Table 5). This contrasts with the significant relationship that Ginsberg (1988) found in his study in Buffalo Springs between group size and availability of forage ($r^2 = 0.376$, $P<0.01$). Ginsberg's study was, however, conducted during the drought of 1983/84 during which food was limited. This supports the hypothesis that food was limited in Barsalinga (chapter 3) and further suggests that conditions in Barsalinga mimic those in the drought in Buffalo Springs.

In contrast, there was no relationship between the general pattern of aggregation and the spatial variation of food in Buffalo Springs. However, both the feeding patterns (chapter 3) and the aggregative behaviour of Grevy's zebra in Buffalo Springs may have been uncoupled from the forage availability. As expressed in chapter 3, there may have been sufficient food resources such that the zebra do not need to make behavioural decisions based on food distribution.

Fretwell & Lucas (1970), Fretwell (1972) and Parker (1970), in the ideal free distribution hypothesis, proposed that redistribution of animals will continue until the profitabilities of all patches are equal. However, the hypothesis assumes that all animals are 'free' to redistribute themselves among patches. In chapter 3, I presented data to show that the use of space by Grevy's zebra was constrained by factors other than the distribution of food. In this chapter, I show that the zebra aggregate in a non-ideal way: there are other factors, such as predators, that cause them to aggregate. Aggregation will, inevitably, result in higher competition among animals when food resources are limiting. Hence, there are many factors which tend to indicate that zebra were not 'ideal free' distributed. However, future work might try to ascertain whether the dynamic dispersal of Grevy's zebra recorded in this study (see chapter 3) can be, at least in part, explained by the decreasing gains derived from increasing competition during the dry season on the aggregated resources, according to principles of ideal-free distribution (Fretwell 1972; Fretwell & Lucas 1970).

Season had a significant effect on the availability of grass, with significant growth of grass during the rains (chapter 3). The forage-maturation hypothesis predicts that zebras should aggregate in the rains to feed on highly nutritious regenerating grass (Hobbs & Swift 1988; McNaughton 1986; 1984). The hypothesis is dependent on a sufficiently long plant growing season to allow for regeneration of plants following their use by herbivores. This makes nutritionally superior regrowth available for further use by herbivores. However, although over all study areas there were no seasonal difference in group sizes (Table 4), in Buffalo Springs groups were larger in the rains. Hence, it was likely that aggregation in Buffalo Springs was, in part, being driven by zebra feeding on the regrowth of grass. In contrast, in Barsalinga, groups were largest during the dry season, which is directly contrary to the pattern predicted by the forage-maturation hypothesis (e.g., Figure 3).

The forage-maturation of plants ~~was~~ probably acts additively on the effect of predation for the determination of patterns of aggregation in Buffalo Springs. The regeneration of grass is confined to the rainy seasons and hence is likely to be more important in mesic ecosystems with long rainy seasons, or where the migration of animals follows the pattern of rainfall (e.g., the Serengeti, Fryxell & Sinclair 1988; Maddock 1979; Sinclair 1977). In general, the plant growing season in semi-arid northern Kenya may not be sufficiently long for forage-maturation to have a strong effect on the aggregation of Grevy's zebra. This pattern would be consistent with empirical evidence for the aggregation of ungulates in other semi-arid systems with equivalent low predictability of rainfall (Fryxell 1991; 1995; Leuthold & Leuthold 1975).

Future studies might consider data on rates and duration of feeding in different group sizes of Grevy's zebra. Theory predicts that aggregation, in reducing risk of predation, also increases the time that an animal can spend feeding as opposed to being vigilant against predators (Lipetz & Bekoff 1982). Therefore, feeding rates and duration could be used to infer the relative importance of predation in determining aggregations.

In conclusion, in the study area where forage was limiting, the spatial variation of forage was most important in determining the aggregation of Grevy's zebra. In the study area from which pastoral people and their domestic livestock were excluded, both the use of space by Grevy's zebra (chapter 3) and their aggregative behaviour suggested that food was less important as a determining factor. Instead, there may have been sufficient forage for feeding and aggregative behaviour was more closely related to predator density.

References

Caro, T. M. & FitzGibbon, C. D. 1992 Large carnivores and their prey: the quick and the dead. In *Natural enemies:The population biology of predators, parasites and diseases* (ed. M. J. Crawley). Oxford: Blackwell Scientific Publications.

Charnov, E. L. 1976 Optimal foraging: the marginal value theorem. *Theoretical Population Biology* **9**, 129-136.

Crawley, M. J. 1993 *GLIM for Ecologists*. Methods in Ecology. Oxford: Blackwell Science.

Duncan, P., Foose, T. J., Gordon, I. J., Gakahu, C. G. & Lloyd, M. 1990 Comparative nutrient extraction from forages by grazing bovids and equids a test of the nutritional model of equid bovid competition and coexistence. *Oecologia* **84**, 411-418.

Estes, R. D. 1976 The significance of breeding synchrony in the wildebeest. *East African Wildlife Journal* **14**, 135-152.

FitzGibbon, C. D. & Lazarus, J. 1995 Antipredator behaviour of Serengeti ungulates: individual differences and population consequences. In *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem* (ed. A. R. E. Sinclair & P. Arcese), pp. 274-296. Chicago: The University of Chicago Press.

Foose, T. J. 1982 Trophic strategies of ruminant versus nonruminant ungulates. Chicago: University of Chicago.

Fretwell, S. D. 1972 *Populations in a seasonal environment.* Princeton: Princeton University Press.

Fretwell, S. D. & Lucas, H. J. J. 1970 On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretika* **19**, 16-36.

Fryxell, J. M. 1987 Seasonal reproduction of white eared kob in boma National Park, Sudan. *African Journal Of Ecology* **25**, 117-124.

Fryxell, J. M. 1991 Forage quality and aggregation by large herbivores. *American Naturalist* **138**, 478-498.

Fryxell, J. M. 1995 Aggregation and migration by grazing ungulates in relation to resources and predators. In *Serengeti II: Dynamics, Management and Conservation of an Ecosystem* (ed. A. R. E. Sinclair & P. Arcese). Chicago: Chicago University Press.

Fryxell, J. M. & Sinclair, A. R. E. 1988 Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution* **3**, 237-241.

Ginsberg, J. R. 1988 Social organization and mating strategies of an arid-adapted equid: the Grevy's zebra. Princeton, New Jersey: Princeton University.

Ginsberg, J. R. 1989 The ecology of female behaviour and male reproductive success in Grevy's zebra, *Equus grevyi. Symposia of the Zoological Society (London)* **61**, 89-110.

Hanby, J. P., Bygott, J. D. & Packer, C. 1995 Ecology, demography, and behavior of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti Plains. In *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem.* (ed. A. R. E. Sinclair & P. Arcese). Chicago: Chicago University Press.

Hobbs, N. T. & Swift, D. W. 1988 Grazing in herds: when are the nutritional benefits realized? *American Naturalist* **131**, 760-764.

Hofer, H. & East, M. 1995 Population dynamics, population size, and the communiting system of Serengeti spotted hyenas. In *Serengeti II: Dynamcis, Management, and Conservation of an Ecosystem* (ed. A. R. E. Sinclair & P. Arcese). Chicago: Chicago University Press.

Jarman, P. J. 1987 Group Size and Activity In Eastern Grey Kangaroos. *Animal Behaviour* **35**, 1044-1050.

Krebs, C. J. 1989 *Ecological methodology.* New York: Harper Collins.

Krebs, J. R. 1978 Optimal foraging: decision rules for predators. In *Behavioural Ecology* (ed. J. R. Krebs & N. B. Davies). Oxford: Blackwell Scientific Publications.

Kruuk, H. 1972 *The Spotted Hyena: A study of predation and social behaviour.* Chicago: Chicago University Press.

Leuthold, W. & Leuthold, B. M. 1975 Patterns of social groupings in ungulates in Tsavo National Park, Kenya. *Journal of Zoology, London* **175**, 405-420.

Lipetz, V. E. & Bekoff, M. 1982 Group size and vigilance in proghorns. *Zeitschrift für Tierpsychologie* **58**, 203-216.

Maddock, L. 1979 The "migration" and grazing succession. In *Serengeti: Dynamics of an Ecosystem* (ed. A. R. E. Sinclair & M. Norton-Griffiths). Chicago: Chicago University Press.

McCullagh, P. & Nelder, J. A. 1987 *Generalised Linear Models.* Monographs on Statistics and Applied Probability. London: Chapman and Hall.

McNaughton, S. J. 1984 Grazing lawns: animals in herds, plant form, and coevolution. *American Naturalist* **124**, 863-886.

McNaughton, S. J. 1986 Grazing lawns: on domesticated and wild grazers. *American Naturalist* **128**, 937-939.

McNaughton, S. J. 1988 Mineral nutrition and spatial concentrations of African ungulates. *Nature* **334**, 343-345.

Moehlman, P. D. 1974 Behaviour and Ecology of Feral Asses. Wisconsin: University of Wisconsin.

Moehlman, P. D. 1979 Behavior and Ecology of feral asses (*Equus asinus*). Washington, D. C.: National Geographic Society.

Parker, G. A. 1970 The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. (Dipterera: Scatophagidae) II. The fertilization rate and the spatial and temporal relationships of each sex around the site of mating and oviposition. *Journal of Animal Ecology* **39**, 205-228.

Payne, R. W., Lane, P. W., Digby, P. G. N., Harding, S. A., Leech, P. K., Morgan, G. W., Todd, A. D., Thompson, R., Tunnicliffe Wilson, G., J., W. S. & White, R. P. 1993 *Genstat 5 Release 3 Reference Manual.* Oxford: Clarendon Press.

Pratt, D. J. & Gwynne, M. D. 1977 *Rangeland management and ecology in East Africa.* Kent: Hodder and Stoughton.

Rowen, M. & Ginsberg, J. R. 1993 Grevy's zebra (*Equus grevyi* Oustalet). In *Equid Action Plan* (ed. P. Duncan). Gland, Switzerland: IUCN.

Rutberg, A. T. 1987 Adaptive hypotheses of birth synchrony in ruminants: an interspcific test. *American Naturalist* **130**, 692-710.

Schaller, G. B. 1972 *The Serengeti Lion: A Study of Predator-Prey Relations.* Chicago: Chicago University Press.

Sinclair, A. R. E. 1977 *The African Buffalo.* Chicago: Chicago University Press.

Sokal, R. R. & Rohlf, F. J. 1995 *Biometry: the principles and practice of statistics in Biological Research.* New York: W. H. Freeman and company.

Western, D. 1975 Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East African Wildlife Journal* **13**, 265-286.

5. Temporal patterns of water use by Grevy's zebra

Summary

1. Three hypotheses are proposed to explain temporal patterns of water use in ungulates: 1) patterns reduce predation risk; 2) patterns reduce the physiological costs of dehydration; and 3) patterns result from interference competition with competitors at water.
2. The hypotheses were tested by studying the water use of Grevy's zebra (*Equus grevyi* Oustalet) in two areas in northern Kenya where the predator densities and composition of ungulate communities differ.
3. Results show that in an area from which pastoral people were excluded, Grevy's zebra drank during the day when the activity and presence of predators at water were lowest. These results support that temporal patterns of water use reduce the risks of predation. In comparison, in the area used by pastoral people, Grevy's zebra drank at night. This may have been a result of their perception of humans as a threat. However, by drinking at night in pastoralist areas, the zebra were vulnerable to an increased risk of predation from hyaenas and lions - even though their densities were low.
4. The costs to Grevy's zebra of moving to and from water were higher in the area used by pastoralists.
5. The observed temporal patterns of water use suggest that theory explaining spatial aggregation can be successfully applied in a temporal dimension. I suggest that temporal aggregations are akin to the predator refuges in predator-prey models and therefore should have stabilising effects on the ecosystem.

Introduction

The decision to move to water can be costly: if animals delay their visits to water, there will be physiological costs (Schmidt-Nielsen 1964); animals may have to move large distances in order to visit a water source (Western 1975); and once there, they are vulnerable to predators or aggressive competitors (du Preez & Grobler 1977; Packer 1986; Pierpont 1986; Schaller 1972). Although these costs generate testable hypotheses to explain the temporal patterns of water use in ungulates, few previous ecological studies have attempted to explain observed patterns. Moreover, there are conflicting explanations in those studies that do attempt to explain the patterns of water use. The explanations for the observed patterns of water use range from interspecific competition (du Preez & Grobler 1977; Weir & Davison 1965), predation (du Preez & Grobler 1977), thermoregulation (Villet & Woodiwiss 1986), and/or human disturbance (Ruggiero 1990). In this study, I test each of the above hypotheses as explanations for patterns of water use in Grevy's zebra (*Equus grevyi* Oustalet) in northern Kenya.

First, I test whether the temporal patterns of water use by ungulates may be explained as reducing the predation risk when drinking (du Preez & Grobler 1977). Models of predator-prey systems have shown that predator refuges, in a spatial dimension, in which the prey species can seek respite from predation, are crucial for the persistence of both predator and prey (Hassell & May 1973; May 1978). I suggest that the concept of spatial refuges can be equally applied in a temporal dimension. This predicts that events such as water use should be aggregated in time. In order to reduce the risk of predation when visiting water, ungulate water use may be aggregated either 1) during high visibility, and therefore daylight hours, so as to reduce predation by increased detection, or 2) during times when predator presence at the water source is predictably low, although these may not be mutually exclusive.

Second, temporal patterns of water use may be explained as reducing the physiological costs of thermoregulation (Villet & Woodiwiss 1986). Although animals living in hot, arid climates are usually adaptively tolerant to heterothermia, they become susceptible to 'explosive heat rise', a potentially lethal condition which results from prolonged dehydration (Grenot 1992; Schmidt-Nielsen 1964). The body temperature of animals fluctuates on a daily basis (Schmidt-Nielsen 1964) and heat stress is likely to occur during the hottest times of the day.

There are two ways of dealing with explosive heat stress, each of which produces different temporal patterns of water use. Drinking water reduces heat stress. This predicts that animals are more likely to drink during the hottest time of the day. An alternative thermoregulatory strategy for animals, in more extreme environments, is to be active only during the coolest times. They would be active at night but seek out shade and remain inactive during the heat of the day (Grenot 1992). This minimises body temperature fluctuations and consequently the amount of water needed to maintain a constant internal temperature. This, in turn, predicts that animals will move to water and drink at night.

Finally, water use patterns may result from interference between potentially competing species at the water source. The outcome of interference competition parallels that of exploitative competition (Case & Gilpin 1974; Case *et al.* 1979; Pierpont 1986). Exploitative competition predicts that when two species with similar resource requirements coexist, niche overlap should be minimal otherwise one species will excluded the other (Diamond & Case 1986; 1934; Gause 1935; Keddy 1989; Law & Watkinson 1989; Simberloff 1984). When this theory is applied to the temporal patterns of water use, it predicts temporal displacement of the subordinate species to less than optimal times. This final hypothesis is, therefore, dependent on the outcome of the above hypotheses as they determine the optimal times over which animals may compete.

Additionally, I assess the energetic costs of moving to water. Water-dependent animals are limited in the distance they can move away from permanent water (Lamprey 1963; Western 1975). As they require water, movement away from water increases the 'commuting' distance animals must travel to drink. Consequently, I infer differential energetic costs by examining the distribution of animals relative to water.

Study areas

I tested these hypotheses by studying the temporal patterns of water use of Grevy's zebra in the semi-arid environment of northern Kenya. Logistical contraints meant the study was conducted in only two, rather than three study areas. Therefore, this part of the study was conducted in Barsalinga, the study area with high densities of pastoral people and domestic livestock, and Buffalo Springs, the area from which the pastoral people are excluded (see chapter 2 for details on the study areas). Water was a rare and localised resource in this environment (see chapter 2 & 3 for details of water distribution).

The choice of study areas facilitated the testing of the above hypotheses: first, the densities of predators within the study areas differed, with higher overall densities of predators, primarily lions, in Buffalo Springs (see chapter 4). There were hyaenas in Barsalinga, but the relative densities were 37-fold lower than the lions densities in Buffalo Springs (chapter 4). Moreover, although cheetahs can take foals, only lions are known to take adult Grevy's zebra (Becker & Ginsberg 1990; Klingel 1974; Rowen 1992). This, therefore, predicts that the pattern of water use by Grevy's zebra in Buffalo Springs will be more affected by the predator presence at water than in Barsalinga. Hence, in Buffalo Springs, the Grevy's zebra were predicted to drink in high visibility, low predator presence times of the day. Second, the temperature difference between the two study areas was quantified (see below). The thermoregulation hypothesis predicts that in the more extreme environment, animals will drink at night. Finally, not only were the densities of pastoral people and their domestic livestock different in the two study areas, but also the community composition of ungulates (and therefore potential competitors at water sources) and their densities were markedly different in the two areas (see chapter 2; Grunblatt *et al.* 1989). The different densities facilitated the testing of interspecific competition for optimal drinking times.

Data collection and analysis

Temperature records

The temperature was recorded in the shade in the research vehicle. The temperature was recorded every time when groups of animals were sighted, when crossing the boundary between two habitats, when changing direction, and, in addition, every half-hour. In order to use independent data points for the analysis, a random sample of 2092 temperature records was selected from the records for the analysis of the diurnal patterns of temperature change. In order to analyse the effect of time of day and study area on the temperature, temperature was used as the response variate in generalised linear models (McCullagh & Nelder 1987), with the square of time of the day, in hours^2 (since the distribution was peaked), and study area taken as the explanatory variables. Temperature was a normally distributed, continuous variate (mean temperature overall = 29.78°C, variance = 15.63), and hence no error structure or transformation was necessary (Crawley 1993).

To analyse whether the peak in temperature corresponded with the peak in use of water by Grevy's zebra, a continuous, normally distributed index of zebra presence at water was fitted as the response variate, with the quadratic of temperature as the explanatory variable (temperature + temperature^2).

Temporal patterns of water use

As outlined in chapter 4, the patterns of water use by all mammal species, including Grevy's zebra, were recorded during the dry season in September 1994 and July 1995 at 'usable' water sources in Buffalo Springs and Barsalinga. The study was conducted during the dry season since that was when all ungulates were constrained to drink at permanent, usable water sources, and interspecific competition was likely to be most acute. During the rains, all animals will drink opportunistically in the widespread or ubiquitous ephemeral water (pers. obs.).

During September 1994, a usable water source in each study area was monitored for 240 one-hour blocks randomly distributed through the 28 days (672 hours) of a lunar month (modified after Kangwana 1993). With the help of trained volunteers, the water sources in each study area were simultaneously monitored. Since the sample size of Grevy's zebra recorded in Barsalinga was relatively low compared with Buffalo Springs (see results) and to test whether the patterns were repeatable, the monitoring of a water source was conducted in Barsalinga alone during July 1995. In this case the water source was monitored continuously, i.e., for 24 hours a day, throughout the lunar month. During both periods, the animals were observed from a hide using binoculars by day and night vision equipment by night. At no stage was there any indication that the drinking animals were aware of the observers.

Data on the temporal use of water were analysed on two levels. On a broad level, data were compared on a diurnal/nocturnal basis - therefore, during high and low visibility hours. These data were so clearly defined, they negated the need for statistics to determine the extent of the observed patterns.

On a fine scale, the number of individuals of each species recorded over the lunar month was grouped into hour blocks. When comparing the drinking times of animals, a generalised linear model with Poisson errors was fitted to the distributions (McCullagh & Nelder 1987), with the number of individuals of each species as the response variate in the model. The data were overdispersed, and hence the dispersion parameter was estimated for the models. The chi-squared (χ^2) used to test a given parameter's effect was calculated by dividing the change in deviance when that explanatory variable was dropped from the model (Crawley 1993).

To analyse any difference in the times of water use among the wild ungulate species in Buffalo Springs, the interaction term between a factor for species and the square of time of the day (fitted as a continuous variate, and squared because the times of water use were peaked - and hence not linear; see below) was fitted to the model with numbers of animals as the response variate. Similarly, to test the difference in temporal use of water between the wild ungulates of Buffalo Springs and the domestic ungulates in Barsalinga, a factor was used to group each group of species. The effect of the interaction term between this factor and the square of time of day was used to examine the difference in times of water use between the groups of species.

Focal watches of Grevy's zebra individuals were also conducted to record the time spent drinking and vigilance behaviour while drinking. The duration of activities were recorded during the focal watches (Altmann 1974). The time was started when an individual came into view. The duration of the following activities was recorded: 1) the time taken to reach water and to start drinking (approaching); 2) the time spent drinking (drinking); 3) the time spent alert, with their head up, having interrupted drinking (vigilant behaviour); and 4) the time to disappear from view (departing). For the purposes of the analyses, a 'drinking bout' was defined as the total time from when an individual lowered its head to water to the time it had left water, and therefore included the time spent with their head up being vigilant during the bout. In contrast, 'drinking' time was the time spent actually ingesting water during a 'drinking bout'. These data also quantified the number of times that the zebra were vigilant during a drinking bout. Vigilance rates of the focal individuals at the water sources were calculated by dividing the drinking bout duration by the number of times that it lifted its head and appeared alert during the bout.

The analysis of factors affecting on the duration of drinking bouts, the duration of drinking and the vigilance rates were conducted using generalised linear models. For the models, each was used as the response variate and all were normally distributed (hence they did not significantly differ from a normal distribution: drinking bout: $\chi^2 = 5.19$, *d.f.* = 5, P = NS; drinking length: $\chi^2 = 5.16$, *d.f.* = 5, P = NS; vigilance rates: $\chi^2 = 6.40$, *d.f.* = 5, P = NS). Study area and sex were the explanatory factors that were added to the models to test for their effect.

Interactions among species at the water source were recorded *ad lib* (Altmann 1974). Although different behavioural measures of dominance may lead to different rank orders (van Hooff & Wensing 1987), only supplant behaviour was suitable from the observations at the water source. Supplants, actively or indirectly, were defined as occurring when an individual(s) of one species interrupted their drinking and moved away from water in deference to an individual(s) of another species (Richards 1974). The original individual then returned to water at a later stage to complete the drinking bout. The interspecific aggressive interactions were used to form a dyadic interaction matrix (Lehner 1996). The dominance hierarchy was determined from the dominance matrix using standard methods (Brown 1975; Lehner 1996). The linearity of the dominance hierarchy was tested by calculating the number of circular triads, d, and testing this against the probabilities of selected values of d for the number of interacting species as given in Appleby (1983).

Animal distributions relative to water

The distribution of animals was calculated relative to usable water (as defined in chapter 2) using the positions of groups of animals recorded during the surveys of the study areas (see chapter 2). For Grevy's zebra, this included the distribution of different classes of females (as defined in chapter 2).

All the analyses in this chapter were conducted using Genstat 5 Release 3.2 (Payne *et al.* 1993).

Results

Temporal patterns of water use

In Buffalo Springs, Grevy's zebra drank during the daylight hours, with a concentrated four-hour peak between 11:00 and 15:00 in which 93% of all observed individuals drank ($N = 1910$). It was notable that foals of less than four months were recorded at water in Buffalo Springs. Similarly, the water use of other wild ungulates in Buffalo Springs was highly aggregated in time. 91% of all individuals drank between 10.00 and 15.00 (Figure 1). In the analysis of whether there were fine differences in the temporal use between the wild ungulates in Buffalo Springs, to determine the extent of interspecific interference competition at water, when the interaction term between the factor for species and the square of time of the day was added to the model with number of individuals of each species as the response variate, the change in deviance was not significant (species.time^2: deviance = 355, dispersion = 149.0, $\chi^2 = 2.38$, $d.f. = 10$, P = NS). Hence, this indicates that interspecific competition between the species was having no effect on their temporal patterns of water use.

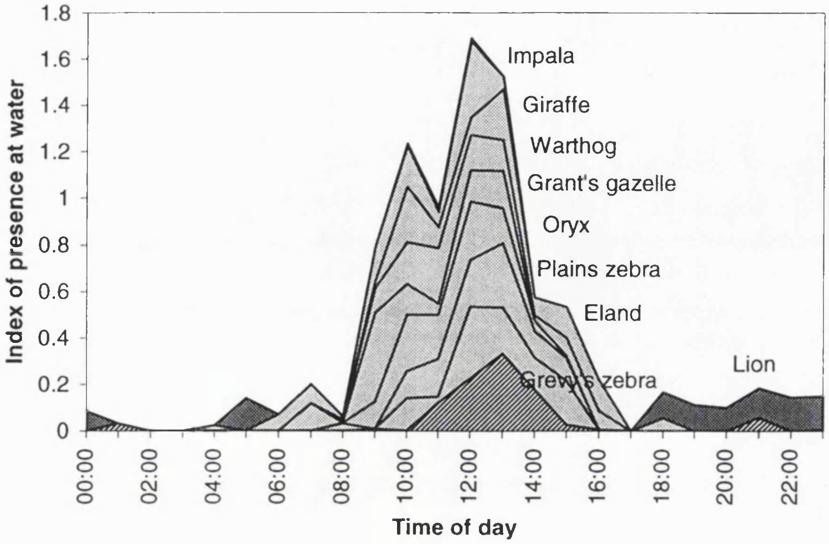


Figure 1. The times of water use by wild ungulates (light grey) in Buffalo Springs, shown in relation to lion (*Panthera leo*, $N = 69$) presence (dark grey) at the water source. The data are for the following ungulate species: eland (*Taurotragus oryx*, $N = 146$), plains zebra (*Equus burchelli*, $N = 488$), beisa oryx (*Oryx b. beisa*, $N = 618$), Grant's gazelle (*Gazella granti*, $N = 94$), warthog (*Phacochoerus aethiopicus*, $N = 115$), giraffe (*Giraffa camelopardalis reticulata*, $N = 147$), impala (*Aepyceros melampus*, $N = 89$) and Grevy's zebra (*E. grevyi*; hatched pattern, $N = 1910$).

Although the analysis for difference in the temporal patterns of water use indicate that interspecific competition was not important, there were antagonistic interactions at water. The dominance matrix on which the dominance hierarchy was based had a total of 70 interspecific interactions (Table 1).

Table 1. The dyadic dominance matrix from aggressive interspecific interactions that provided the basis for generating the dominance hierarchy.

		Winners						
		Elephant	Giraffe	Oryx	Eland	Grevy's zebra	plains zebra	warthog
Losers	Elephant		0	0	0	0	0	0
	Giraffe	5		0	0	0	0	0
	Oryx	8	1		0	0	0	0
	Eland	1	1	2		0	0	0
	Grevy's zebra	20	2	5	1		0	0
	Plains zebra	17	1	1	0	0		0
	Warthog	4	0	1	0	0	0	
	Wins	55	5	9	1	0	0	0
	Losses	0	5	9	4	28	19	5

The dominance hierarchy determined from the dominance matrix (Table 1) from interactions between the ungulates species in Buffalo Springs was:

Elephant
↓
Giraffe
↓
Oryx
↓
Eland
↓
Grevy's zebra, plains zebra, warthog

However, linearity of the hierarchy was not significant (for the number of circular, $d = 3.75$, for 7 interacting species, hence $P < 0.069$, Appleby 1983).

In Buffalo Springs, lions were the most frequently observed predators at the water source. 93% of lion sightings occurred at night (N=69; Figure 1). Hyaenas were not recorded in Buffalo Springs - neither during the monitoring of the water sources nor during any of the surveys. This may have reflected that hyaenas were using other water sources within Buffalo Springs. However, the evidence that there were no hyaenas in Buffalo Springs was supported since no hyaena calls were heard either during the water source monitoring or throughout the rest of the study.

In both months of observation in Barsalinga, the Grevy's zebra drank at night. Only 4% (N=1 observation) of observed animals drank during the day during September 1994. No individuals were observed drinking during the day in July 1995 (September 1994, N=104; and July 1995, N=55 observations; Figure 2). Foals of less than four months were not recorded at water in Barsalinga. There were no differences in the patterns of water use between September 1994 and July 1995. Grevy's zebra in Barsalinga drank when no other species were present at the water sources, and therefore no interspecific interactions were recorded.

The domestic ungulates in Barsalinga used the water source during the daylight hours (Figure 2), similar to the broad pattern of use by the wild ungulates in Buffalo Springs. 96% of all observation of drinking Grevy's zebra occurred between 08.00 and 16.00. Indeed, the analysis comparing the temporal patterns of water use by wild ungulates (Grevy's zebra, plains zebra, oryx, Grant's gazelle, impala, giraffe, warthog) in Buffalo Springs and domestic ungulates (cattle, smallstock and donkeys)

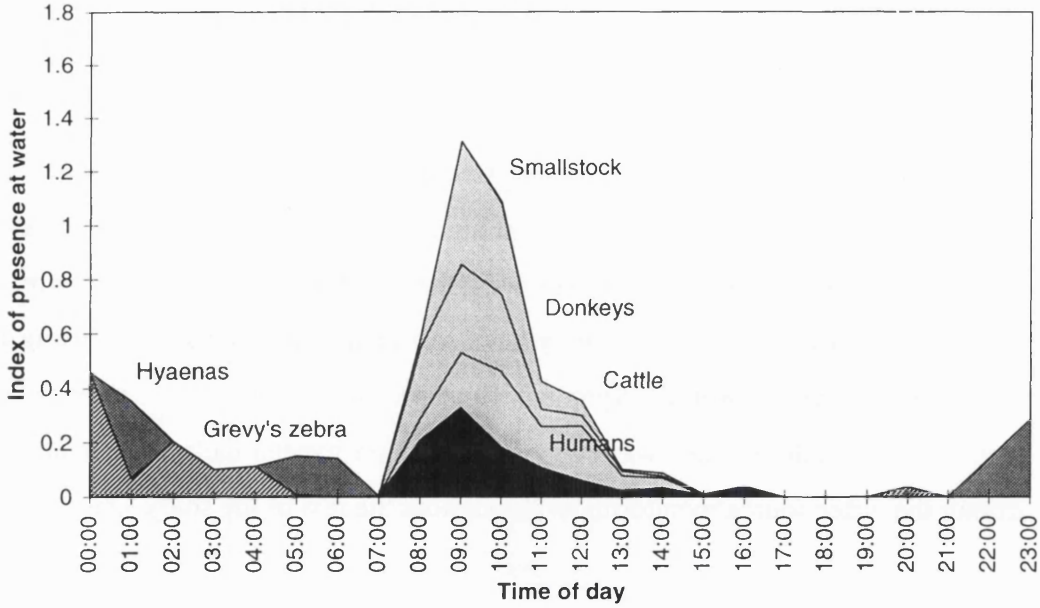


Figure 2. The times of water use by Grevy's zebra (hatched, *N* = 104) in Barsalinga in September 1994, in relation to use of water by domestic livestock species (light grey), humans (solid black, *N* = 392) and hyaenas (dark grey, *N* = 3). The domestic ungulates included cattle (*N* = 4323), smallstock (*N* = 5903) and donkeys (*N* = 790).

in Barsalinga showed there was no significant difference between the two. Hence, when the interaction term between the factor distinguishing the groups of species and the square of time of day was dropped from the model with the number of animals as the response variate, the change in deviance was not significant (factor.time^2: deviance = 314, dispersion = 233, $\chi^2 = 1.35$ *d.f.* = 1, *P* = NS).

In contrast to Buffalo Springs, giraffe, oryx and Grant's gazelle, all of whom are not obligate drinkers (Kingdon 1979; Kingdon 1997) and although present in Barsalinga (pers. obs.), were not observed drinking in Barsalinga. Interestingly, the only wild ungulates that drank in Barsalinga were Grevy's zebra and plains zebra, or species found predominantly in the vicinity of water (impala and warthog). The warthog and impala used the water source during the daylight hours but at times when humans and domestic livestock species were not present (Figure 3). The difference between the water use patterns of impala and warthog, and those of Grevy's zebra may be explained by the human activity in and around the *manyattas* (pastoralist villages) during the day. This activity may have formed an effective barrier to Grevy's zebra, preventing them from moving down to water during the day.

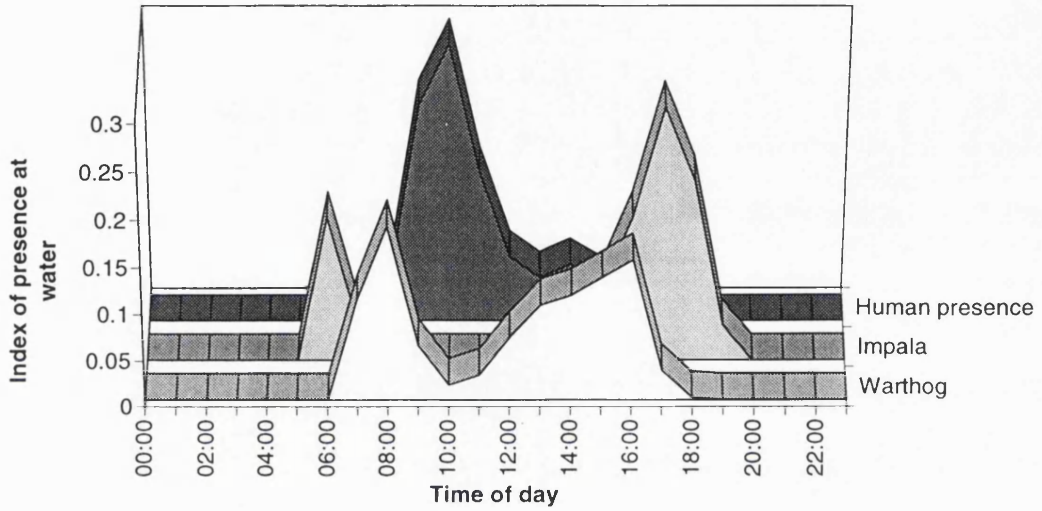


Figure 3. The times of water use by warthog ($N = 370$) and impala ($N = 26$) relative to the presence of humans ($N = 628$) at the water source in Barsalinga. Data from July 1995.

The pastoralist people in Barsalinga built their *manyattas* at a mean distance of 3.6km (standard error = ±0.3; N=40) from permanent water sources. The result of which was a '*manyatta* line', formed by a continuous band of *manyattas* (see chapter 3, Figure). Since the human activity around the *manyattas* ceased at dusk, the Grevy's zebra could only move down to water at night. In contrast, warthog and impala lived predominately within the *manyatta* line. Therefore, they were not prevented from reaching the water during the daylight hours and drank during the day.

Further evidence that the *manyatta* line formed a barrier to Grevy's zebra came from data collected in Karole in Marsabit District, Kenya. This area was surveyed during June 1995 as part of a census of small, potentially isolated populations of Grevy's zebra (Wisbey 1995). The area was also used by both pastoralists and Grevy's zebra.

Here, there was no *manyatta* line. Instead, pastoralists lived in scattered *manyatta*s and in the town of Kargi. The data collected at Karole demonstrated that in the absence of the *manyatta* line, Grevy's zebra will come in to drink during the day once human activity at the water source has ceased (Figure 4). This predicts that, like impala and warthog in Barsalinga, Grevy's zebra will not drink at night in Karole.

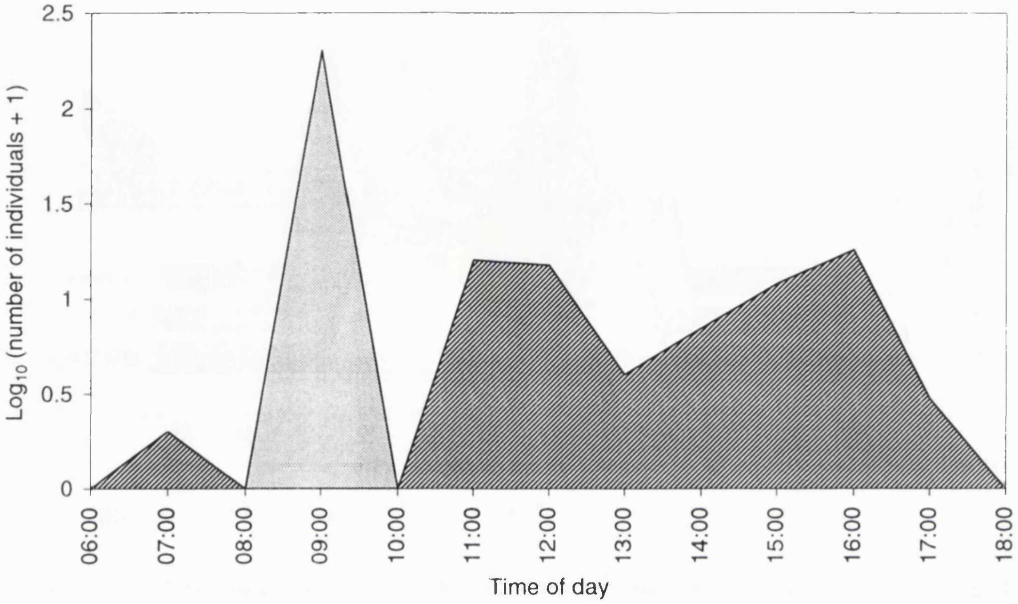


Figure 4. The times that Grevy's zebra (hatched) and domestic livestock species (light grey) were recorded visiting the spring at Karole. These data come from the three days that this area was surveyed as part of a census of small populations of Grevy's zebra in northern Kenya. $N_{\text{DOMESTIC LIVESTOCK}}$= >200; $N_{\text{GREVY'S ZEBRA}}$= 69. Note that the *y*-axis is a $\log_{10}(N + 1)$ scale, and that only daylight hours are shown.

As in Buffalo Springs, wild predator water use in Barsalinga was restricted to night. No lions were recorded during the September 1994 water source monitoring, but during July 1995 one individual was seen at night. Hyaenas were also recorded in Barsalinga only at night (September 1994, N=3; July 1995, N=7; Figure 2).

Human water use in Barsalinga was restricted to the daylight hours, with the peaks of water use between 08.00 and 13.00 (September 1994, 90% of observations, N=392) and 08.00 and 12.00 (July 1995, 72% of observations, N=628; Figure 2).

Diurnal temperature

Temperature, over both study areas, varied significantly through the day and had a peaked distribution: the effect of dropping hours² from the model was significant ($F_{1,2091}$=301.49; P < 0.001). Buffalo Springs was also significantly hotter than Barsalinga ($F_{1,2090}$=191.49, P<0.001; $mean_{\mathrm{BS}}$ = 30.9 *s.e.*= ±0.11; $mean_{\mathrm{BAR}}$ = 28.7 *s.e.*= ±0.12; N_{BS}=1052, N_{BAR}=1040). Peak temperature in both study areas was between 14.00 and 15.00. Minimum temperature occurred just before dawn between 04.00 and 06.00.

In the model used to assess whether the peaks in temperature and Grevy's zebras' temporal use of water, the quadratic of temperature did not have a significant effect on the presence of Grevy's zebra ($F_{2,9}$ = 2.40, P = 0.146). However, there was a trend for Grevy's zebra to drink during the hottest time of the day (Figure 5). In contrast, in Barsalinga, Grevy's zebra drank in the cool of the night.

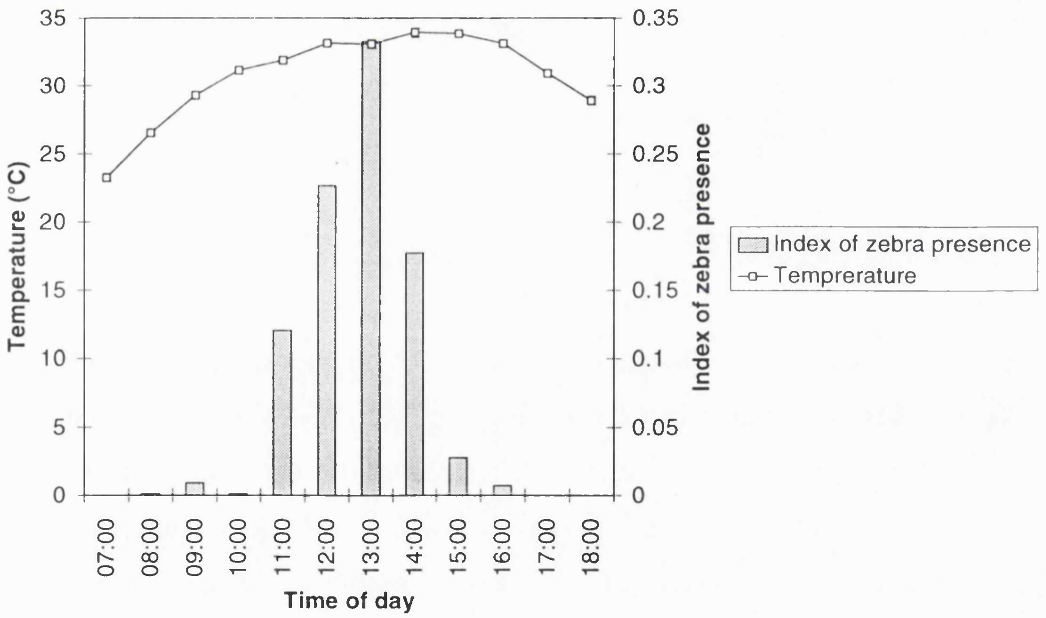


Figure 5. The relationship between the times of the day when Grevy's zebra drank in Buffalo Springs, and the mean temperature (with error bars representing the standard error about the mean) as measured over the course of the study.

Focal watches

Analysis of the focal watches on drinking Grevy's zebra individuals showed that drinking bouts in Buffalo Springs were significantly longer than those in Barsalinga ($mean_{BS}$=376; $mean_{BAR}$=186 seconds; $F_{1,73}$=6.97, P=0.01, N_{BS}=59, N_{BAR}=16). However, there was no difference in the drinking times ($F_{1,73}$=2.18, P=0.14). The difference in the vigilance rates of the individuals between Buffalo Springs and Barsalinga was also not significant ($F_{1,73}$=3.26, P=0.075; $mean_{BS}$ = 45 ± 4; $mean_{BAR}$ = 62 ± 12; N_{BS}=48, N_{BAR}=28).

In Buffalo Springs, there were no differences between the sexes in the duration that individuals spent at water, the duration of drinking or their rates of vigilance ($F_{1,52}$=3.15, P=0.082; $F_{1,52}$=0.03, P=0.85; $F_{1,52}$=0.32, P=0.57, respectively; $N_{FEMALES}$=23, N_{MALES}=31). Since Grevy's zebra visited Barsalinga at night, and the resolution of the night vision equipment was not sufficient to distinguish the sexes with certainty, the data could not be compared.

With increasing group size, the rates of vigilance decreased. The regression between the rate of vigilance and log group size of Grevy's zebra was significant (r^2=0.073, $F_{1,62}$=4.86, P=0.031), with the regression coefficient = -14.96. When log of the total number of all ungulate species individuals was used the fit of the regression improved (r^2=0.091, $F_{1,62}$=6.23, P=0.015).

Animal distributions relative to water

The analysis of the distribution of Grevy's zebra, overall and by different classes of female was presented in chapter 3. In brief, the effect of area could not be tested since the distribution of water in the three study areas meant they were not comparable. However, the distributions, when visually compared showed that Grevy's zebra in the two areas used by pastoral people were found further from water than in Buffalo Springs (Figure 6). Hence, groups of Grevy's zebra in Barsalinga and Ngare Ndare were rarely found less than 5km from usable water, while all the Grevy's zebra in Buffalo Springs were found within 5km of water (since they were constrained to be so; Figure 6).

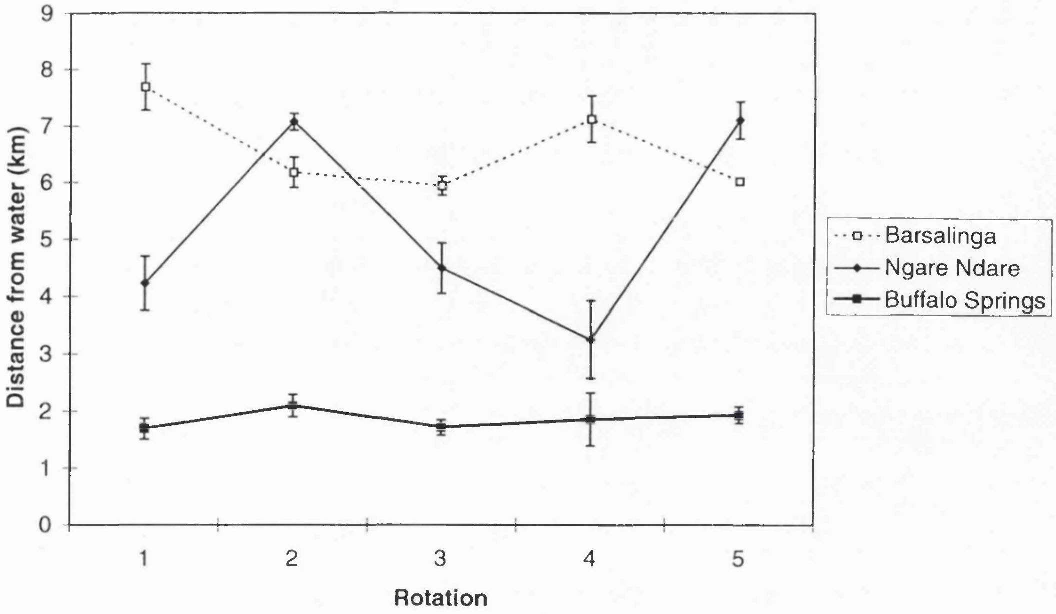


Figure 6. The mean distance (± the standard error about the mean) of groups of adult females relative to usable water in the three study area.

The analysis of the distribution of lactating females, relative to other females, relative to water showed that in Barsalinga, the lactating females were closer to water sources than other classes of female (chapter 3, Table 6). There was no effect of class of female in the other two study areas (chapter 3, Table 6).

Discussion

The results strongly suggested that in Buffalo Springs, where there were no constraints from pastoralists, the temporal patterns of water use by Grevy's zebra were explained by their avoidance of predation. Hence, they drank during the day - thus, high visibility hours - when predator presence was predictably low. In comparison, in Barsalinga, Grevy's zebra drank only at night. This was when the pastoral people and their domestic livestock were not monopolising the water sources. The water use by Grevy's zebra in Barsalinga was, therefore, temporally displaced, relative to Buffalo Springs. It was likely that this was due to their perception of humans as a threat. That the patterns of water use recorded here were real was supported, first, by the re-sample in July 1995 in Barsalinga which were not different from the previous September. Second, Grevy's zebra were not recorded to drink during the day in Barsalinga throughout the surveys of the study areas. Similarly, in Buffalo Springs there was no evidence to suggest that there was any deviation from the patterns recorded during the water source monitoring. Finally, the patterns recorded in previous studies in Buffalo Springs, although conducted only during daylight hours, mirrored the patterns reported here (Ginsberg 1988; Rowen 1992).

Previous studies have shown that not only are the activity patterns of predators lowest at midday, but also predators are more likely to kill at night (Hanby *et al.* 1995; Kruuk 1972; Schaller 1968; Schaller 1972) and in the vicinity of water (Schaller 1972). In this study, the presence of predators at the water sources in Buffalo Springs was also lowest at midday (Figure 1). Therefore, by drinking around midday in Buffalo Springs, Grevy's zebra were avoiding predation (Figure 1).

The temporally aggregated use of the water source by all ungulate species in Buffalo Springs may have been adaptive behaviour to further reduce the risks of predation, both through increased vigilance (Fitzgibbon 1990a; Lipetz & Bekoff 1982) and/or by dilution (Bertram 1978; Estes 1974; Jarman 1974). These concepts are widely accepted as explaining the spatial aggregations of large herbivores (see chapter 4; Fryxell 1991), but here I apply them in a temporal dimension. This was supported by the negative regression between vigilance rates and the aggregations at water. This effect was similar to that of group size on vigilance rates in feeding ungulates, where the rate of vigilance decreases with group size, allowing individuals greater feeding time (Fitzgibbon 1989; 1990b; 1995). This behaviour is directly attributed to anti-predator behaviour.

By drinking at night in Barsalinga, it appeared as if Grevy's zebra were avoiding humans, domestic livestock or both (Figure 2). However, the degree of overlap between the ungulate species in Buffalo Springs clearly indicated that interference among wild ungulates played no measurable role in determining the patterns of water use (Figure 1). There was no temporal displacement among the species, even though interspecific aggression at the water source was recorded (Table 1).

It may have been that the presence of the humans - both at water with the herds of livestock, but also in and around the manyattas - was an important factor in determining the temporal patterns of water use by Grevy's zebra in Barsalinga and may have resulted from zebras perceiving humans as a threat. This hypothesis could be tested in an area used by domestic livestock species, but in which there are no humans. I predict that in such an area, there would be an overlap in the times of water use of Grevy's zebra and the domestic livestock species similar to that recorded among the ungulates in Buffalo Springs.

The concept that Grevy's zebra perceived humans as a threat was less obvious. That humans are a threat is supported by empirical evidence in this and other studies. In this study, 58% of the dead zebra, where the cause of death was certain (N=12), could be attributed to killings by humans. That humans spear wildlife that destroy their hand dug wells would reinforce the avoidance of humans by Grevy's zebra (S. D. Williams, unpublished data; Spencer 1965; Spencer 1973; Thouless 1992; 1993). Finally, whereas the wild ruminants that are non-obligate drinkers (i.e., giraffe, oryx, Grant's gazelle) all drank regularly in Buffalo Springs, they were not recorded drinking in Barsalinga. This provided further, indirect, support that wild ungulates behave towards humans as a threat.

By drinking at night in Barsalinga, the zebra were more vulnerable to predation from lions and hyaenas, even though these were at very low densities. This was particularly true of foals that appeared to be left in 'kindergartens' since, unlike in Buffalo Springs, they were not observed at the water source. The formation of kindergartens in Grevy's zebra has been recorded in previous studies of Grevy's zebra (Becker & Ginsberg 1990; Klingel 1974; Rowen 1992; Rubenstein 1986) and is thought to result from energetic constraints on the foals (Rubenstein 1986). These studies reported the formation of kindergartens, and hence energetic constraint, of foals in Buffalo Springs. The formation of kindergartens, therefore, was even more likely since in Barsalinga all reproductive classes of Grevy's zebra were found farther away from water than those in Buffalo Springs (Figure 6). When this was coupled with the lack of anti-predator defence strategies (Klingel 1974), and with their formation at night, the foals were probably more susceptible to predation.

Furthermore, the distribution of Grevy's zebra in Barsalinga meant that moving to and from water was energetically more costly for Grevy's zebra than in Buffalo Springs (Figure 6).

Both predictions from the thermoregulatory hypothesis conflicted with the observed patterns of water use. If thermoregulation was an important determining factor, a consistent pattern for the water use by Grevy's zebra was expected for both Barsalinga and Buffalo Springs. There was no such consistency. Indeed, there was little evidence that the ungulates were constrained by their thermoregulatory requirements and could be active both by day or night, regardless of the temperature. That Grevy's zebra in Buffalo Springs drank towards the hottest time of the day was coincidental with reduced predator activity at that time of the day.

In conclusion, I suggest that in this study the concept of spatial aggregation can be successfully applied in a temporal dimension. The temporal aggregations are akin to the predator refuges in predator-prey models that have been shown to been crucial to the persistence of both predator and prey (Hassell & May 1973; May 1978) and should have stabilising effects on the community (Hanski 1994). The presence of humans at water sources and in the vicinity of the *manyatta*s temporally displaced the water use of Grevy's zebra in Barsalinga to times when wild predators were active, albeit at low densities. This may have had important consequences for the persistence of Grevy's zebra in Barsalinga, and particularly their juveniles. I examine this issue in the next chapter.

References

Altmann, J. 1974 Observational study of behaviour: sampling methods. *Behaviour* **49**, 227-265.

Appleby, M. C. 1983 The probability of linearity in hierarchies. *Animal Behaviour* **31**, 600-608.

Becker, C. D. & Ginsberg, J. R. 1990 Mother infant behavior of wild Grevy's zebra: adaptations for survival in semi-desert east Africa. *Animal Behaviour* **40**, 1111-1118.

Bertram, B. C. R. 1978 Living in groups:predators and prey. In *Behavioural Ecology* (ed. J. Krebs & N. B. Davies), pp. 64-96. Oxford: Blackwell Scientific Publications.

Brown, J. L. 1975 *The Evolution of Behaviour.* New York: W. W. Norton.

Case, T. J. & Gilpin, M. E. 1974 Interference competition and niche theory. *Proceedings of the National Academy of Sciences (USA)* **71**, 3073-3077.

Case, T. J., Glipin, M. E. & Diamond, J. M. 1979 Overexploitation, interference compeition, and excess density compensation in insular faunas. *American Naturalist* **113**, 843-854.

Crawley, M. J. 1993 *GLIM for Ecologists.* Methods in Ecology. Oxford: Blackwell Science.

Diamond, J. M. & Case, T. J. 1986 *Community Ecology.* New York: Harper & Row.

du Preez, J. S. & Grobler, I. D. 1977 Drinking times and behaviour at aterholes of some game species in the Ethosha National Park. *Madoqua* **10**, 61-69.

Estes, R. D. 1974 Social organisation of the African Bovidae. In *The behaviour of ungulates and its relation to management.* (ed. V. Geist & F. Walther). Morges, Switzerland.: IUCN.

Fitzgibbon, C. D. 1989 A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Animal Behaviour* **37**, 508-510.

Fitzgibbon, C. D. 1990a Mixed species grouping in Thomson and Grant gazelles: the antipredator benefits. *Animal Behaviour* **39**, 1116-1126.

Fitzgibbon, C. D. 1990b Why do hunting cheetahs prefer male gazelles? *Animal Behaviour* **40**, 837-845.

FitzGibbon, C. D. & Lazarus, J. 1995 Antipredator behaviour of Serengeti ungulates: individual differences and population consequences. In *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem* (ed. A. R. E. Sinclair & P. Arcese), pp. 274-296. Chicago: The University of Chicago Press.

Fryxell, J. M. 1991 Forage quality and aggregation by large herbivores. *American Naturalist* **138**, 478-498.

Gause, G. F. 1934 *The struggle for existence.* New York: Hafner.

Gause, G. F. 1935 Experimental demonstration of Volterra's periodic oscillation in the number of animals. *Journal of Experimental Biology* **12**, 44-48.

Ginsberg, J. R. 1988 Social organization and mating strategies of an arid-adapted equid: the Grevy's zebra. Princeton, New Jersey: Princeton University.

Grenot, C. J. 1992 Ecophysiological characteristics of large herbivorous mammals in arid Africa and the Middle East. *Journal of Arid Environments* **23**, 125-155.

Grunblatt, J., Said, M. Y. & Nutira, J. K. 1989 Livestock and wildlife summary 1987 - 1988 for Kenya Rangelands. Nairobi, Kenya: Department of Resource Surveys and Remote Sensing, Ministry of Planning and National Development.

Hanby, J. P., Bygott, J. D. & Packer, C. 1995 Ecology, demography, and behavior of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti Plains. In *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem.* (ed. A. R. E. Sinclair & P. Arcese). Chicago: Chicago University Press.

Hanski, I. 1994 Spatial scale, patchiness and population dynamics on land. *Philosophical Transactions of the Royal Society, London B.* **343**, 19-25.

Hassell, M. P. & May, R. M. 1973 Stability in insect host-parasite models. *Journal of Animal Ecology* **42**, 693-736.

Jarman, P. J. 1974 The social organization of antelope in relation to their ecology. *Behaviour* **48**, 215-267.

Kangwana, K. 1993 Elephants and Maasai: Conflict and Conservation in Amboseli, Kenya. Cambridge: Cambridge University.

Keddy, P. A. 1989 *Competition.* London: Chapman.

Kingdon, J. 1979 *East African Mammals: An Atlas of Evolution in Africa.* Chicago: Chicago University Press.

Kingdon, J. 1997 *The Kingdon Guide to African Mammals.* San Diego: Academic Press.

Klingel, H. 1974 Social organisation and behaviour of the Grevy's zebra. *Zeitscrift für Tierpsychologie* **36**, 36-70.

Kruuk, H. 1972 *The Spotted Hyena: A study of predation and social behaviour.* Chicago: Chicago University Press.

Lamprey, H. K. 1963 Ecological separation of large mammal species in Tarangire Game Reserve, Tanzania. *East African Wildlife Journal* **1**, 1-20.

Law, R. & Watkinson, A. R. 1989 Competition. In *Ecological Concepts* (ed. J. M. Cherret & R. Law). Oxford: Blackwell Scientific Publications.

Lehner, P. N. 1996 *Handbook of Ethological Methods.* Cambridge: Cambridge University Press.

Lipetz, V. E. & Bekoff, M. 1982 Group size and vigilance in proghorns. *Zeitschrift für Tierpsychologie* **58**, 203-216.

May, R. M. 1978 Host-parasitoid systems in patchy envirnments: a phenomological model. *Journal of Animal Ecology* **47**, 833-843.

McCullagh, P. & Nelder, J. A. 1987 *Generalised Linear Models.* Monographs on Statistics and Applied Probability. London: Chapman and Hall.

Packer, C. 1986 The ecology of socality in felids. In *Ecological aspects of social evolution* (ed. D. I. Rubenstein & R. W. Wrangham). Princeton: Princeton University Press.

Payne, R. W., Lane, P. W., Digby, P. G. N., Harding, S. A., Leech, P. K., Morgan, G. W., Todd, A. D., Thompson, R., Tunnicliffe Wilson, G., J., W. S. & White, R. P. 1993 *Genstat 5 Release 3 Reference Manual.* Oxford: Clarendon Press.

Pierpont, N. 1986 Interspecific aggression and the ecology of woodcreepers (Aves: Dendrocolaptidae). Princeton: Princeton University.

Richards, S. M. 1974 The concept of dominance and methods of assessment. *Animal Behaviour* **22**, 914-930.

Rowen, M. 1992 Mother-infant behavior and ecology of Grevy's zebra, *Equus grevyi.* Yale: Yale University.

Rubenstein, D. I. 1986 Life history and social organisation in arid adapted ungulates. In *Ecological aspects of social evolution.* (ed. D. I. Rubenstein & R. W. Wrangham). Princeton: Princeton University Press.

Ruggiero, R. 1990 The effects of poaching disturbance on elephant behaviour. *Pachyderm* **13**, 42-44.

Schaller, G. 1968 Hunting behaviour of the cheetah in the Serengeti National Park, Tanzania. *East African Wildlife Journal* **6**, 95-100.

Schaller, G. B. 1972 *The Serengeti Lion: A Study of Predator-Prey Relations.* Chicago: Chicago University Press.

Schmidt-Nielsen, K. 1964 *Desert Animals: Physiological Problems of Heat and Water.* Oxford: The Clarendon Press.

Simberloff, D. S. 1984 Properties of coexisting bird species in two archipelagoes. In *Ecological Communities: Conceptual issues and evidence* (ed. D. R. Strong, D. S. Simberloff, L. G. Abele & A. B. Thistle). Princeton, New Jersey: Princeton University Press.

Spencer, P. 1965 *The Samburu.* London: Routledge & Kegan Paul.

Spencer, P. 1973 *Nomads in Alliance.* London: Oxford University Press.

Thouless, C. R. 1992 Samburu and Laikipia elephant count 1992. Nairobi, Kenya: Kenya Wildlife Service Laikipia Elephant Project.

Thouless, C. R. 1993 Laikipia Elephant Project: Final Report. Nairobi, Kenya.

van Hooff, J. A. R. A. M. & Wensing, J. A. B. 1987 Dominance and its behavioural measures in a captive wolf pakc. In *Man and Wolf* (ed. H. Frank), pp. 219-252. Dordrecht, Netherlands: Dr W. Junk Publishers.

Villet, M. H. & Woodiwiss, S. L. 1986 Resource partitioning and daily drinking patterns in communities of African game mammals. *Lamergeyer* **36**, 34-39.

Weir, J. & Davison, E. 1965 Daily occurrence of African game animals at waterholes during the dry season. *Zoologica Africana* **1**, 353-368.

Western, D. 1975 Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East African Wildlife Journal* **13**, 265-286.

Wisbey, J. 1995 The population status of Grevy's zebra (*Equus grevyi*) in selected areas of northern Kenya. London: University College London.

6. Patterns of reproduction and juvenile survival of Grevy's zebra in a heterogeneous environment

Summary

1. Temporal and spatial patterns of seasonality in breeding and juvenile survival in Grevy's zebra (*Equus grevyi* Oustalet) were studied in three study areas in northern Kenya.
2. Results showed that breeding in Grevy's zebra was explained by condition dependent oestrus, with a peak in births that corresponded to environmental conditions one gestation period prior to the study.
3. These results did not indicate that Grevy's zebra were aseasonal in their breeding. The evidence suggested their oestrus and conception was highly dependent on the seasonal variation in forage and water availability, which in turn was dependent on patterns of rainfall. Therefore, their breeding was highly influenced by stochastic patterns of climatic variation.
4. Juvenile survival was related to the distance that animals have to move to and from water, and the predictability of dispersal from areas.
5. The predictability and frequency of oestrus, and juvenile survival were lowest in the areas used by pastoral people. The conditions in these areas mimicked the effects of drought as recorded in Buffalo Springs by Ginsberg (1988).

Introduction

Fecundity and mortality rates are critical determinants of animal population dynamics, yet despite their practical importance, they remain unavailable for most species. These parameters may vary at the population level within species. Differences may arise within metapopulations exposed to different environmental conditions (Hanski & Gilpin 1991; Spendelow *et al.* 1995; Stearns 1992), or even within populations living in a heterogeneous environment (e.g., Paradis & Croset 1995).

Breeding in many animal species is affected by the broad pattern of seasons even in ecosystems with high environmental stochasticity (Roff 1992; Stearns 1992). Therefore, few animals are truly aseasonal. Breeding that is influenced by season is generally explained in two ways: 1) optimal birth seasons; or 2) condition dependent oestrus (Deutsch & Ofezu 1994).

Seasonality in births is thought to increase juvenile survival (Baker 1938; Clutton-Brock 1991), either as an adaptive response to temporal variation in forage abundance (Nefdt 1996; Rosser 1989; Rutberg 1987; Sinclair 1983) or by reducing the risk of predation on juveniles (Estes 1976; Fryxell 1987b; Rutberg 1987). Although not mutually exclusive, the first of these hypotheses predicts that births should be during the plant growing season, while the second predicts that females should give birth in large aggregations (Estes 1976). Aggregations that occur in time and space, reduce the risks of predation through dilution (Fryxell 1991). Furthermore, an interbirth interval of about 12 months (or a multiple of 12) would be expected for birth seasonality to remain synchronised with a predictable annual season.

In contrast to birth seasonality, condition dependent oestrus is a physiological response to ambient environmental conditions (Belonje & van Niekerk 1975). Condition dependent oestrus will, therefore, be highly influenced by stochastic patterns of environmental variability. Although animals whose pattern of breeding is determined by condition dependent oestrus could have seasonal births, they will remain in anoestrus during times of low forage abundance until the condition of the range, and, therefore, their body conditions improve (Andrews & McKenzie 1941; Burkhardt 1948; Day 1939; Quinlan *et al.* 1951; van Niekerk & van Heerden 1972). This predicts that birth patterns will be independent of environmental conditions at the time that offspring are born. Instead the birth patterns will be dependent on conditions one gestation period prior to the births, when the animals come into oestrus in response to an improvement of the nutritional plane. Therefore, the number of females in a population that come into oestrus in synchrony, when the nutritional plane improves, will be dependent on the length of the period of low resource availability prior to a period of relative forage abundance. The longer the period of low resource availability, the greater the resulting peak in births. Another prediction that arises from condition dependent oestrus is that the stochastic variation in an environment should be reflected in the interbirth intervals. The greater the environmental unpredictability, the greater the variation in the recorded interbirth intervals.

Age-effects on survival have been emphasized for many large- and medium-sized mammals (Deevey 1947), usually with three stages (Caughley 1966): 1) a juvenile stage with low survival; 2) a prime-adult stage with a high survival rate; and 3) a senescent stage with a decreasing survival rate. Of these stages, survival of juveniles in ungulates appears to be particularly sensitive to environmental conditions (Fryxell 1987a; Gaillard *et al.* 1993; McNaughton & Georgiadis 1986; Owen-Smith 1990). This predicts that there will be differences in juvenile survival within populations, whose distribution is spread over a heterogeneous environment.

Grevy's zebra (*Equus grevyi* Oustalet) live in a seasonally unpredictable environment in northern Kenya. The very unpredictability of this environment provides an opportunity to test the hypotheses for seasonal breeding and to study the effect of a heterogeneous environment on juvenile survival. The study was conducted on two scales. The breeding patterns were studied on a regional scale since this is the level at which seasons affect the environment (Jätzold & Bake 1995). Furthermore, the mobility of the species (see chapter 3; Ginsberg 1988; Klingel 1974) would make it difficult to determine the environmental conditions that influence breeding on a smaller scale. But because adult females with young foals are sedentary (Ginsberg 1989; Klingel 1974), foal survival can be studied in relation to the area in which they are born.

Methods

In order to test the hypotheses I chose three study areas with marked differences associated with their land use (see chapter 2 for descriptions of the study areas). The study areas were surveyed in rotation throughout the duration of the study, with each rotation starting in Barsalinga and finishing in Buffalo Springs (see chapter 2). Over the duration of the study, six complete rotations of the study areas were conducted. In addition, in June 1995, a seventh survey of Buffalo Springs and the two adjacent national reserves - Samburu and Shaba - was conducted as part of a larger survey for Grevy's zebra in northern Kenya (Wisbey 1995). This final survey was used only in the capture-mark-recapture analyses of survival. During each survey, the season was recorded (as defined in chapter 2).

On encountering groups of Grevy's zebra during the surveys, individuals were identified using their natural markings, using a technique developed by Rubenstein (1986), but modified by Ginsberg (1988) (see chapter 2 for details on the technique used to identify Grevy's zebra).

The first time an individual was identified, and thus its stripe pattern drawn, it was considered 'captured and marked'. Subsequent sightings of that individual were considered as 'resightings', along the lines of capture-mark-recaptures (CMR) principles (Jolly 1965). For each female identified, the reproductive class, including whether she had a foal and/or was an oestrus female, and her body condition were recorded (as defined in chapter 2).

Over the duration of the study, a capture-resighting history (Clobert *et al.* 1987; Jolly 1965) was constructed for each 'marked' individual over the seven surveys. In particular, capture-resighting histories were constructed for the foals. A foal's history was initiated when an adult female was seen to be in the last trimester of pregnancy. The foal was then monitored until the foal was weaned. In Rowen's (1992) study of mother-infant behaviour of Grevy's zebra, she recorded a mean weaning age of 11.5 months (standard deviation (SD), ± 1.4 months). Therefore, the mare-foal pairs were monitored until 10 months following the birth of the foal (mean - SD; 11.5 - 1.4 = 10.1).

Foal survival was recorded by noting the presence or absence of the foal. If a mare was seen without her foal before it was 10 months old, then the foal was recorded as being dead. It was highly unlikely that foals would be incorrectly recorded as being dead. Foals are in constant association with their mother (Becker & Ginsberg 1990; Rowen 1992), with the exception of foals of less than four months old. When mothers of these foals move to water to drink, the foals are left in 'kindergartens' (Becker & Ginsberg 1990; Klingel 1974; Rowen 1992). There was a higher likelihood that foals in Buffalo Springs would be mistakenly recorded as being dead since surveys were conducted during daylight hours, which was when animals in Buffalo Springs drank (see chapter 5). Furthermore, the surveys in each study area were conducted in two three-day periods. Mares with foals that were recorded as being dead by their absence in the first survey were checked on the second.

In most circumstances, early lactation females are sedentary, and tend not to disperse from the area in which the foal was born until it was at least six months old (Ginsberg 1989; Rowen 1992). However, in this study mare-foal pairs were recorded to disperse because of resource depletion (see chapter 3). Mare-foal pairs that did disperse were classified as 'transitory' (cf. Rowen 1992). In contrast mare-foal pairs that remained in an area until the foal was weaned or died were classified as 'sedentary'. If the foal of 'transitory' mare-foal pairs was recorded as being dead, the death was attributed to the area in which it was born.

During the surveys, predator sightings were also recorded.

Since the availability of resources in semi-arid areas of northern Kenya reflect the abundance of rainfall (chapter 3; Ginsberg 1988; Herlocker 1993), I tested the above predictions by examining the rainfall records, both during and prior to the study, for the area in which the study was conducted.

Data analysis

Oestrus and births

The patterns of oestrus and births over time and among study areas were analysed in a similar way. The number of post-partum and cycling oestrus females, and births were analysed as a proportion of the total adult female population recorded during any given rotation through all study areas, rather than in any given study area and survey. The reason for adopting this approach was that, unlike lactating, and particularly early-lactation females, non-reproductive females are not constrained to remain sedentary by their need for water (Ginsberg 1989; Rowen 1992). Therefore, there were surveys in particular areas when the greater proportion of females in that area were lactating simply because the non-reproductive females had dispersed. Using the total number of adult females per rotation gave a better representation of the real population of females either with young foals (and therefore births) or in oestrus relative to the whole population.

In order to test for peaks in, and the effect of study area on, oestrus and births, generalised linear models with binomial errors (for analysing proportional data) were fitted to the data, using Genstat 3.2 (Crawley 1993; McCullagh & Nelder 1987; Payne *et al.* 1993). The number of births and oestrus (both for post-partum oestrus and all oestrus) females was used as the response variate, with the total number of females in each rotation of all the study areas as the binomial denominator. Peaks, over all study areas and within each, were detected by adding time and $(\text{time})^2$ to the model. Study area was also added to the model to assess differences among the three study areas.

Interbirth intervals

The mean interbirth interval was calculated using censored data such as those used when calculating the mean age to death in survival analyses (Crawley 1993; Fedigan & Rose 1995). This meant that when a known female was seen to produce two foals over the course of the study, and therefore the interbirth interval (here equivalent to age to death) was known, it was considered as censored. In contrast, there were females who produced a foal, and by the end of the study, but at a time greater than the minimum interbirth interval of 13.5 months[1], had neither produced a second foal nor showed signs of a second pregnancy. Obviously there was no way of knowing when these females would produce another foal. Nonetheless, they contributed to the equivalent of the survival function in survival analysis, although not directly to the interbirth interval. In order to account for these females in the calculation of interbirth intervals, the mean interbirth interval was weighted with a censoring indicator, which for censored females = 1, and uncensored females = 0. A model, with Poisson errors, a log link function, and log time as an offset (Crawley 1993), was then fitted to the data, with the censoring indicator as the response variate. The mean interbirth interval was then calculated from the natural antilog of the parameter estimates from the model.

Patterns of dispersal

The study areas were not closed. There was no barrier, except distance, impeding the movement of animals among the study areas. The movement of individuals within and among study areas was assessed using the repeated sightings of individually identified females. Those females only recorded once throughout the study, and therefore the 'single sightings', were removed from these analyses, even though, by definition, they were using more than one area unless they died. However, they obviously did not provide information on the others areas that they are using.

For the analysis of comparing the degree of dispersal - and hence the proportion of 'transitory' and 'sedentary' early-lactation females among the areas, models, fitted with binomial errors for proportional data, were used with the number of transitory females as the response variate and the total number of females as the binomial denominator. A factor indicating study area was added to the model to assess the differences between the study areas.

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[1] Grevy's zebra have a post-partum oestrus two weeks after giving birth to a foal (Ginsberg 1988). Therefore, with a 13 month gestation period (King 1965), in theory, the minimum interbirth interval was 13.5 months.

Juvenile survival

The analysis of survival in animals can be conducted using three types of data: 1) known deaths, where all individuals known to die are recorded; 2) recoveries of deaths, data which are often incomplete; and 3) incomplete recoveries of the survivors and therefore using CMR histories (Clobert *et al.* 1985; Lebreton *et al.* 1993). Since very few juvenile carcasses were recovered during this study ($N = 4$ skeletons; $N = 1$ fresh carcass), I focused on analyses of data on known deaths and CMR histories.

Initially, I analysed survival using the number of known deaths and the total number of foals born. Within these analyses, foal survival was first estimated as:

$$\phi_i = 1 - \left(\frac{d_i}{T_i}\right) \tag{1}$$

where ϕ_i was the survival of foals in area i, d_i was the number of foals born in that area but were known to have died as defined above, and T_i was the total number of foals recorded to have been born in that area. This gave a high estimate of survival, since it assumed the survival of all the foals of the mare-foal pairs that were not resighted.

I therefore constructed a further estimate of survival using the data on recorded deaths. This incorporated the rate of survival in the animals not re-sighted, by assuming their rate of survival was similar to that of transitory females. Therefore,

$$\phi_i = 1 - \frac{\left(d_i + m\left(\frac{d_m}{d_m + q_m}\right)\right)}{T_i} \tag{2}$$

where d_m was the number of transitory foals that were known to have died, q_m was the number of transitory foals known to have survived, and m was the number of mare-foal pairs, where neither the mare nor foal was re-sighted following their last sighting, and nor before 10 months since the birth of the foal. The effect of study area on both the survival estimates was analysed using generalised linear models, fitted with binomial errors, for proportional data. The survival rate was taken as the response variate, with a binomial denominator of 1, and study area as the explanatory factor.

The second method to estimate survival of foals used recently developed CMR models, extensively reviewed in Lebreton *et al.* (1992). Such models have the following simplified capture-resighting history for the population over the duration of a study, in this case consisting of seven surveys, as their basis:

$$1 \xrightarrow{\phi_1} \underset{P_2}{2} \xrightarrow{\phi_2} \underset{P_3}{3} \xrightarrow{\phi_3} \underset{P_4}{4} \xrightarrow{\phi_4} \underset{P_5}{5} \xrightarrow{\phi_5} \underset{P_6}{6} \xrightarrow{\phi_6} \underset{P_7}{7}$$

Here, ϕ_i is the estimated survival between samples n and $n + 1$, while P_i is the probability of resighting individuals from sample n in sample $n + 1$. This history is simplified since it does not show the successive cohorts 'captured' during sequential sampling.

Initially, the Cormack-Jolly-Seber (CJS) model was fitted to the data. In the CJS model, both the survival rate (ϕ) and resighting probability (P) are time-dependent ($\phi_t P_t$). Goodness-of-fit (GOF) tests of the model to the data were conducted using RELEASE software (Burnham *et al.* 1987; Cooch *et al.* 1996; Pollock *et al.* 1990).

CMR models have four basic assumptions: 1) each foal in the population has an equal probability of survival or resighting; 2) each foal has an equal probability of surviving from one sampling period to the next; 3) marks are neither lost nor overlooked; and 4) all samples are instantaneous and individuals are released immediately following marking. The CJS model was rejected for the overall data set (see results). This indicated that either the underlying assumptions to the model were violated and therefore the choice of the starting model was inappropriate. Alternatively, the data were either over- or under-dispersed for the CJS model, in which case lack of fit was due to extra-nomial variation (Lebreton *et al.*, 1992). The GOF tests were conducted for a time and area dependent model (ϕ_{A*t} P_{A*t}), thus testing whether the lack of fit in the CJS model was due to differences in the survival rates and resighting probabilities among the three areas. This model was accepted as the starting point for model selection, although the data were overdispersed (see results). Therefore, when selecting models, the procedure to correct for overdispersed data was followed (Anderson *et al.* 1994; Burnham *et al.* 1995a;

Burnham *et al.* 1995b). The variance inflation factor, *c*, (Cooch *et al.* 1996; Lebreton *et al.* 1992) was, therefore, calculated from the sum of the χ^2 derived from tests conducted in the GOF test, divided by the total degrees of freedom - i.e., the number of parameters - in the $\phi_{A*t} P_{A*t}$ model.

Using the area dependent CJS as the starting model, models were selected. Selection was an active process, with models being fitted to the data and then compared. Two methods of model comparison for data that is overdispersed are recommended by Lebreton *et al.* (1992). The first uses a modified or quasi-Akaike information criterion (QAIC after Anderson *et al.* 1994),

$$QAIC = \frac{Dev}{c} + 2np \tag{3}$$

where, *Dev* is the deviance of the model, *c* is the variance inflation factor, and *np* the number of parameters in the model. The second is a test statistic, *F*, used for comparison of models fitted to overdispersed data, where

$$F_{df,rdf} = \frac{\chi^2 / df}{c} \tag{4}$$

F is derived from the likelihood ratio tests (LRT) for nested models *i* and *j*, where $\chi^2 = Dev_i - Dev_j$, the degrees of freedom from the number of parameters (*np*), where $df = |np_i - np_j|$, and finally, *c*, the variance inflation factor.

Comparison of the QAIC results for each model facilitated the selection of the most parsimonious set of models, but those that do not necessarily have to be nested (e.g., Hutchison 1978). The models with the lowest QAIC were selected. The principles behind such model comparison are consistent with quasi-likelihood theory (Lebreton *et al.* 1992). The steps and parameters used in the model selection process, and the resulting QAICs are reported in the results. These analyses were conducted using SURGE4 software (Lebreton *et al.* 1992; Pradel & Lebreton 1991).

Specific hypothesis testing was done using the *F*-statistic between nested models among the selected group of parsimonious models. First I tested for an effect of time on survival (ϕ_{A*t}). Therefore, the model with different survival rates for each period (time between rotations) was fitted to the data. I then tested fitted a model in which rotations conducted in the dry season were grouped. This model assumed the same survival rate for rotations in the dry season (ϕ_{A*s}). The modelling process indicated that 'period 4', the time between the fourth and fifth rotations, may have had an effect on the survival rate. Therefore, a model was fitted that assumed the same the survival rate for all rotations, but a different rate in period 4 (ϕ_{A*per4}). Again, from the modelling process and from the survival analysis using 'known deaths', Buffalo Springs and Ngare Ndare had similar survival rates (see results). Therefore, this was incorporated in a model, where they were assumed to have the same survival rate, with Barsalinga having another ($\phi_{(A1/A2 + A3)}$). The factor for area was then dropped from the model to ascertain whether there was an overall area effect on survival.

Finally, since the final survey was conducted in Buffalo Springs and the adjacent National Reserves, but not in either Barsalinga or Ngare Ndare, the effect of this was tested on the resighting probabilities ($P_{A*5/1}$). All other possible variation in the resighting probability was also modelled. However, in the results, I present those models with the structure in resighting probability that led to the most parsimonious models.

Results

Oestrus and births

There was a significant peak in the birth rate between the second and fourth survey periods inclusive, with 71% of all recorded births occurring during this period (Table 1; Figure 1a). This was the case throughout the population ($\chi^2 = 167.2$, $df = 2$, $P<0.0001$), and in each of the study areas (Barsalinga: $\chi^2 = 161.9$, $df = 2$, $P<0.0001$; Ngare Ndare: $\chi^2 = 9.403$, $df = 2$, $P<0.01$; and Buffalo Springs: $\chi^2 = 64.94$, $df = 2$, $P<0.001$). However, area had a very significant effect on the model ($\chi^2 = 76.08$, $df = 2$, $P<0.0001$), and inspection of the χ^2 values for each of the study areas indicated that Barsalinga showed the most significant peak in births.

Table 1. The number of births recorded in the three study areas over the duration of the study, shown by rotation. The total number of foals by area were: Barsalinga: 175; Ngare Ndare: 57; Buffalo Springs: 88.

	Rotation A	1	2	3	4	5
Barsalinga	9	23	76	65	1	1
Ngare Ndare	5	10	19	2	5	16
Buffalo Springs	2	10	32	34	9	1
Total	16	43	127	101	15	18

Figure 1a shows the rainfall records for Archer's Post, a weather station adjacent to Buffalo Springs (see chapter 2, Figure 1), over the duration of this study. The pattern of births and oestrus are also shown on Figure 1a. The greater proportion of the births (53%) occurred during the late dry season in the early part of 1994, before the April/May rains. The rainfall recorded from February - August 1994, which covered the period in which 71% of the births occurred, was 77mm - 43% of the long-term mean for that time of the year.

Figure 1b shows the rainfall records for Archer's Post recorded for two years prior to the study, and in particular, one gestation period before the peak in the births. Of the 22 months between January 1991 and November 1992, only two have rainfall higher than the long-term monthly means (May and July 1991), with only one other month having average rainfall (December 1991). During all other months in this period the rainfall was below the monthly long-term mean. Overall, the rainfall in this 22 month period was 47% of the long-term mean. In contrast, the rainfall between November 1992 and January 1993 was 69% higher than average rainfall. Assuming that the peak in the births recorded in this study would be reflected in the peak in oestrus, but one gestation period before the births, then the pattern of oestrus would have appeared as shown on Figure 1b, with a peak falling only two months following the rainfall.

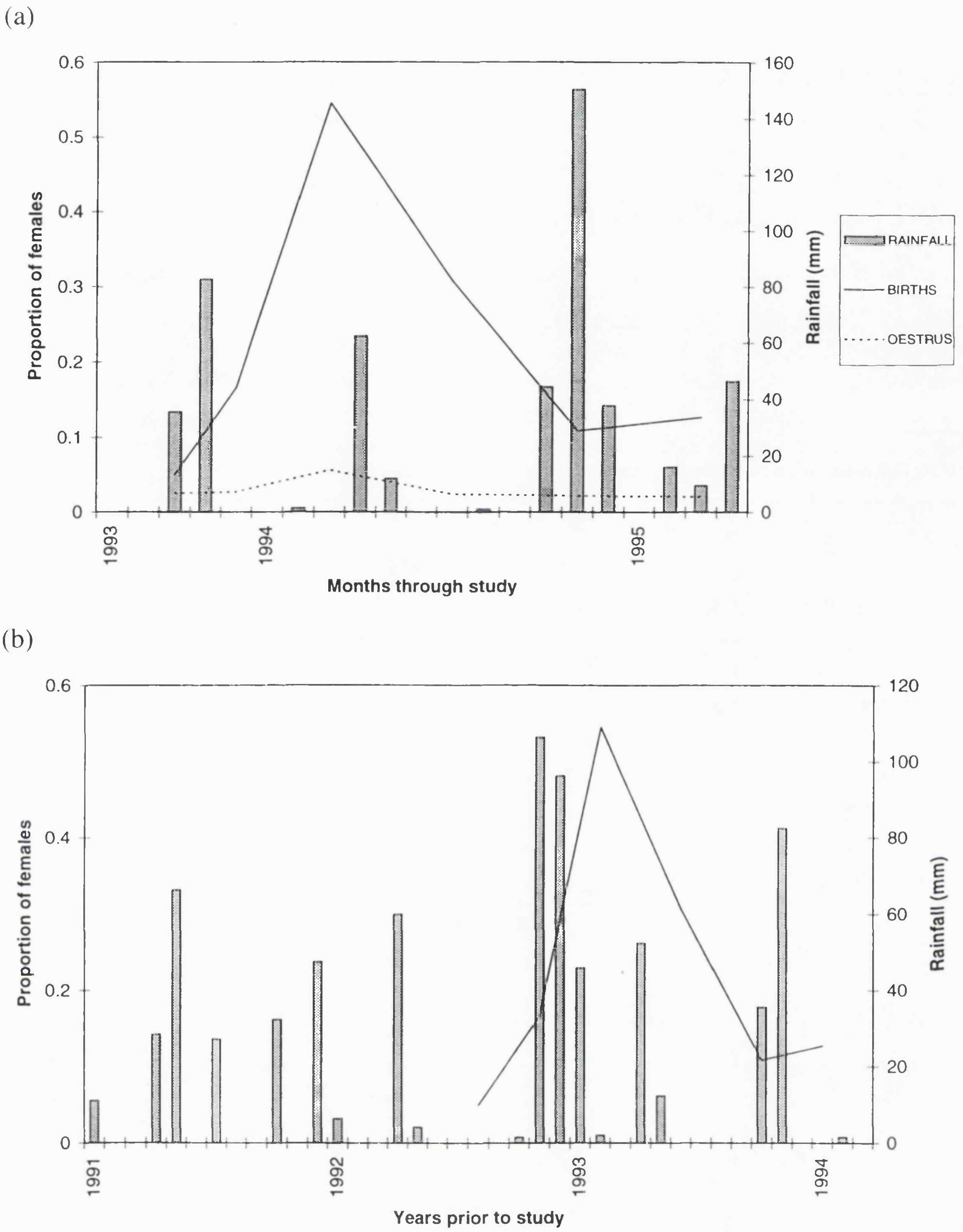

Figure 1 (a): The pattern of births and oestrus, in all study areas, shown as a proportion of the total number of adult females that had given birth to foals (BIRTHS) or were recorded to be in oestrus (OESTRUS) during rotation through the study. The results are presented in relation to the rainfall in Archer's Post - a weather station adjacent to Buffalo Springs. (b) The predicted pattern of oestrus one gestation period (13 months) prior to the births peak shown in Figure 1a. The pattern of oestrus is also shown in relation to the rainfall in Archer's Post. Rainfall data from the Kenya Meteorological Department.

In contrast to the pattern of births, there was no significant peak in the frequency of oestrus recorded in this study (χ^2 = 2.148, *df* = 2, NS; see Table 2 and Figure 1a), even though, if resources are abundant, Grevy's zebra have a post-partum oestrus. However, examination of the frequency of post-partum oestrus in each of the three study areas revealed that there was a significant peak in Buffalo Springs (χ^2 = 11.95, *df* = 2, P<0.005) and Ngare Ndare (χ^2 = 9.619, *df* = 2, P<0.05), but no significant peak in Barsalinga (χ^2 = 3.455, *df* = 2, NS).

Table 2. The number of females in oestrus - both cycling and post-partum (see chapter 2 for definitions) - in the three study areas over the duration of the study.

		Rotation					
		A	1	2	3	4	5
Barsalinga	Cycling	3	1	0	0	1	1
	Post-partum	1	0	3	0	0	0
	Total	4	1	3	0	1	1
Ngare Ndare	Cycling	2	1	2	0	1	0
	Post-partum	2	0	0	0	0	2
	Total	4	1	2	0	1	2
Buffalo Springs	Cycling	0	4	4	4	1	0
	Post-partum	0	1	4	4	0	0
	Total	0	5	8	8	1	0
	Total	8	7	13	8	3	3

Overall, area did not have an effect on oestrus (χ^2 = 0.0, *df* = 1, NS), although there was a significant effect of the interaction term between area and rotation (area.rotation: χ^2 = 29.38, *d.f.* = 10, P < 0.005). However, in pairwise analyses between the areas, there was a higher frequency of oestrus in Buffalo Springs than the other two study areas (Figure 2). The differences were significant: Barsalinga vs.

Buffalo Springs, $\chi^2 = 4.674$, $df = 1$, $P<0.05$; Ngare Ndare vs. Buffalo Springs, $\chi^2 = 4.670$, $df = 1$, $P<0.05$. The difference between Barsalinga and Ngare Ndare was not significant ($\chi^2 = 0$, $df = 1$, NS).

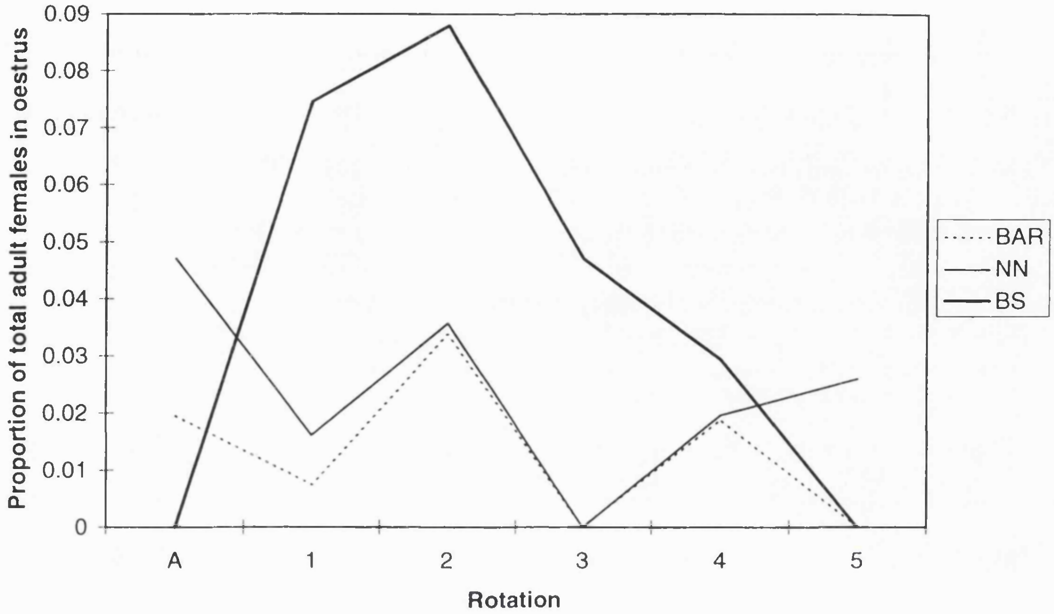

Figure 2. The proportion of females in oestrus in the three study areas, Barsalinga (BAR), Ngare Ndare (NN), and Buffalo Springs (BS), by rotation. The proprotion was calculated from the number of females in oestrus in each study area and the total number of females sighted across all areas.

Interbirth intervals

Out of a total of 162 females that could have had two foals over the duration of the study, 71 did and were, therefore, censored in the analysis to calculate the mean interbirth interval. The remaining 91 females were included in the analysis as being not censored. Using the parameters estimate from modelling the censoring indicator, *w*, the mean interbirth interval was calculated to be 37.71 months (which compared with the mean of 16.18 months for those females with known interbirth interval).

Dispersal

The main results of dispersal analysis are presented in chapter 3.

From known mares and foals that were recorded as being sedentary and transitory, there appeared to be a greater tendency for those from Barsalinga to be transitory than in the other study areas. Area had a significant effect on the model of proportion of females that were transitory (χ^2=7.61, *df*=2, *P*<0.025, Table 3). The differences were significant between Barsalinga and Buffalo Springs (χ^2 = 7.44, *df* = 1, *P*<0.01), but not with Ngare Ndare (χ^2 = 2.27, *df* = 1, NS). There was no difference between Ngare Ndare and Buffalo Springs (χ^2 = 1.19, *df* = 1, NS).

Survival: known deaths

Table 3 shows the results of the survival calculations for each of the study areas using the initial methods of estimation. This included the different survival estimates for the known transitory and sedentary foals. The results showed that there was a tendency, with the notable exception of Barsalinga, for transitory foals to have a lower survival rate. The differences between the known sedentary and transitory foal survival was, however, not statistically significant for any of the areas (Barsalinga: χ^2 = 0.47, *df* = 1; Ngare Ndare: χ^2 = 0.61, *df* = 1; Buffalo Springs: χ^2 = 0.98, *df* = 1).

Analysis of the results of the second estimation of survival using equation (2), showed that there was a significant effect of area on the survival of foals (χ^2 = 9.67, *df* = 2, *P*<0.01). There was a significant effect of area between Barsalinga and both Ngare Ndare and Buffalo Springs (χ^2=5.91, *df*=1, *P*<0.025; χ^2=6.65, *df*=1, *P*<0.01 respectively), but that there was no difference in the survival between Buffalo Springs and Ngare Ndare (χ^2=0.02, *df*=1, NS).

Table 3. The number of foals recorded in each study area, by category: 1) known survivors: those foals that were known to survive to greater than 10 months old; 2) known deaths: mothers who had had a foal and was recorded without her foal when it should have been less than 10 months old; and 3) the total number of individually identified foals in each area and overall. This number included the number of single sighted mare-foal pairs (which were, therefore, by definition 'transitory', but since they were not resighted, gave no information about survival). Thereafter, the estimates of the foal survival in the three study areas are given using these data on known deaths. Estimate 1 was the high estimate of survival since it assumed the survival of all foals of transitory females. In contrast, Estimate 2 incorporates the rate of survival of transitory females, and therefore was thought to be a more accurate estimate of foal survival.

		Barsalinga	Ngare Ndare	Buffalo Springs	Total
Known survivors					
Transients		13	8	6	27
Sedentary		6	12	17	35
Total, known survivors		19	20	23	62
Known deaths					
Transients		14	5	4	23
Sedentary		10	4	5	19
Total		24	9	9	42
Total foals seen		160	58	82	300
Survival estimates					
Estimate 1	All foals	0.85	0.84	0.89	
	Sedentary	0.375 (16)	0.75 (16)	0.77 (22)	
	Transitory	0.48 (27)	0.62 (13)	0.6 (10)	
Estimate 2	All foals	0.47	0.65	0.64	

Table 4. The results of the goodness-of-fit tests for the initial CJS model (ϕ_t P_t) and subsequent area and time dependent model (ϕ_{A*t} P_{A*t}) to the data. See text for details.

	TEST 2			TEST 3			TEST 2 + 3			
	χ^2	*df.*	*P*	χ^2	*df.*	*P*	χ^2	*df.*	*P*	*c*
ϕ_t P_t	15.7	7	0.03	29.1	9	<0.01	44.8	16	<0.01	2.8
BAR	9.1	7	0.2	19.4	8	0.01	28.5	15	0.02	1.90
NN	4.5	5	0.5	13.3	8	0.1	17.8	13	0.2	
BS	16.7	7	0.02	11.4	8	0.2	28.1	15	0.02	1.87
ϕ_{A*t} P_{A*t}							74.4	43	0.002	1.73

Survival: CMR models

The results of the goodness-of-fit tests suggested that the CJS model should be rejected (Table 4). The goodness-of-fit tests for area dependent CJS model (ϕ_{A*t} P_{A*t}) were not completely satisfactory (Table 4). However, the *c* value obtained (mean deviance, $c = 1.7305$) was indicative of overdispersion in the data rather than use of an inappropriate model (Anderson *et al.* 1994). This suggested that the initial rejection of the CJS model was due to area heterogeneity. The area-dependent CJS model (ϕ_{A*t} P_{A*t}) was then accepted as the starting point of the model selection process (Figure 3), using the overdispersion correction factor, $c = 1.7305$ to calculate QAIC2 values for model selection.

The model selection process resulted in model 8 (ϕ $\phi_{(A1/A2+A3)*per4)}$ P_A) being chosen as that with best fit according both to its low QAIC value and the tests using the *F*-statistic (Table 5). Table 6 show the survival estimates derived from model 8.

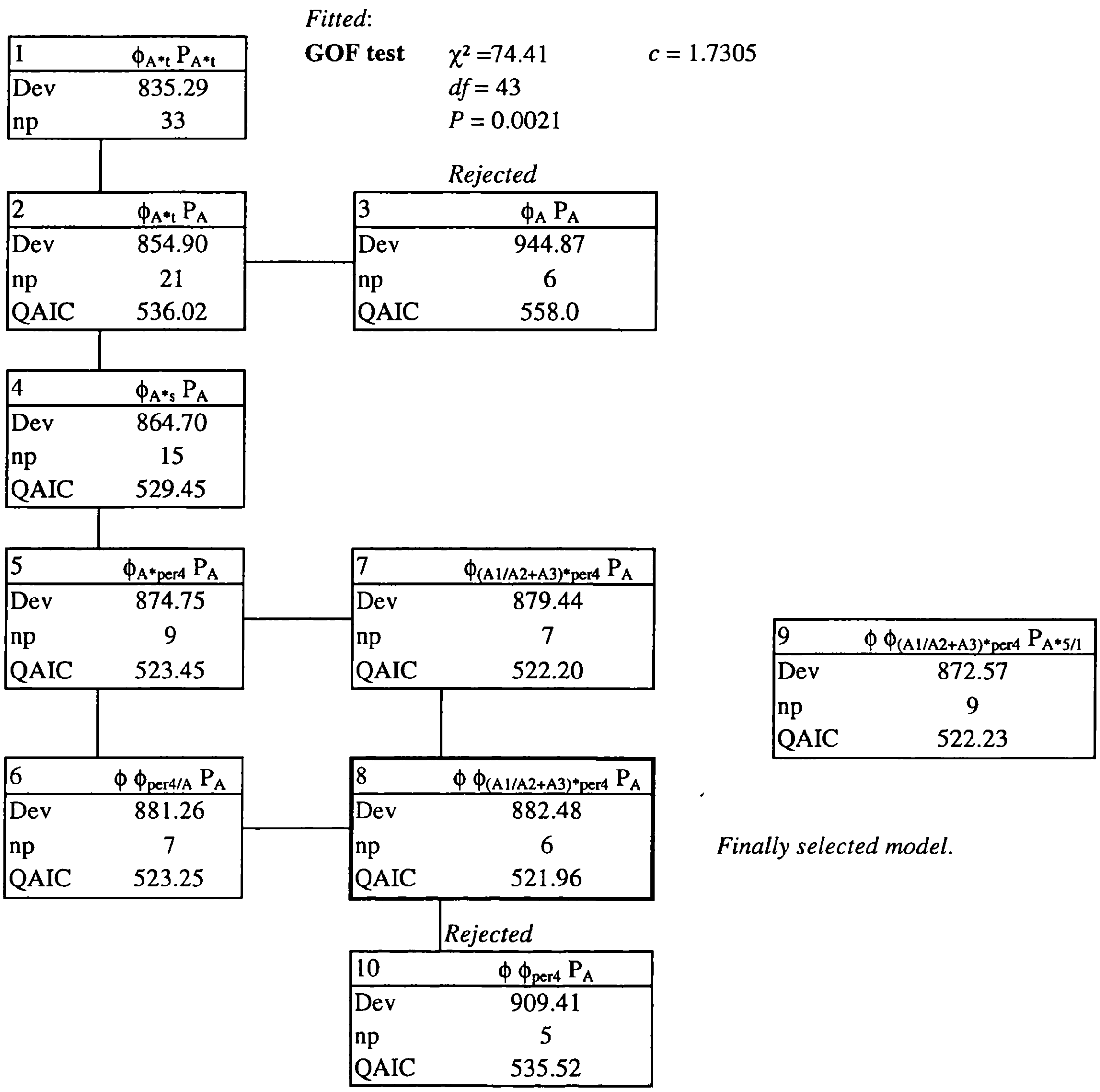

Figure 3. A diagrammatic representation of the model selection process, showing the most parsimonious set of models. The starting model was the area and time dependent model (ϕ_{A*t} P_{A*t}), that was accepted with the caveat that the model selection process use correction factors for overdispersed data. Model 8 was finally selected as the model of best fit. For each model, the deviance (*Dev*), estimated number of parameters (np), and quasi-Akaike Information Criterion (QAIC) are presented. For each model, the effects tested on the survival rate (ϕ) and resighting probabilities (P) are indicated in subscript beneath either the ϕ or P; these are more fully explained in Table 5. In the subscript text the following symbols are used: t - time; A - area, where A1 is Barsalinga, A2 Ngare Ndare, and A3 Buffalo Springs; s - season, where surveys conducted in the dry season were assumed to have the same survival; 5/1 - where the resighting probabilities among the first six surveys are taken as being the same, in contrast with that from the seventh and final survey; per4 - indicated the seperation of the period between surveys 4 and 5, testing whether the lower survival in Barsalinga was attributable to this period alone; * - indicate interactive effects between parameters; and + indicates additive effects between parameters in the model.

Table 5. Descriptions of the most parsimonious models from the selection process, explaining the parameters used in each, and which correspond to Figure 3. Model 8 was the finally selected model.

no.	Model	Description
1	$\phi_{A*t}\ P_{A*t}$	ϕ and P both time and area dependent: used as starting model
2	$\phi_{A*t}\ P_{A}$	ϕ time dependent in each area; P area dependent
3	$\phi_{A}\ P_{A}$	ϕ and P area dependent
4	$\phi_{A*s}\ P_{A}$	ϕ seasonal dependent (for dry season surveys) in each area; P area dependent
5	$\phi_{A*per4}\ P_{A}$	ϕ the survival for each area split into period 4 and all periods but period 4; P area dependent
6	$\phi\ \phi_{A*per4}\ P_{A}$	ϕ assumed to be the same for all areas and periods, but for period 4, where each area has a separate survival rate; P area dependent
7	$\phi_{(A1/A2+A3)*per4}\ P_{A}$	ϕ A2 and A3 survival grouped, A1 separate, all assumed to have the same survival for all periods but period 4; P area dependent
8	$\phi\ \phi_{(A1/A2+A3)*per4}\ P_{A}$	ϕ as with model 6, but A2 and A3 assumed to have the same survival, A1 different in period 4; P area dependent
9	$\phi\ \phi_{(A1/A2+A3)*per4}\ P_{A*5/1}$	ϕ as with model 8; P area dependent, the effect of the final survey
10	$\phi\ \phi_{per4}\ P_{A}$	ϕ effect the same for all areas and periods but for period 4, when there was no area effect; P area dependent

The modelling process first tested the temporal effects on survival. There was an effect of time, taken as the rotations among the study areas, on survival in each of the areas. Hence, from the starting model, in which survival was time dependent (ϕ_{A*t}), when time was dropped, the effect was significant (ϕ_{A*t} P_A vs. ϕ_A P_A, $F_{15,43}=3.47$, $P<0.01$). Time, therefore, had to remain in the models, and the model with just area dependent survival was rejected. The effect of time was explained further by grouping periods into seasons (dry and rains), and examining this effect on survival (ϕ_{A*t} P_A vs. ϕ_{A*s} P_A, $F_{6,43}=0.94$, NS). The temporal effects on survival were most accurately (the equivalent of the temporal 'minimum adequate model') explained by grouping the survival in all periods, but 'period 4' (ϕ_{A*s} P_A vs. ϕ_{A*per4} P_A, $F_{6,43}=0.97$, NS). This implied that during the fourth period between surveys, there was low survival while in all other periods, there was a constant, high survival of juveniles.

The modelling process then considered the spatial effects on survival - hence, the differences among the study areas. An area dependent model was accepted as the starting model (see above), but the model was improved effect by grouping Buffalo Springs and Ngare Ndare. Therefore, the model was fitted assuming that the survival in Buffalo Springs and Ngare Ndare was the same, while that in Barsalinga was different (ϕ_{A*per4} P_A vs. $\phi_{(A1/A2\ +\ A3)*per4}$ P_A, $F_{2,43}=1.88$, NS). That area, itself, had a significant effect was tested by dropping it from the model. Since the effect was significant, the model, with only time dependent survival, was rejected ($\phi_{(A1/A2\ +\ A3)*per4}$ P_A vs. ϕ ϕ_{per4} P_A, $F_{1,43}=11.52$, $P<0.01$).

The most parsimonious model for resighting probability was that with an area effect alone and, therefore, area was included in all the models (P_A). When the effect of the final survey, which was conducted in Buffalo Springs and the adjacent National Reserves but not Barsalinga and Ngare Ndare, was added to the model the effect was not significant ($\phi_{(A1/A2\ +\ A3)*per4}$ P_A vs. $\phi_{(A1/A2\ +\ A3)*per4}$ $P_{A*5/1}$, $F_{3,43}=1.91$, NS). The survival estimates from these two models were not different (Table 6).

Hence, in conclusion, the most parsimonious model was one which included the following effects: 1) survival in all periods and in all areas was the same except for that in 'period 4' (ϕ in Table 6); 2) survival was the same in Buffalo Springs and Ngare Ndare in period 4 ($\phi_{NN + BS, per4}$ in Table 6); and 3) survival was unique in period 4 in Barsalinga ($\phi_{BAR, per4}$ in Table 6). The survival estimates for these parameters are presented on Table. Two models are shown on Table: these are the models in which the resighting probability differed as explained above, though, of the two, the most parsimonious was model 8 - that with the area effect alone. However, there was no significant difference with the model that included a different resighting probability for all periods but the final one. Hence, this model was not rejected, and the results are presented as well.

Table 6. The survival estimates derived from models of best fit: 8 and 9. In the notation, Barsalinga ≡ BAR; Ngare Ndare ≡ NN; Buffalo Springs ≡ BS; CI were the 95% confidence intervals of the estimates; *sd* was the standard deviation.

	Model 9			Model 8		
	ϕ estimate	CI	*sd*	ϕ estimate	CI	*sd*
ϕ	0.886	0.779 - 0.946	0.042	0.894	0.783 - 0.951	0.041
$\phi_{BAR, per4}$	0.140	0.08 - 0.233	0.038	0.146	0.083 - 0.245	0.041
$\phi_{NN + BS, per4}$	0.610	0.410 - 0.778	0.098	0.611	0.910 - 0.780	0.099

I then re-examined the data on movements of the animals sighted in Barsalinga in the fourth and fifth surveys in order to establish the processes behind these patterns. Of the 104 females with foals that were sighted in Barsalinga during survey 4, only 4 were resighted in survey 5 in Barsalinga (one of which was sighted in Buffalo Springs in between surveys 4 and 5 in Barsalinga), while 27 were resighted in either Buffalo Springs or Ngare Ndare, obviously indicating they had emigrated from Barsalinga. The remaining 72 individuals were not resighted again through the remainder of the study - again indicative of their emigration from Barsalinga, but neither to Ngare Ndare nor Buffalo Springs.

Discussion

The results indicated that breeding in Grevy's zebra was driven by condition dependent oestrus. Evidence suggested that there was a peak in oestrus prior to the study that probably resulted from an improvement of the nutritional plane following a period of above average rainfall (Belonje & van Niekerk 1975; Quinlan *et al.* 1951; van Niekerk & van Heerden 1972). In contrast, birthing was not related to the seasonal patterns of forage availability. This did not indicate that Grevy's zebra were aseasonal in their breeding. The evidence suggested their oestrus and conception was highly dependent on the seasonal variation in forage and water availability, which in turn was dependent on patterns of rainfall. Therefore, their breeding was highly influenced by stochastic patterns of climatic variation. The environment in northern Kenya is highly seasonal, but on an annual scale, it is highly unpredictable, which was, in turn, reflected in the breeding patterns of Grevy's zebra.

That the results were not simply stochastic variation was supported by temporal patterns recorded in previous studies. Rowen (1992) recorded births throughout her study with no apparent peaks or troughs. This degree of asynchrony is consistent for the effects of condition dependent oestrus in the extended period of higher than average rainfall following a period of average rainfall that spanned her study. Similarly, Ginsberg (1988) recorded a low predictability and frequency of oestrus during a period of drought. However, he also recorded a peak in oestrus at the onset of rainfall following the drought. This peak in oestrus recorded by Ginsberg (1988) predicts a peak in births similar to that recorded in this study.

Support for condition dependent oestrus also came in a spatial dimension and was related to the availability of resources. In Buffalo Springs, the predictability and frequency of oestrus was higher than recorded in Barsalinga and Ngare Ndare (Table 2). This corresponded to the relatively high resource availability in Buffalo Springs (chapter 3). Similarly, in his study in Buffalo Springs, Ginsberg (1988) found that Grevy's zebra females come into oestrus only when they were in good condition - this was when food and water were abundant. Therefore, with low predictability and frequency of oestrus, Barsalinga and Ngare Ndare appear to mimic the effects of drought on the reproduction of Grevy's zebra that were recorded by Ginsberg (1988).

In contrast to the support for condition dependent oestrus, there was strong evidence that birthing of Grevy's zebra was not seasonal. Contrary to the prediction that seasonal birthing should occur during period of predictable resource abundance (Nefdt 1996; Rosser 1989; Rutberg 1987; Sinclair 1983), the recorded peak in the births primarily fell during the late dry season (Figure 1). This was when forage availability was both predicted and measured to be at its lowest (see chapter 3). Similarly, Ginsberg (1988) recorded a small, but consistent peak in births in his study that fell at the time of the year when rain was absent in his study.

The breeding of Grevy's zebra contrasted with annual breeders such as wildebeest, whose birthing peaks occur on an predictable annual basis within a two week period (Estes 1976). The temporal aggregation of wildebeest births is facilitated by their interbirth interval, which closely approximates to 12 months (Estes 1976). In contrast, the interbirth intervals of Grevy's zebra, both recorded and modelled (16.2 and 37.7 months respectively), did not tend towards being equal or under 12 months, or a multiple of 12, as was expected for animals with annual seasonality.

Kiltie (1985) has argued that the cost of time lost in evolving synchronised innate cycles is high. The cost is greatest in species with short minimum interbirth intervals (e.g., Uganda kob, Deutsch & Ofezu 1994), or those longer than a year. Seasonal birthing was, therefore, unlikely to evolve in an animal such as Grevy's zebra that has supra-annual interbirth intervals, unless selection - through a highly predictable and abundant growth period and high predator pressures - was overwhelming. Indeed, a principal precondition for the evolution of seasonality would be a highly predictable growing season (Baker 1938). Individuals would then benefit through high juvenile survival if they gave birth during the periods of high resource abundance, and, therefore, selection would favour birth seasonality. Clearly, in the unpredictable environment of northern Kenya, this is not the case. Hence, as in Uganda kob (Deutsch & Ofezu 1994), rather than time births with unpredictable seasons, Grevy's zebra may have been selected to maximise reproduction rates by coming into oestrus when conditions allow. The very fact that Grevy's zebra can have a post-partum oestrus supports this hypothesis.

Like the breeding patterns, survival of juveniles in Grevy's zebra was also susceptible to environmental stochasticity. This is supported by previous studies that show juvenile survival to be related to season (Ginsberg 1988) and the amount that mothers moved (Rowen 1992).

The analyses of known deaths and the CMR modelling process showed that juvenile survival lowest in Barsalinga (Tables 3 & 5). In contrast, there was little difference in the survival rate between Ngare Ndare and Buffalo Springs.

The use of the CMR modelling differentiated the critical stages when the survival in Barsalinga was lowest. This was in the period between the fourth and fifth surveys, which coincides with a large scale emigration of lactating females from Barsalinga (see chapter 3). Earlier in this thesis, I showed that the distribution of zebra relative to water differed markedly among the study areas (see chapters 3 and 5). The distance to water were largest distances in Barsalinga. Hence, the low survival of 'sedentary' foals may be related to the distance that animals have to move to and from water. It was, therefore, probable that the costs of moving, both when 'sedentary' and particularly when emigrating, were responsible for low juvenile survival in Barsalinga. That juvenile survival is related to the extent to which mare-foal pairs are mobile, was also supported in previous work. Rowen (1992) demonstrated that mare-foal pairs that remained in a small area had higher survival than those that moved in and out of her study area.

An explanation for the relationship between juvenile survival and the extent to which they move is that they may be energetically constrained. Rubenstein (1986) used the suggestion that foals are energetically constrained to explain the formation of 'kindergartens'. The formation of kindergartens allows them to conserve large amounts of energy by not making the daily trip to and from water with their mothers. The suggestion that foals are energetically constrained is further supported by Becker & Ginsberg (1990) who observed that kindergartens are more frequently formed in dry conditions when mares have further to walk to and from water. Therefore, given the distance that animals have to move to and from water, and the higher predictability of dispersal from that area (see chapters 3 and 5), lower juvenile survival would be expected in Barsalinga on energetic grounds alone.

The formation of kindergartens at night may also contribute to the lower juvenile survival of Grevy's zebra foals in Barsalinga by exposing them to higher rates of predation. Klingel (1974) remarked on the vulnerability of foals when in kindergartens, noting that unlike many species of ungulate, they had no specific anti-predator behaviour. They would be especially vulnerable to predation at night, when predators are more active (see chapter 5). In this study, I did not measure the predation rates on juveniles; future work might attempt to study predation of juveniles in area such as Barsalinga, especially at night when their mothers are drinking.

In this study, I have shown that the effects on Grevy's zebra in Barsalinga mimic those of drought, as recorded by Ginsberg (1988) in Buffalo Springs. There are two factors which allow these results to be generalised to the Grevy's zebra population in the southern part of their range (Rowen & Ginsberg 1993; Williams 1998). First, in studies that have focused on the condition of the range in northern Kenya, descriptions of rangelands and the impact of pastoral people and their livestock are equivalent throughout the region (Bronner 1990; Grunblatt *et al.* 1992; Herlocker 1990; Herlocker 1992; Herlocker 1993; Mäckel & Walther 1994). The two areas used by pastoral people in this study, Barsalinga and Ngare Ndare, are included in the areas described in those studies. Hence, it is unlikely that the environmental conditions that have resulted in the reported patterns of oestrus, births and juvenile survival are restricted to the study areas alone. Second, the population of Grevy's zebra in the southern part of their natural range is the largest, and in conservation terms, the most important (Rowen & Ginsberg 1993; Williams 1998). The estimated size of this population is c. 1,500 of a total estimated wild population of 4,500 animals (Grunblatt *et al.* 1989; Rowen 1992; Rowen & Ginsberg 1993; Williams 1998). In this study, I recorded the births of 300 foals (Table 3). Given that there is an equal male:female ratio, and that all females are unlikely reproductively mature or viable, this represents a large proportion of possible births.

Consequently, recruitment of Grevy's zebra is constrained, particularly in the areas used by pastoral people. Obviously, the periods of low recruitment are predicted to be punctuated by periods of high fecundity, similar to that recorded in Rowen's (1992) study. In high rainfall years, the frequency of oestrus and conception will be high, similar to the peak in oestrus predicted to have occurred prior to this study. However, as in this study, the survival of those foals will be dependent on the maintenance of the periods of abundance for at least 19 months post-conception - thus, until the foals are greater than six months old. If the foals are born in an area used by pastoralists or during a low rainfall year in Buffalo Springs, then juvenile survival will be correspondingly low. The implications of the results for the population dynamics of Grevy's zebra are, therefore, critical and the recovery from the decline in number recorded between 1977 and 1988 (Dirschl & Wetmore 1978; Grunblatt *et al.* 1989) may be unlikely if conditions in northern Kenya continue as they are at present.

References

Anderson, D. R., Burnham, K. P. & White, G. C. 1994 AIC model selection in overdispersed capture recapture data. *Ecology* **75**, 1780-1793.

Andrews, F. N. & McKenzie, F. F. 1941 Estrus, ovulation and related phenomena in the mare. *Research Bulletin of the Mo. Experimental Station* **29**.

Baker, J. R. 1938 The evolution of breeding seasonality. In *Essays on aspects of evolutionary biology preseneted to Professor E. S. Goodrich.* (ed. G. R. de Beer). Oxford.: Oxford University Press.

Becker, C. D. & Ginsberg, J. R. 1990 Mother infant behavior of wild Grevy's zebra: adaptations for survival in semi-desert east Africa. *Animal Behaviour* **40**, 1111-1118.

Belonje, P. C. & van Niekerk, C. H. 1975 A review of the influence of nutrition upon the oestrous cycle and early pregnancy in the mare. *Journal of Reproduction and Fertility, Supplement* **23**, 167-169.

Bronner, G. 1990 *Vegetation and land use in the Matthews Range area, Samburu District.* Dissertationes Botanicae. Berlin: J. Cramer.

Burkhardt, J. 1948 Some clinical problems of horse breeding. *Veterinary Record* **60**, 243-248.

Burnham, K. P., Anderson, D. R. & White, G. C. 1995a Selection among open population capture recapture models when capture probabilities are heterogeneous. *Journal of Applied Statistics* **22**, 611-624.

Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C. & Pollock, K. H. 1987 *Design and analysis methods for fish survival experiments based on release-recapture.* American Fisheries Society Monograph. 5410 Grosvenor Lane, Bethesda, MA 20814.: American Fisheries Society.

Burnham, K. P., White, G. C. & Anderson, D. R. 1995b Model selection strategy in the analysis of capture recapture data. *Biometrics* **51**, 888-898.

Caughley, G. 1966 Mortality patterns in mammals. *Ecology* **47**, 906-918.

Clobert, J., Lebreton, J.-D. & Allaine, D. 1987 A general approach to survival estimation by capture or resightings of marked birds. *Andrea* **75**, 133-142.

Clobert, J., Lebreton, J.-D., Clobert-Gillet, M. & Coquillart, H. 1985 The estimation of survival in bird populations by recaptures or sightings of marked individuals. In *Statistics in Ornithology.*, vol. 29 (ed. B. J. T. Morgan & N. P.M.). Berlin.: Springer-Verlag.

Clutton-Brock, T. H. 1991 *The evolution of parental care.* Monographs in Behaviour and Ecology. Princeton: Princeton University Press.

Cooch, E. G., Pradel, R. & Nur, N. 1996 *A practical guide to mark-recapture analysis using SURGE.* Montpellier, France.: CNRS.

Crawley, M. J. 1993 *GLIM for Ecologists.* Methods in Ecology. Oxford: Blackwell Science.

Day, F. T. 1939 Sterility in the mare associated with irregularities of the oestrous cycle. *Veterinary Record* **51**, 1113-1119.

Deevey, E. S. 1947 Life tables for natural populations of animals. *Quarterly Review of Biology* **22**, 283-314.

Deutsch, J. C. & Ofezu, A. A. 1994 Uganda kob reproductive seasonality: optimal calving seasons or condition dependent oestrus? *African Journal of Ecology* **32**, 283-295.

Dirschl, H. J. & Wetmore, S. P. 1978 Grevy's zebra abundance and distribution in Kenya, 1977. Nairobi, Kenya: Kenya Rangeland Ecological Monitoring Unit.

Estes, R. D. 1976 The significance of breeding synchrony in the wildebeest. *East African Wildlife Journal* **14**, 135-152.

Fedigan, L. M. & Rose, L. M. 1995 Interbirth interval variation in 3 sympatric species of Neotropical monkey. *American Journal of Primatology* **37**, 9-24.

Fryxell, J. M. 1987a Food limitation and demography of a migratory antelope, the white-eared kob. *Oecologia* **72**, 83-91.

Fryxell, J. M. 1987b Seasonal reproduction of white eared kob in boma National Park, Sudan. *African Journal Of Ecology* **25**, 117-124.

Fryxell, J. M. 1991 Forage quality and aggregation by large herbivores. *American Naturalist* **138**, 478-498.

Gaillard, J. M., Delorme, D., Boutin, J. M., Vanlaere, G., Boisaubert, B. & Pradel, R. 1993 Roe deer survival patterns a comparative analysis of contrasting populations. *Journal of Animal Ecology* **62**, 778-791.

Ginsberg, J. R. 1988 Social organization and mating strategies of an arid-adapted equid: the Grevy's zebra. Princeton, New Jersey: Princeton University.

Ginsberg, J. R. 1989 The ecology of female behaviour and male reproductive success in Grevy's zebra, *Equus grevyi*. *Symposia of the Zoological Society (London)* **61**, 89-110.

Grunblatt, J., Ottichilo, W. K. & Sinange, R. K. 1992 A GIS approach to desertification assessment and mapping. *Journal of Arid Environments* **23**, 81-102.

Grunblatt, J., Said, M. Y. & Nutira, J. K. 1989 Livestock and wildlife summary 1987 - 1988 for Kenya Rangelands. Nairobi, Kenya: Department of Resource Surveys and Remote Sensing, Ministry of Planning and National Development.

Hanski, I. & Gilpin, M. 1991 Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**, 3-16.

Herlocker, D. J. 1990 Rangeland Vegetation of Isiolo District. Nairobi, Kenya: Ministry of Livestock.

Herlocker, D. J. 1992 Vegetation types. In *Range Management Handbook of Kenya, Volume II, 2: Samburu District* (ed. S. B. Shaabani, M. Walsh, D. J.

Herlocker & D. Walther). Nairobi, Kenya: Republic of Kenya, Ministry of Livestock Development (MOLD).

Herlocker, D. J. 1993 Vegetation types. In *Range Management Handbook of Kenya, Volume II, 5: Isiolo District* (ed. D. J. Herlocker, S. B. Shaabani & S. Wilkes). Nairobi, Kenya: Republic of Kenya, Ministry of Agriculture, Livestock Development and Marketing.

Hutchison, G. E. 1978 *An introduction to population ecology.* New Haven, Conn.: Yale University Press.

Jätzold, R. & Bake, G. 1995 The climatology of northern and north-eastern Kenya. In *Range Management Handbook of Kenya, Vol. II.* (ed. D. Herlocker, M. Nicholson & S. Allanson). Nairobi, Kenya.: Ministry of Agriculture, Livestock Development and Marketing (MALDM).

Jolly, G. M. 1965 Explicit estimates from capture-recapture data with both death and immigration stochastic model. *Biometrika* **52**, 225-247.

Kiltie, R. A. 1985 Gestation as a constraint on the evolution of season breeding in mammals. In *Mammalian population biology and life history evolution.* (ed. M. S. Boyce). Yale: Yale University Press.

King, J. M. 1965 A field guide to the reproduction of the Grant's zebra and the Grevy's zebra. *East African Wildlife Journal* **3**, 99-117.

Klingel, H. 1974 Social organisation and behaviour of the Grevy's zebra. *Zeitscrift für Tierpsychologie* **36**, 36-70.

Lebreton, J. D., Pradel, R. & Clobert, J. 1993 The statistical analysis of survival in animal populations. *Trends in Ecology & Evolution* **8**, 91-95.

Lebreton, J.-D., Burnham, K. P., Clobert, J. & Anderson, D. R. 1992 Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**, 67-118.

Mäckel, R. & Walther, D. 1994 *A field guide to soil erosion & its management implications in northern Kenya (Range Monitoring Series No. 2).* Nairobi, Kenya: Republic of Kenya, Ministry of Agriculture, Livestock Development and Marketing (MALDM).

McCullagh, P. & Nelder, J. A. 1987 *Generalised Linear Models.* Monographs on Statistics and Applied Probability. London: Chapman and Hall.

McNaughton, S. J. & Georgiadis, N. J. 1986 Ecology of grazing and browsing mammals. *Annual Review of Ecology and Systematics* **17**, 39-65.

Nefdt, R. J. C. 1996 Reproductive seasonality in Kafue lechwe antelope. *Journal of Zoology* **239**, 155-166.

Owen-Smith, N. 1990 Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros* in relation to rainfall. *Journal of Animal Ecology* **59**, 893-913.

Paradis, E. & Croset, H. 1995 Assessment of habitat quality in the Mediterranean pine vole (*Microtus duodecimcostatus*) by the study of survival rates. *Canadian Journal of Zoology - Revue Canadienne de Zoologie* **73**, 1511-1518.

Payne, R. W., Lane, P. W., Digby, P. G. N., Harding, S. A., Leech, P. K., Morgan, G. W., Todd, A. D., Thompson, R., Tunnicliffe Wilson, G., J., W. S. & White, R. P. 1993 *Genstat 5 Release 3 Reference Manual.* Oxford: Clarendon Press.

Pollock, K. H., Brownie, C. & Hines, J. E. 1990 Statistical inference for capture-recapture experiments. *Wildlife Monographs.* **107**, 1-97.

Pradel, R. & Lebreton, J.-D. 1991 *User's manual for program SURGE version 4.1.* Montpellier, France: CEFE-CNRS.

Quinlan, J., van Rensburg, S. W. J. & Steyn, H. P. 1951 The oestrous cycle of the mare when maintained uder stable conditions iwth restricted exercise at Onderstepoort. *Onderstepoort Journal of veterinary research.* **25**, 105-119.

Roff, D. A. 1992 *The evolution of life histories: theory and analysis.* New York: Chapman & Hall.

Rosser, A. M. 1989 Environmental and reproductive seasonality of puku, *Kobus varoni* in Luangwa Valley, Zambia. *African Journal of Ecology* **27**, 77-88.

Rowen, M. 1992 Mother-infant behavior and ecology of Grevy's zebra, *Equus grevyi.* Yale: Yale University.

Rowen, M. & Ginsberg, J. R. 1993 Grevy's zebra (*Equus grevyi* Oustalet). In *Equid Action Plan* (ed. P. Duncan). Gland, Switzerland: IUCN.

Rubenstein, D. I. 1986 Life history and social organisation in arid adapted ungulates. In *Ecological aspects of social evolution.* (ed. D. I. Rubenstein & R. W. Wrangham). Princeton: Princeton University Press.

Rutberg, A. T. 1987 Adaptive hypotheses of birth synchrony in ruminants: an interspcific test. *American Naturalist* **130**, 692-710.

Sinclair, A. R. E. 1983 The adaptations of African ungulates and their effects on community function. In *Tropical Savannas* (ed. F. Bourliere). Amsterdam: Elsevier.

Spendelow, J. A., Nichols, J. D., Nisbet, I. C. T., Hays, H., Cormons, G. D., Burger, J., Safina, C., Hines, J. E. & Gochfeld, M. 1995 Estimating annual survival and movement rates of adults within a metapopulation of roseate terns. *Ecology* **76**, 2415-2428.

Stearns, S. C. 1992 *The evolution of life histories.* Oxford: Oxford University Press.

van Niekerk, C. H. & van Heerden, J. S. 1972 Nutrition and ovarian activity of mares in the early breeding season. *Journal of the South African Veterinary Medicine Association* **43**, 351-360.

Williams, S. D. 1998 Grevy's zebra. In *Zebras, Asses, and Horses: An Action Plan for the Conservation of Wild Equids* (ed. P. Moehlman). Gland, Switzerland: IUCN.

Wisbey, J. 1995 The population status of Grevy's zebra (*Equus grevyi*) in selected areas of northern Kenya. London: University College London.

7. Concluding discussion: competition and conservation

In this study I have examined the ecology and behaviour of Grevy's zebra (*Equus grevyi* Oustalet) to test the hypothesis that Grevy's zebra compete for critical resources with pastoral people and their domestic livestock. On the basis of the definition of competition that I presented in the first chapter of this thesis, I conclude that competition exists between Grevy's zebra, and pastoralists and their livestock. The inclusion of humans in the ecological unit with which Grevy's zebra compete was justified since humans are present in areas such as Barsalinga and Ngare Ndare to exploit the resources through diversified animal husbandry (Coppock *et al.* 1986a; Coppock *et al.* 1986b; Coughenour *et al.* 1985).

Resource use

There are two ways in which species may influence each other's resource use: either exploitatively or through interference (Case & Gilpin 1974; Case *et al.* 1979; Pierpont 1986).

Overall, Barsalinga had significantly lower biomass of forage than both Ngare Ndare and Buffalo Springs. Buffalo Springs, in turn, had the highest forage availability. This was not consistent through all rotations, since the availability of forage in Ngare Ndare was lower than Barsalinga following the low April 1994 rainy season, but higher than Buffalo Springs following the heavy November 1994 rains (chapter 3, Figure 1). The fluctuation in forage availability in Ngare Ndare may have been be attributed to 1) the density of domestic livestock, or that 2) high rainfall in November 1994 caused a large growth of grass, which was suggested by the variation of forage availability over seasons in Ngare Ndare. The difference between Barsalinga and

Buffalo Springs was most acute in the dry season. The low forage availability in Barsalinga corresponded to the high numbers of grazing ungulates, which was heavily skewed by the presence of the domestic livestock species. This provided evidence for exploitative competition, which occurs when individuals interact indirectly and respond to resource levels which have been depressed by competitors (Keddy 1989; Law & Watkinson 1989), particularly because, in Barsalinga, Grevy's zebra and domestic livestock were constrained to using the same habitats. In Barsalinga there was a significant negative relationship between the number of Grevy's zebra and the distance to the nearest group of domestic livestock (chapter 3).

Comparison of Barsalinga and Buffalo Springs indicated that in Barsalinga, Grevy's zebra were temporally displaced to using water at night because of the presence of humans and their domestic livestock at water, and in and around their *manyatta*s (chapter 5). Since humans were included in the ecological unit for competition, I conclude that it was interference that displaced the zebra, where interference competition is the direct conflict, or avoidance of conflict between individuals (Case *et al.* 1979; Pierpont 1986). Furthermore, in Ngare Ndare, the space use of Grevy's zebra was negatively influenced by human presence (chapter 3). This indicted that zebra were also avoiding humans in this area.

Limited resources

The main evidence that resources were limited came from the dispersal patterns of the zebra. The extent of the dispersal of Grevy's zebra has not previously been measured, although it was recognised as occurring in previous studies (Ginsberg 1988; Klingel 1974; Rowen 1992). Klingel's (1974) study, in a pastoralist area on the Il Bonyeki plains north of Buffalo Springs, was in what he described as a 'wet season area', thereby acknowledging that there was seasonal movement of animals. Ginsberg (1988) and Rowen (1992) both recognised dispersal in Grevy's zebra. However, their studies were confined to Buffalo Springs, and, therefore, did not record the dynamic way in which animals were moving.

That dispersal was restricted to the dry season suggested that forage abundance was seasonally limited. During the dry season, Grevy's zebra from Barsalinga and Ngare

Ndare responded to declining food resources by dispersal. In contrast, during this period, the number of Grevy's zebra in Buffalo Springs *increased* (chapter 3, Figure 7). This indicated that Buffalo Springs may act as a refuge for animals when forage is less abundant elsewhere. This idea is supported in Ginsberg's (1988) study which spanned a drought. During the drought (which he defined as a complete rainy period being missed) there were large numbers of Grevy's zebra using the area, again indicating that Grevy's zebra were coming in from the surrounding, depleted areas.

Only males which were territorial were 'resident' in Buffalo Springs; other non-territorial males and females used the area when its resource availability was higher than surrounding areas. That these animals ultimately dispersed may have suggested that the food resources in Buffalo Springs were, to a relatively small degree, limiting. However, an alternative explanation is that there may have been recovery of the vegetation and therefore higher resource availability elsewhere. This was the case in Ginsberg's (1988) study, when the animals, including territorial males, dispersed from Buffalo Springs following the drought when rain had fallen elsewhere.

I propose the hypothesis that there were three thresholds of resource limitation for dispersal for different sex classes of Grevy's zebra. The non-reproductive females had the lowest threshold: they were the first to disperse from the areas where the forage availability was diminishing. Unlike lactating females with young foals, who were constrained by their need for a predictable water supply, non-reproductive females were able to disperse. (Since bachelor males are also not constrained by resources or territoriality, I predict that they also dispersed with the non-reproductive females. These data were not collected in this study.) Therefore, lactating females had a higher threshold - they remained in an area until the forage abundance further dwindled - than non-reproductive females, which was also observed in Ngare Ndare and Barsalinga. The final threshold was for territorial males, who are constrained not by their need for resources but by their sociality (Ginsberg 1988; 1989; Klingel 1974). In neither Barsalinga nor Ngare Ndare did the territorial males disperse at any stage in the study.

These patterns of dispersal for females contrasted with the description of 'migration' by Klingel (1974). In his study, he reported two thresholds, one for 'mares, foals, and non-territorial stallions' and another for 'territorial stallions'. Klingel (1974) did not distinguish between the effects of food and water, but he attributed the dispersal of animals both to declining forage availability and to water sources drying up. However, the description of his study area does not mention any permanent water sources and forage abundance was not measured, although he reported them to be 'definitely bad'. This he attributed 'above all to the excessive use of the area by several thousand Samburu cattle'.

If forage abundance was determining the dispersal in Klingel's (1974) study, since he did not report two thresholds for reproductive classes of female, either he did not pick up the patterns or the decline in forage abundance was so dramatic that all classes of female dispersed simultaneously. However, if water had been driving the dispersal, then a simultaneous dispersal of all classes of female would be expected. That dispersal was not driven by competition for use of water in this study was demonstrated by the staggered, rather than simultaneous, dispersal of the different classes of Grevy's zebra female.

Throughout the study, the availability of water was mapped, particularly at water sources known to be used by Grevy's zebra and domestic livestock. Water, itself, was never limiting - hence, the water sources never dried up regardless of what extent they were used by people, livestock or wild ungulates. I have demonstrated that access to water is confined to a limited number of usable sources, and second, that the number of high visibility - and therefore daylight - hours are limited.

Energetic costs

The greater distances that animals have to move to and from water meant higher energetic costs incurred by individuals living in Barsalinga and Ngare Ndare when compared to Buffalo Springs (chapters 3 and 5).

The higher predictability and frequency of dispersal of Grevy's zebra from Barsalinga and Ngare Ndare compared with Buffalo Springs meant that animals using these areas faced a higher risk of incurring the costs of dispersal. This may have been related to the extent to which adult females were energetically constrained Rubenstein (1986) suggested that this was the case with foals who, since they cannot meet the energetic requirements to make daily journeys to and from water, remain in 'kindergartens' (this study; Ginsberg 1988; Klingel 1974; Rowen 1992; Rubenstein 1986). During the dry season, if the distance between food and water becomes too great, the adult females may also become constrained. Therefore, there may be an energetic threshold which will contribute to animals' decision to disperse.

Fitness costs

In this study, I recorded low frequencies of oestrus and juvenile survival in Barsalinga, as a result of the highly dynamic response of Grevy's zebra to measured levels of forage availability. This was consistent with Rowen's (1992) work in Buffalo Springs where she found that foals of 'transient', i.e. mobile, females had lower survival than foals of 'resident' females. The results in Barsalinga also mirrored the effects of drought conditions reported by Ginsberg (1988). Ginsberg (1988) found that foal mortality in Buffalo Springs was higher in the late dry and drought than in other seasons. This he attributed to the higher costs of moving to and from water during the drought when the disjunction between food and water increased.

The lower juvenile survival in Barsalinga may, in part, be attributable to the higher predation risks faced by animals drinking at night. Grevy's zebra females have been observed in Buffalo Springs leaving their foals of less than four months in a 'kindergarten' while they move down to water (see above). Since no foals were sighted at water during the water source monitoring in Barsalinga, I assumed that the foals were also forming kindergartens during nocturnal visits to water by their mothers. This would make them vulnerable to predation, even though predator densities in Barsalinga were relatively low: Klingel (1974) remarked on foal vulnerability when in kindergartens and noted that unlike other species of ungulate, they have no specific anti-predator behaviour. Even if the foals were accompanying their mothers down to water because of the increased predation risks, low juvenile survival is still predicted on energetic grounds.

Clearly Grevy's zebra are adapted to the unpredictable environment that forms their natural range (Ginsberg 1988; 1989; Klingel 1974; Rowen 1992; Rubenstein 1986). However, as I have shown in this study, competition with domestic livestock in the areas used by pastoral people mimics the effects of drought, thereby constraining the recruitment rates of Grevy's zebra. Periods of low recruitment are, nonetheless, likely to be punctuated by periods of high fecundity, at least in protected areas, as recorded in Rowen's (1992) study. In high rainfall years, the frequency of oestrus and conception will be high or similar to the peak in oestrus that must have occurred prior to this study. The survival of those foals will be dependent on periods of resource abundance for at least 19 months post-conception - thus until the foals are greater than six months old. If, however, foals are born into a low rainfall year in Buffalo Springs, or in an area used by pastoralists, then juvenile survival will be low.

I have also argued that these results can be generalised to the Grevy's zebra population in the southern part of their range (Rowen & Ginsberg 1993; Williams 1998), since range conditions are described as being similar throughout the region - including the two areas used by pastoral people in this study (Bronner 1990; Grunblatt *et al.* 1992; Herlocker 1990; Herlocker 1992; Herlocker 1993; Mäckel & Walther 1994). Hence, it is unlikely that the environmental conditions that have resulted in the reported patterns of oestrus, births and juvenile survival are restricted to the study areas alone. Second, this study represents a large sample of that southern population, the estimated size of which is c. 1,500 of a total estimated wild population of 4,500 animals (Grunblatt *et al.* 1989; Rowen 1992; Rowen & Ginsberg 1993; Williams 1998). For example, in this study, I recorded the births of 300 foals. Given that there is an equal male:female ratio, and that all females are unlikely to be reproductively mature or viable, this represents a large proportion of possible births.

I predict that there are also social costs to Grevy's zebra that use pastoralist areas such as Barsalinga. Ginsberg (1989), Becker and Ginsberg (1990) and Rowen (1992) all report that females with young foals are more predictable in their behaviour than other classes of female. They usually remain and mate with one male, whose territory has access to water. This contrasted with the females in early lactation in

Barsalinga that had to travel far to water, potentially crossing several territories, but certainly not remaining in those territories with access to water. Indeed, during the day, it was rare to see territorial or other males less than four kilometres from water. This begs the question of whether there are any territories with access to water? If so, are they only functional at night? Are they, therefore, more unstable, in contrast to territories in Buffalo Springs which may be held by the same individual for seven years or more (Ginsberg 1988; 1989)? If so, what are the implications for the population? These questions were not addressed in this thesis, but in showing that there are marked ecological constraints in areas used by pastoralists, like Barsalinga and Ngare Ndare, compared to National Reserves like Buffalo Springs, it becomes clear that the behavioural plasticity in breeding strategies would be an interesting topic of study.

I also did not study other costs on females that may contribute to reducing reproductive success. These include the harassment of oestrus females by males when crossing territories to move to water (e.g., Berger 1983), increased disease risk to animals exposed to high livestock densities (e.g., Dobson 1995) and lost feeding time through time spent moving (e.g., Mayes & Duncan 1986). Nonetheless, these would only add to the costs measured in this study: the consequence of low juvenile survival, low frequency and predictability of oestrus, and social costs already predicts that the reproductive success of individuals using the pastoralist areas would be low.

In broader, evolutionary terms, the persistence of equids is explained by their ability to extract more nutrients, per unit time, than ruminants, provided there is sufficient biomass of forage to sustain their high intake rates (Duncan *et al.* 1990; Foose 1982; Janis 1976). That Grevy's zebra were able to derive sufficient nutrients to survive from low quality forage was apparent in this study. However, what was also apparent was that, in the face of competition, recruitment into the population was constrained. As such, this study is consistent with theoretical models for the taxonomic and ecological displacement of equids by ruminants which suggest that it is the reproduction of equids that must be constrained if displacement is to occur (Duncan 1992; Duncan *et al.* 1990).

Conservation

Overall, the results of this study highlight the importance of National Reserves, like Buffalo Springs, for the persistence of Grevy's zebra in their natural environment. Maintenance of these areas is particularly important to sustain recruitment into the population. Effective protected areas for Grevy's zebra are very few and far between. Buffalo Springs, together with Samburu and Shaba National Reserves, cover approximately 0.4% (800km^2) of the natural range of Grevy's zebra in northern Kenya (Grunblatt *et al.* 1989; Shaabani *et al.* 1992). Their importance, recognised by Rowen and Ginsberg (1993), is clearly supported by the results of this study.

The study provided direct evidence that pastoral people maintain high stocking rates of domestic livestock, which were similer to surrounding areas used by pastoral people (Grunblatt *et al.* 1989). The continued maintenance of these stocking rates, with some degree of density-independence, is expected. Density-independence, or alternatively, elevation of the thresholds of density-dependence, may continue through activities such as re-supply of drought-related losses of pastoralist livestock by international NGOs (Drought Monitoring Project Reports, 1993 - 1995). Veterinary care will also decrease losses from disease, allowing high stocking rates to be maintained. Maintenance of domestic livestock stocking rates will mean that competition, as measured in this study, will be similarly maintained.

For the persistence of Grevy's zebra outside of protected areas, the pastoralists' dependence on high stocking rates must be reduced. This study, therefore, supports recent efforts by the Kenya Wildlife Service to achieve this goal through implementation of 'community conservation'. Here, the community benefits directly from the wildlife in their area, utilising it under their own constructed management scheme. The community conservation scheme has been implemented in Barsalinga, but is still in its infancy. For this scheme to be successful, pastoralists will have to lower stocking rates. This will be feasible only once the benefits of wildlife management scheme are tangibly felt by the pastoralists, and when domestic livestock are not their only entrance into a market economy. It will take a great deal of education to change the insurance practice where the number of animals matters more than their productivity (Saidi 1992; Spencer 1965). However, only with a reduction in the stocking rates of the pastoral people in areas such as Barsalinga will Grevy's zebra be competitively released, thereby improving the likelihood of their persistence in their natural range.

References

Becker, C. D. & Ginsberg, J. R. 1990 Mother infant behavior of wild Grevy's zebra: adaptations for survival in semi-desert east Africa. *Animal Behaviour* **40**, 1111-1118.

Berger, J. 1983 Induced abortion and social factors in wild horses. *Nature* **303**, 59-61.

Bronner, G. 1990 *Vegetation and land use in the Matthews Range area, Samburu District.* Dissertationes Botanicae. Berlin: J. Cramer.

Case, T. J. & Gilpin, M. E. 1974 Interference competition and niche theory. *Proceedings of the National Academy of Sciences (USA)* **71**, 3073-3077.

Case, T. J., Glipin, M. E. & Diamond, J. M. 1979 Overexploitation, interference compeition, and excess density compensation in insular faunas. *American Naturalist* **113**, 843-854.

Coppock, D. L., Ellis, J. E. & Swift, D. M. 1986a Livestock feeding ecology and resource utilization in a nomadic pastoral ecosystem. *Journal of Applied Ecology* **23**, 573-583.

Coppock, D. L., Swift, D. M. & Ellis, J. E. 1986b Seasonal nutritional characteristics of livestock diets in a nomadic pastoral ecosystem. *Journal of Applied Ecology* **23**, 585-595.

Coughenour, M. B., Ellis, J. E., Swift, D. M., Coppock, D. L., Galvin, K., McCabe, J. T. & Hart, T. C. 1985 Energy extraction and use in a nomadic pastoral ecosystem. *Science* **230**, 619-625.

Dobson, A. 1995 The ecology and epidemiology of rinderpest virus in the Serengeti and Ngorongoro Conservation Area. In *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem* (ed. A. R. E. Sinclair & P. Arcese). Chicago: Chicago University Press.

Duncan, P. 1992 *Horses and grasses: the nutritional ecology of equids and their impact on the Camargue.* Ecological Studies. New York: Springer-Verlag.

Duncan, P., Foose, T. J., Gordon, I. J., Gakahu, C. G. & Lloyd, M. 1990 Comparative nutrient extraction from forages by grazing bovids and equids a test of the nutritional model of equid bovid competition and coexistence. *Oecologia* **84**, 411-418.

Foose, T. J. 1982 Trophic strategies of ruminant versus nonruminant ungulates. Chicago: University of Chicago.

Ginsberg, J. R. 1988 Social organization and mating strategies of an arid-adapted equid: the Grevy's zebra. Princeton, New Jersey: Princeton University.

Ginsberg, J. R. 1989 The ecology of female behaviour and male reproductive success in Grevy's zebra, *Equus grevyi. Symposia of the Zoological Society (London)* **61**, 89-110.

Grunblatt, J., Ottichilo, W. K. & Sinange, R. K. 1992 A GIS approach to desertification assessment and mapping. *Journal of Arid Environments* **23**, 81-102.

Grunblatt, J., Said, M. Y. & Nutira, J. K. 1989 Livestock and wildlife summary 1987 - 1988 for Kenya Rangelands. Nairobi, Kenya: Department of Resource Surveys and Remote Sensing, Ministry of Planning and National Development.

Herlocker, D. J. 1990 Rangeland Vegetation of Isiolo District. Nairobi, Kenya: Ministry of Livestock.

Herlocker, D. J. 1992 Vegetation types. In *Range Management Handbook of Kenya, Volume II, 2: Samburu District* (ed. S. B. Shaabani, M. Walsh, D. J. Herlocker & D. Walther). Nairobi, Kenya: Republic of Kenya, Ministry of Livestock Development (MOLD).

Herlocker, D. J. 1993 Vegetation types. In *Range Management Handbook of Kenya, Volume II, 5: Isiolo District* (ed. D. J. Herlocker, S. B. Shaabani & S. Wilkes). Nairobi, Kenya: Republic of Kenya, Ministry of Agriculture, Livestock Development and Marketing.

Janis, C. 1976 The evolutionary strategy of equidae and the origins of rumen and cecal digestion. *Evolution* **30**, 757-774.

Keddy, P. A. 1989 *Competition.* London: Chapman.

Klingel, H. 1974 Social organisation and behaviour of the Grevy's zebra. *Zeitscrift für Tierpsychologie* **36**, 36-70.

Law, R. & Watkinson, A. R. 1989 Competition. In *Ecological Concepts* (ed. J. M. Cherret & R. Law). Oxford: Blackwell Scientific Publications.

Mäckel, R. & Walther, D. 1994 *A field guide to soil erosion & its management implications in northern Kenya (Range Monitoring Series No. 2).* Nairobi, Kenya: Republic of Kenya, Ministry of Agriculture, Livestock Development and Marketing (MALDM).

Mayes, E. & Duncan, P. 1986 Temporal patterns of feeding behavior in free ranging horses. *Behaviour* **96**, 105-129.

Pierpont, N. 1986 Interspecific aggression and the ecology of woodcreepers (Aves: Dendrocolaptidae). Princeton: Princeton University.

Project, D. M. 1993 - 1995 The Drought Monitoring Bulletin: Isiolo District. Maralal, Kenya.

Rowen, M. 1992 Mother-infant behavior and ecology of Grevy's zebra, *Equus grevyi.* Yale: Yale University.

Rowen, M. & Ginsberg, J. R. 1993 Grevy's zebra (*Equus grevyi* Oustalet). In *Equid Action Plan* (ed. P. Duncan). Gland, Switzerland: IUCN.

Rubenstein, D. I. 1986 Life history and social organisation in arid adapted ungulates. In *Ecological aspects of social evolution.* (ed. D. I. Rubenstein & R. W. Wrangham). Princeton: Princeton University Press.

Saidi, K. 1992 Human ecology. In *Range Management Handbook of Kenya, Volume II, 2: Samburu District* (ed. S. B. Shaabani, M. Walsh, D. J. Herlocker & D. Walther). Nairobi, Kenya: Republic of Kenya, Ministry of Livestock Development (MOLD).

Shaabani, S., Herlocker, D. J., Walther, D., Walsh, M., Schwartz, H. J. & Wilkes, S. 1992 *Range Management Handbook of Kenya, Volumes II, 1-5.* Nairobi, Kenya: Republic of Kenya, Ministry of Livestock Development.

Spencer, P. 1965 *The Samburu.* London: Routledge & Kegan Paul.

Williams, S. D. 1998 Grevy's zebra. In *Zebras, Asses, and Horses: An Action Plan for the Conservation of Wild Equids* (ed. P. Moehlman). Gland, Switzerland: IUCN.