



Saurashtra University

Re – Accredited Grade 'B' by NAAC
(CGPA 2.93)

Priyadarshini, K. V. R., 2005, “*Interactions Between Forage, Recruitment and Activity Patterns of the Indian Blackbuck*”, thesis PhD, Saurashtra University

<http://etheses.saurashtrauniversity.edu/id/eprint/582>

Copyright and moral rights for this thesis are retained by the author

A copy can be downloaded for personal non-commercial research or study, without prior permission or charge.

This thesis cannot be reproduced or quoted extensively from without first obtaining permission in writing from the Author.

The content must not be changed in any way or sold commercially in any format or medium without the formal permission of the Author

When referring to this work, full bibliographic details including the author, title, awarding institution and date of the thesis must be given.

Saurashtra University Theses Service
<http://etheses.saurashtrauniversity.edu>
repository@sauuni.ernet.in

**INTERACTIONS BETWEEN FORAGE, RECRUITMENT AND
ACTIVITY PATTERNS OF THE INDIAN BLACKBUCK**
(Antilope cervicapra)

**Dissertation Submitted to Saurashtra University, Rajkot , Gujarat, for the
award of the Degree of Doctor of Philosophy in Wildlife Science.**

K. V. R. PRIYADARSHINI

**Wildlife Institute of India
Dehradun**

July 2005



भारतीय वन्यजीव संस्थान
Wildlife Institute of India

July 1, 2005

CERTIFICATE

This is to certify that the thesis titled "**Interactions between forage, recruitment and activity patterns of the Indian blackbuck (*Antelope cervicapra*)**" submitted for the award of degree of **Doctor of Philosophy in Wildlife Science** to Saurashtra University, Rajkot, is a record of original and independent research work carried out by **Ms. K. V. R. Priyadarshini** under my guidance. No part of this thesis has been submitted in part or full to any other University/Institution for the award of any other degree and it fulfils all the requirements laid down by Saurashtra University.

Dr. Y. V. Jhala
Sr. Reader & Head,
Dept. of Animal Ecology
& Conservation Biology

Forwarded

Mr. P. R. Sinha
Director
Wildlife Institute of India

Director
Wildlife Institute of India
Dehradun

ACKNOWLEDGEMENTS

Many institutions and individuals supported me during this study and dissertation writing. This study is part of Wildlife Institute of India (WII) – United States Fish and Wildlife Service (USFWS) collaborative project on the Conservation of Indian wolf. I would like to thank USFWS, which provided the primary funding support for this work. Additional funding and logistic support was given by Earthwatch and Conservation Treaty Support Fund. I am grateful to the present and earlier Directors of WII for permitting me to use the institutional facilities during the study period and dissertation writing. I thank the Gujarat State Forest Department for permission to work in Velavadar National Park and am grateful to Mr. L. N. Jadeja (Park Director) and Mr. V. A. Rathod (the then Range Officer) for their help and logistic support. I would like thank Dr. Indra Gadvi and his family for all their support and hospitality in Bhavnagar. I am grateful to Deepak bhai and his team at Satvik Garage for the much-needed help with vehicles and equipment. Several people in Velavadar made my fieldwork memorable. I would like to thank the entire forest staff of VNP and the villagers of Velavadar Bhal for all the good times that I had during my stay in VNP. I would like to thank Kavita Isvaran for sending me relevant literature and for her company in the field. Three excellent project staff, Ramesh, Lalu and Rajinder, assisted in data collection and extended crucial support in the field. I am extremely grateful to them.

I am grateful to Dr. Y. V. Jhala for his support, guidance and supervision of this work. I have benefited greatly from the inputs given to this study by Dr. S. P. Goyal and Dr. G. S. Rawat. Dr. Goyal and Dr. Rawat gave valuable comments on an earlier draft of this dissertation. I would like to thank Drs. K. Ramesh and Ashish David for having proof read this dissertation at a short notice. I would like to thank Dr. Goyal, Dr. H. C. Bohra (Principal Scientist, CAZRI) and Mr. O. P. Gupta (Apex laboratories, Dehradun) for helping me with laboratory analysis of grass samples. I am grateful to Dr. G. S. Rawat, Mr. M. M. Babu and Mr. P. L. Saklani for identifying plant specimens. I benefited immensely from the inputs given by Dr. Barry Noon and K. Yoganand (Yogi) on statistical analysis. In addition, Yogi provided many field equipment, helped in analysing and discussing the results, read through several drafts of this dissertation and gave valuable comments which helped improve the dissertation on the whole. I would like to thank all WII library staff; technicians at

the WII laboratory, especially Rakesh Sundriyal and Shyamlalji; staff of the computer cell, especially Muthu Veerappan, Dinesh Pundir, Virendra Sharma, and Harendra Kumar; and finally the USFWS Projects office at WII, especially Sajwan Sir and Rajeev Gupta for their excellent support.

Several people at WII helped me at various stages of this work. I sincerely appreciate the help of Gopi, G. V., Rajapandian, Bhaskar Acharya and Ashish David for helping me with sorting samples and checking errors in my drafts. I thank Mr. Shirish Kyatham for his help in preparing the study area map. I appreciate the support and encouragement of Aree, Jayapal, Ramesh, Suresh, Vijay, Siva, Rina, Anil, Anu and Bivash all along the study.

A special thanks to my brother-in-law for getting me a laptop PC that helped me a lot while writing up. I am extremely grateful to all my family members for their encouragement and support throughout the study period. Without the unstinting support of my parents and my husband, I cannot imagine how this work could have been possible.

*Dehradun
July 2005*

K. V. R. Priyadarshini

CONTENTS

	Page No.
Acknowledgements	iii
List of Tables and Appendix	vi
List of Figures	vii
List of plates	x
Abstract	xi
Chapter 1 General Introduction	1
Chapter 2 Review of Literature	5
Chapter 3 Study Area Description	13
Chapter 4 Seasonality of calving in blackbuck in the grasslands of Velavadar National Park	
4.1. Introduction	19
4.2. Methods	24
4.3. Results	31
4.4. Discussion	50
4.5. Summary	61
Chapter 5 Activity patterns and time budgets of blackbuck herds in Velavadar National Park	
5.1. Introduction	63
5.2. Methods	66
5.3. Results	69
5.4. Discussion	81
5.5. Summary	87
Chapter 6 Effects of grass harvesting and grazing (biomass removal and fertilization) on grassland productivity and grass quality.	
6.1. Introduction	89
6.2. Methods	93
6.3. Results	98
6.4. Discussion	105
6.5. Summary	110
Literature Cited	112
Appendix	130

LIST OF TABLES AND APPENDIX

		Page No.
Table 4.1	Seasonal differences in above-ground biomass (g/m^2), moisture content (%), crude protein, ADF, lignins, silica content of grass ($\text{g}/100\text{g}$ dry weight), and body condition factor scores of blackbuck females in Velavadar National Park.	34
Table 4.2	Relationships among various forage quality variables in Velavadar National Park.	41
Table 4.3	Correlations among the body condition ranks of five body parts of blackbuck females in Velavadar National Park and PCA component loadings.	42
Table 4.4	Relationships between monthly means of body condition factor scores of blackbuck females and various forage quality variables in Velavadar National Park.	44
Table 4.5	Length and other characteristics of the calving seasons in Velavadar National Park.	46
Table 4.6	Summary of relationships between monthly mean proportions of blackbuck females calving and the different predictor variables in Velavadar National Park.	48
Table 5.1	The effect of season and period of day on % time spent in various activities (arcsine transformed) as assessed by a 2-way factorial ANOVA.	75
Table 5.2	Differences between periods of day in % of time spent in various activities by blackbuck as determined by post-hoc pair-wise comparisons.	78
Table 6.1	Differences in means of accumulated biomass (g/m^2) and accumulated Nitrogen in grasses (g/m^2) among various treatments during the experiment year 2001-02.	101
Table 6.2	Differences in accumulated biomass (g/m^2) between pairs of treatments in both years of the experiment.	102
Appendix 1	List of plant species recorded in Velavadar National Park during the study period (2000-2002).	130

LIST OF FIGURES

Figure No.		Page No.
Figure 3.1	Map of Velavadar National Park.	14
Figure 4.1	A plot of cumulative weekly proportion of blackbuck female calving (lactating) in year 2000.	28
Figure 4.2	Total monthly rainfall recorded in the grassland in Velavadar National Park.	31
Figure 4.3	Monthly means of dry biomass of grass in Velavadar National Park.	32
Figure 4.4	Seasonal differences in grass biomass in Velavadar National Park.	33
Figure 4.5	Monthly means of moisture content (%) of grasses in Velavadar National Park.	35
Figure 4.6	Seasonal differences in moisture (%) content of grasses in Velavadar National Park.	35
Figure 4.7	Monthly means of crude protein content (g/100g dry weight) of grasses in Velavadar National Park.	36
Figure 4.8	Seasonal differences in crude protein content (g/100g dry weight) of grasses in Velavadar National Park.	37
Figure 4.9	Monthly means of Acid Detergent Fibre (ADF; g/100g dry weight) of the grasses in Velavadar National Park.	38
Figure 4.10	Monthly means of lignins (g/100g dry weight) in grasses in Velavadar National Park.	38
Figure 4.11	Monthly means of silica (g/100g dry weight) in grasses in Velavadar National Park.	39
Figure 4.12	Seasonal differences in Acid Detergent Fibre (ADF; g/100g dry weight) of grasses in Velavadar National Park.	39
Figure 4.13	Seasonal differences in the lignins content (g/100g dry weight) of grasses in Velavadar National Park.	40
Figure 4.14	Seasonal differences in silica content (g/100g dry weight) of grasses in Velavadar National Park.	40
Figure 4.15	Monthly means of body condition factor scores (from PCA) of blackbuck females in Velavadar National Park.	43
Figure 4.16	Seasonal differences in body condition of blackbuck females in Velavadar National Park.	43
Figure 4.17	Weekly mean proportion (%) of females calving (lactating) and weekly total rainfall in Velavadar National Park.	45
Figure 4.18	Monthly mean proportion (%) of females calving	45

	(lactating) and monthly total rainfall in Velavadar National Park.	
Figure 4.19	Monthly mean proportion (%) of blackbuck females calving, standardised (range transformed to vary from 0 to 1) values of monthly means of body condition factor scores of females, and main forage quality variables in Velavadar National Park.	49
Figure 5.1	Dry season hourly mean % of blackbuck occupied with various activities, and the mean hourly ambient temperature in Velavadar National Park.	70
Figure 5.2	Wet season hourly mean % of blackbuck occupied with various activities, and the mean hourly ambient temperature in Velavadar National Park.	70
Figure 5.3	Cold season hourly mean % of blackbuck occupied with various activities in Velavadar National Park.	71
Figure 5.4	Hourly % (a) feeding, (b) resting, and (c) moving activity of blackbuck herds in Velavadar National Park in different seasons.	72
Figure 5.5	Time budget of blackbuck herds for feeding, resting/ruminating, moving and other activities in different seasons in Velavadar National Park.	73
Figure 5.6	Variability in the time spent feeding by three blackbuck herds in dry, wet and cold seasons in Velavadar National Park.	74
Figure 5.7	Distance moved during the day by three blackbuck herds in different seasons in Velavadar National Park.	75
Figure 5.8	Percent of blackbuck feeding in different periods of day in different seasons.	76
Figure 5.9	Percent of blackbuck resting/ruminating in different periods of day in different seasons.	77
Figure 5.10	Percent of blackbuck moving in different periods of day in different seasons.	77
Figure 5.11	Relationship between hourly % time spent feeding by blackbuck and hourly temperature in Velavadar National Park.	79
Figure 5.12	Relationship between % time investment in feeding by blackbuck herds and biomass (g/m^2) of grasses in the foraging ranges of the herds during the periods of activity sampling.	79
Figure 5.13	Relationship between % time investment in feeding by blackbuck herds and moisture (%) of grasses in the	80

	foraging ranges of the herds during the periods of activity sampling.	
Figure 6.1	Accumulated biomass in treatment plots during year 2000 experiment and the standing biomass during the month of maximum biomass. (a) Box plots of biomass in different treatment plots and (b) mean accumulated biomass in different treatment plots	99
Figure 6.2	Accumulated biomass in treatment plots during year 2001-02 experiment and the standing biomass during the month of maximum biomass. (a) Box plots of biomass in different treatment plots and (b) mean accumulated biomass in different treatment plots	100
Figure 6.3	Nitrogen content of grasses in the different treatment plots and standing biomass plots during year 2000 experiment.	104
Figure 6.4	Nitrogen content of grasses in the different treatment plots and standing biomass plots during year 2001-02 experiment.	104

LIST OF PLATES

Plate No.		Following Page No.
Plate 1:	Grassland habitat in Velavadar National Park.	14
Plate 2a:	<i>Prosopis juliflora</i> patch and barren ground habitat in Velavadar National Park. A female dominated blackbuck herd is seen moving between grassland patches through barren ground.	14
Plate 2b:	Saline habitat in Velavadar National Park.	14
Plate 3a & 3b:	Body parts used for ranking body condition of female blackbuck in the field.	30
Plate 4a & 4b:	Blackbuck fawn hiding in the grassland and lying out in a saline patch of land.	30
Plate 5:	Lactating blackbuck female with clearly visible teats and a non-lactating female with retracted teats that are not distinctly visible.	30
Plate 6a:	Sampling of blackbuck activity by scan sampling, using a spotting scope.	68
Plate 6b:	Female dominated mixed herds of blackbuck grazing and moving through grassland habitat in Velavadar National Park.	68
Plate 7a:	An enclosure put up in the grassland of Velavadar National Park to study the effects of grazing and grass harvesting on above-ground productivity and quality of grasses.	111
Plate 7b:	Harvesting of grass by local people in Velavadar National Park.	111

ABSTRACT

Grasslands and grassland ungulates are considered to be inter-dependant, often to have co-evolved, and the interactions between them substantially influence each other in various ways. In this study in Velavadar National Park (VNP), Gujarat, western India, conducted from October 1999 to January 2003, I investigated certain aspects of interactions between blackbuck (*Antilope cervicapra*) and the semi-arid grassland it inhabits. Specifically, I studied seasonality in calving, body condition and foraging activity of blackbuck and assessed the relationships of these with forage availability and quality. Additionally, I examined the effects of grazing and grass harvesting on above-ground productivity and quality of grasses in the study area.

I assessed the seasonal patterns in forage availability, quality and body condition of blackbuck females, and examined if changes in these variables influenced calving seasonality. Forage variables that were measured are above-ground grass biomass, moisture, crude protein, Acid detergent fibre (ADF), lignins and silica content of grasses. Body condition of females was assessed by visual ranking of body parts. Blackbuck were sampled in different blocks of the study area to estimate proportion of females lactating and this was used as a measure of proportion of females calving.

Above-ground grass biomass was highest in cold season, and moisture and crude protein content were highest in wet season. The other forage variables did not show substantial seasonal changes. Body condition of females was best in wet season and worst in dry season. Blackbuck calving was clustered during two separate periods of a year (dry and wet seasons), but a basal level calving (5 to 15%) occurred throughout the year. The calving (lactation) season lengths ranged from 7 to 15 weeks. The calving seasons appeared to be cyclical, occurred with an interval of 23 to 28 weeks between successive calving peak points, which corresponded with inter-calving interval in blackbuck. There was no evidence of calving synchrony in VNP.

Lactation status of females was not related to body condition ($B = -0.174 (\pm 0.18)$, Wald statistic= 0.94, $df = 1$, $P = 0.33$, $\exp(B) = 0.84$), but showed seasonality. Calving frequency, overall, was not strongly related to any of the predictor variables assessed, but the two calving peaks had

different relationships with the predictor variables. The dry season calving peak preceded the crude protein peak, and the wet season calving peak followed the crude protein peak, and coincided with high biomass availability and high body condition of females. The dry season calving peak was probably timed to the impending peak in forage quality, and the females that calved in the wet season perhaps provided greater maternal nutritional investment to the young.

I compared the seasonal changes in daily activity patterns, time investment in feeding and resting/ruminating activities, and examined if these were influenced by changes in air temperature, forage quality and quantity. Activity of blackbuck was sampled using scan sampling method. Each season, three herds were followed from dawn to dusk and their activities studied. Temperature was measured using an automatic temperature logger. Forage variables (grass biomass and moisture content, as a correlate of crude protein content) were measured in eight plots from the foraging range of each herd in each season. Over 60% of blackbuck spent their time feeding during 11 hours (out of 13 daylight hours) in wet season, 8 hours (out of 11 hours) in cold season, and 6 hours (out of 13 hours) in dry season. There was intensive feeding activity in the early morning, afternoon and late evening periods. Hourly changes in resting/ruminating activity had a pattern that was reverse to that of feeding activity. Blackbuck spent a major part of the day feeding (66%, 80% and 69% of daytime in dry, wet, and cold seasons, respectively). Feeding, resting/ruminating, and moving activities did not show significant seasonal differences, but showed significant differences among periods of day. Daily activity pattern of blackbuck showed a cyclical pattern, mainly alternating between feeding and resting/ruminating peaks. The air temperature did not seem to affect feeding activity, as blackbuck continued to feed during periods even when temperatures were high ($> 40^{\circ}\text{C}$). Time investment in feeding activity by blackbuck did not seem to have a relationship with either of the forage variables. This was probably because blackbuck spent a large proportion of time feeding in both periods, when forage quality and abundance were low and high. Also, the magnitudes of changes in forage quality among seasons were not large (a maximum of 2.3%

change in crude protein among all pairs of seasons) and therefore, it may not have been a strong factor to influence changes in time investment in feeding. It seems that blackbuck in VNP were influenced more by intake rate, rumination time, and other limitations posed by morphological and physiological attributes, rather than by seasonal differences in forage quality and quantity.

Lastly, I studied the effects of grass harvesting (biomass removal) and simulated grazing (biomass removal along with urine fertilisation) on above-ground productivity and quality (in terms of Nitrogen content) of grasses in VNP, by way of an experiment. Three levels of treatment – low, medium and high intensities of harvesting and grazing were applied to plots in 12 enclosures distributed systematically in the study area. The treatments were applied monthly, in the grass-growing season, and the experiment was conducted for two years (2000 and 2001-02).

All harvesting and grazing treatments increased above-ground biomass and Nitrogen content of grasses (as compared to maximum standing biomass), but there were no substantial differences among the different treatments. Small effect sizes and high variability in the treatment plots seems to have rendered the effect of treatments statistically not significant. Even after controlling for some of the variability by using grass-cover as a covariate, and accounting for variability in local environmental conditions by standardising the treatment biomass with maximum standing biomass, the magnitude of treatment effects remained uncertain. It seems that there might have been unknown factors such as root biomass, and soil quality that had confounded the effect of treatments and added to the variability, leading to equivocal results. In this study, the upper limits to harvesting and grazing, so as to maintain increased productivity of grasslands and at the same time control it from being over-grazed/harvested, could not be determined.

The results of this study, in addition to contributing to the knowledge on ecology of blackbuck and semi-arid grasslands, have many implications for conservation of grassland and blackbuck in VNP. These are discussed in this dissertation.

CHAPTER 1. GENERAL INTRODUCTION

Grasslands represent approximately one third of the earth's terrestrial surface and they are subject to varying degrees of pressures and management by humans (Verchot *et al.* 2002). As recently as 200 years ago, most of these grasslands supported large populations of wild ungulates. However, global expansion of cropland and increased fodder needs of livestock have greatly decreased the area of natural grasslands (Verchot *et al.* 2002). Most of the grasslands in India, as in other parts of the world, have been converted to croplands and the remaining grasslands have been highly degraded due to over-grazing by domestic livestock (Dabadghao and Shankaranarayan 1973, Misra 1979, Singh and Joshi 1979a, 1979b). These grasslands support high abundance and diversity of wild fauna and the decline of these grasslands would endanger the wild animals that depend on these habitats. This study is about certain ecological interactions between a large herbivore species and its habitat, a tropical semi-arid grassland. Specifically, I studied the effects of forage availability and quality on breeding seasonality and foraging activity of blackbuck (*Antelope cervicapra*) in Velavadar National Park (VNP), western India. Further, I studied the effects of grazing and grass harvesting on forage productivity and grass quality. This study is expected to lead to an improved understanding of these important aspects of ecology of grasslands and grazing ungulates. The results of this study have conservation implications and may contribute to theoretical knowledge.

Grasslands and grassland ungulates are considered to be inter-dependant, often to have co-evolved and the interactions between them substantially influence each other in various ways (McNaughton 1979, 1984, Owen-Smith 2002). Grassland ungulates depend on grasses for sustenance and grasses in turn are affected in their growth and form by ungulate use (McNaughton 1979, 1985, Milchunas *et al.* 1988, Milchunas and Lauenroth 1993, Hobbs 1996, Detling 1998). Grasses determine many aspects of the biology of grassland ungulates: their abundance, population dynamics, community structure and behaviour (Bell 1970, 1971, Jarman 1974, Sinclair 1977a, 1977b, 1979, Jarman and Sinclair 1979, McNaughton *et al.* 1988,

Owen-Smith 1994, 2002). Forage availability and quality have remarkable influence on reproduction of ungulates (Sadleir 1969, Sinclair 1977b, Rutberg 1987, Bronson 1989, Ims 1990a, Sinclair *et al.* 2000). The timing and frequency of reproduction, reproductive success, and recruitment of young are greatly determined by the abundance and nutritive quality of forage available in the habitat (Sadleir 1969, Field and Blankenship 1973, Sinclair 1977b, Rutberg 1987, Bronson 1989, Ims 1990a, Sinclair *et al.* 2000, Langvatn *et al.* 2004). Forage availability and quality also determine the physiological condition of individuals in a population, the time that they invest in foraging and other activities, and the social interactions among individuals (Jarman 1974, Kamil *et al.* 1987, Robbins 1993). Although grassland productivity is directly influenced by climatic factors to a great extent, ungulate grazing also affects their productivity and quality (Cumming 1982, Hobbs 1996, Frank 1998,). For example, moderate level of ungulate grazing is known to promote grass growth (McNaughton 1979, 1985, Augustine and McNaughton 1998), while high-levels of grazing deters growth (Detling 1988, Milchunas and Lauenroth 1993, Van de Koppel *et al.* 1997, Verchot *et al.* 2002). Further, ungulate grazing, by means of fertilization by urine improves the nutritive quality of grasses (Day and Detling 1990, Frank and McNaughton 1992, Ruess and Seagle 1994, Hobbs 1996, Frank and Groffman 1998). The complex interactions between grassland habitats and ungulates that inhabit them are thus important and interesting to study.

The present knowledge on breeding biology of ungulates is largely based on studies on African (tropical) and temperate ungulates (Dasmann and Mossman 1962, Sadleir 1969, Estes 1976, Rutberg 1987, Bronson 1989, Sinclair *et al.* 2000). Studies on grassland ecosystems and ungulates in India have been relatively few so far, and more studies on them could add to theoretical knowledge and an improved understanding of their ecology would aid in their conservation. Further, limited work has been done on ecological aspects of dry grasslands in India. The present knowledge on effects of grazing on dry grasslands is based on studies on African (McNaughton 1979, 1983, 1985, Van de Koppel *et al.* 1997), North and South American grasslands communities that include temperate and tropical grasslands

(Detling 1988, Frank and McNaughton 1992, Chaneton *et al.* 1996, Frank and Groffman 1998). Similar studies from Indian dry grassland ecosystems are urgently needed. Understanding the interactions between grasslands and ungulates would help in management, such that their interactions are sustained. Some of the ungulates and grasslands may have co-evolved and it is important to conserve the co-evolution partners for posterity. For an endangered ungulate, manipulation of an important forage component can impact or improve breeding success and an understanding of such interactions would be important for appropriate management of the habitat and for the conservation of the endangered ungulate. On the other hand, changes in grazing intensities would influence grassland productivity, by modifying the effects of the environmental variables, community structure and composition, and by affecting the interactions between different species of grass in the community (Detling 1988, Hobbs 1996). Therefore, knowing the effects of different intensities of grazing on grassland productivity and quality is essential for setting limits to grazing and thereby for conservation of grasslands and wild ungulates.

Blackbuck is a tropical antelope endemic to the Indian sub-continent. It is distributed widely in the Indian subcontinent and is commonly seen in some arid and semi-arid areas (Ranjithsinh 1989, Rahmani 1991). The biology of this antelope has been studied by a few researchers, but there is yet to be a study that concerns the interactions that it has with its grassland habitat. Arid and semi-arid areas in India experience seasonal changes due to monsoonal rainfall and consequently, the forage availability and quality too would vary among seasons. These changes could influence the blackbuck in various ways. It is important to understand the effects of varying forage availability and quality on reproduction, activity patterns and time budgets of blackbuck. Additionally, the effects of grazing and grass harvesting on the productivity and quality of grasslands need to be investigated, as these may have a great effect on reproduction and even survival of blackbuck. In this context, I studied certain aspects of interactions between blackbuck and its habitat in VNP. I examined whether calving seasons existed for blackbuck and whether this population showed synchrony in reproduction. I investigated whether

seasonal changes in forage availability and quality influenced reproduction in blackbuck. In addition, I studied the activity patterns and time budgets of female-dominated blackbuck herds, and examined if these were related to seasonal forage availability and quality. I further examined the influence of temperature on daily activity patterns of blackbuck herds. By way of an experiment, I investigated the effects of (i) different intensities of biomass removal (harvesting), and (ii) different intensities of grazing (biomass removal + addition of urine), on grassland productivity and grass quality in VNP.

In this dissertation; Chapter 2 contains a brief review of literature that forms the background for the hypotheses and discussion in this dissertation. Chapter 3 gives a brief description of the study area (VNP). In chapter 4, I describe the breeding seasonality in blackbuck and assess the influencing factors. In Chapter 5, I describe the activity patterns of blackbuck, time investment in foraging activity and assess the influence of forage availability and quality on these aspects of behaviour. In Chapter 6, I describe the effects of grazing and grass harvesting on grassland productivity and grass quality. Detailed introductions to the different aspects of this study are given in the respective chapters.

CHAPTER 2. REVIEW OF LITERATURE

2.1. EARLIER ECOLOGICAL RESEARCH ON BLACKBUCK

An early description of blackbuck behaviour and activity was made by Schaller (1967), based on his observations of a Central Indian population (Kanha National Park, Madhya Pradesh). He reported two rutting (lekking and display of males) and two calving seasons of blackbuck in a year. Mungall's (1978) monograph presented a review of research done by workers in different parts of the world on captive and introduced, free-ranging blackbuck. It is the most comprehensive report yet available on the biology of blackbuck. She detailed descriptions of age classification (from dentition and field observations), activity, anatomy, and lactation, and presented some information on certain aspects of physiology (e.g. oestrus cycle), based on her studies on introduced populations in Texas, U. S. A. Later, Ranjithsinh (1989) reviewed the distribution and population status of blackbuck in India, based on personal observations and from Forest Department records. Rahmani (1991) compiled information on distribution and populations of blackbuck in India based on information collected during the Great Indian bustard (*Ardeotis nigriceps*) survey that he had undertaken, and from Forest Department records and various literature.

Studies on aspects of blackbuck ecology and behaviour that are relevant to this study are summarised here. Prasad (1985) examined the activity budgets of a blackbuck population occupying an agrarian landscape in Mudmal, Andhra Pradesh. Some time periods of the day in certain seasons were not sampled during that study and his observations seem to have been made largely opportunistically. He did not find any seasonal variation in time investment in feeding by blackbuck. Feeding activity constituted the greatest proportion, however, it was much lower than what has been generally reported for ruminant ungulates in the tropics (Owen-Smith 2002). Chattopadhyay and Bhattacharya (1986) studied the seasonal diet of blackbuck population in Ballavpur in West Bengal, India, based on faecal pellet analysis. They reported seasonal shifts in diet of blackbuck, similar to

that reported by Schaller (1967) in Kanha National Park and Mungall (1978) in Texas. Howery *et al.* (1989) reported that the blackbuck in Texas calved throughout the year, without any distinct monthly or seasonal pattern. Jhala (1991) studied the habitat and population dynamics of wolf and blackbuck in VNP. He studied the nutritional ecology of blackbuck in VNP using feeding trials (Jhala 1997), and made detailed observations on captive animals, complementary to field observations. He found seasonal changes in digestibility of forage, in addition to seasonal changes in their diet in VNP. Isvaran and Jhala (2000) studied the lekking behaviour of blackbuck in VNP and Isvaran (2003) assessed the mating strategy in blackbuck and reported lekking to be a flexible mating system in blackbuck. With this background of information that was available on blackbuck behavioural ecology, this study was planned. Its focus was on reproductive seasonality in blackbuck, activity patterns and time investment in different activities, and the effects of harvesting and grazing on grassland productivity and quality in VNP.

2.2. SEASONALITY OF CALVING

One of the aspects examined in this study is the reproductive seasonality in blackbuck in VNP (Chapter 4). Climatic factors (such as rainfall, photoperiod, temperature, and humidity), ecological factors (such as food abundance and population density), and social factors (socially induced oestrus cycles that are commonly seen in mammals, McClintock 1978) have been suggested to be responsible for seasonal reproduction in animals (Sadleir 1969, Bronson 1989, Ims 1990a). Although internal cues or existence of endogenous rhythms as cues for seasonal reproduction has been suggested, evidence is sparse and it has remained difficult to test these hypotheses (Ims 1990a).

Seasonal and synchronised reproduction is commonly seen in mammals, and is especially common in ungulates, both in the temperate and tropical regions (Sadleir 1969, Estes 1976, Rutberg 1987, Bronson 1989, Ims 1990a, Sinclair *et al.* 2000, Langvatn *et al.* 2004). Ims (1990a) divided the causal factors for seasonal and synchronised reproduction into two types: socio-biological and ecological. Socio-biological causes include factors such as communal foraging, where births are synchronised to optimise search for

feeding areas or maternal defence. Ecological factors would include factors such as food abundance and quality, predation, and density dependant factors (Emlen and Oring 1977, Ims 1990a, 1990b, Langvatn *et al.* 2004, Keyser *et al.* 2005). Food availability and quality have been reported to influence seasonality in reproduction. Both food and predation have been reported to cause synchronised birthing (Rutberg 1987, Ims 1990a, Ims 1990b, Sinclair *et al.* 2000).

The environment affects forage availability and quality, and these, in turn, are expected to greatly influence reproduction, as the process of reproduction is energetically demanding for ungulates (Sadleir 1969, Sinclair 1977b, Bronson 1989, Robbins 1993, Schmidt-Nielsen 1997, Pekins *et al.* 1998, Sinclair *et al.* 2000). In the temperate areas, seasonality in reproduction is more pronounced, since high quality food is available only for a short period (Bronson 1989, Langvatn *et al.* 2004). In the tropics, seasonal rainfall affects food abundance and quality, which in turn affects reproduction (Field and Blankenship 1973, Jarman 1974, Sinclair 1977b, Sinclair *et al.* 2000). Several species of tropical ungulates have been reported to have a seasonal pattern of reproduction (Dasmann and Mossman 1962, Field and Blankenship 1973, Sinclair 1977b, Rutberg 1987, Sinclair *et al.* 2000).

Studies have shown that some ungulate species employ synchronised reproduction as a unique anti-predatory strategy called “predator satiation” (Estes 1976, Rutberg 1987, Bronson 1989, Ims 1990a, Sinclair *et al.* 2000). For example, the wildebeest (*Connochaetus taurinus*) in Serengeti, give birth to highly conspicuous and precocial young and all births occur within a span of seven to ten days. Consequently, the predators are swamped with numerous newborn prey and can only predate a limited fraction of the newborns from the population (Kruuk 1972, Estes 1976). Additionally, with prey being plentiful, the predator is also confused about selecting prey (Ims 1990a). By following this strategy, wildebeest ensure survival of a definite percentage of offspring each year.

Rutberg (1987) examined reproductive seasonality and synchrony in 27 species of ruminant ungulates. He classified these species into two ecologically distinct groups, as 'hidiers' and 'followers'. 'Hidiers' were those species in which the newborn young were hidden, concealed or inconspicuous. 'Followers' were those with highly conspicuous, precocial newborn that would follow the mother immediately after birth. He found that the reproductive pattern in the 'hidiers' group was influenced by climatic seasonality and synchronised reproduction in 'followers' group was an anti-predatory strategy. Geist (1981) in his review of reproductive strategies in ungulates also suggested the same. The most commonly accepted theory for seasonal reproduction in ungulates seemed to be food related, but there has been no unanimity on synchronised birthing. In this context, and conceding that blackbuck live in a seasonal environment, and have hiding newborn (Mungall 1991), I studied the influence of food availability on reproduction in blackbuck, and examined the results based on the above-mentioned hypotheses suggested for reproductive seasonality and synchrony.

2.3. ACTIVITY PATTERNS AND BUDGETS

Ungulates divide a day's time for various activities that include foraging, resting, travelling, vigilance, and other social interactions (Jarman 1974, Alcock 1984, Bunell and Gillingham 1985, Lucas 1987, Bunell and Harestad 1989). The daily activity pattern of an ungulate is influenced by energy requirements, distribution of food, predators and thermal stress (Bunell and Gillingham 1985, Parker and Robbins 1985, Bunnell and Harestad 1989, Schmidt-Nielsen 1997). The time spent by ungulates in different activities is influenced by two major factors: the energy demands of the ungulate and the constraints that the ungulate encounters (Bunnell and Gillingham 1985, Lucas 1987, Bunnell and Harestad 1989, Dove 1996). The former would be influenced by age, sex, weight, and physiological state of an ungulate (Hudson and White 1985, Robbins 1993, Schmidt-Nielsen 1997). The latter would encompass daylight time, ambient temperature, anatomical (such as type of mouth parts and size of rumen) and metabolic attributes, potential predation, time demands of social interactions such as displays and mother-young interactions (Jarman and Jarman 1973, Jarman 1974, Underwood

1982, Sih 1992, Spalinger and Hobbs 1992, Krebs and Davies 1993, Caro 1994, Owen-Smith 1994, 2002, Fitzgibbon and Lazarus 1995). Importantly, abundance, quality, and distribution of forage, in time and space, would greatly influence the activity patterns and time investment of ungulates in different activities (Arnold 1985, Bunnell and Gillingham 1985, Lucas 1987, Bunnell and Harestad 1989, Robbins 1993, Dove 1996). Low abundance of food would result in higher time spent searching for it and low quality of food would lead to lower energy gained per unit food ingested, and also higher would be the time invested in searching for appropriate food (Arnold 1985, Bunnell and Gillingham 1985, Robbins 1993, Dove 1996, Owen-Smith 2002). The spatial distribution of forage would affect the movement of ungulates from one patch to another and also the time spent searching for these patches (Stephens and Krebs 1986, Kamil *et al.* 1987, Lucas 1987, Owen-Smith 2002). This search for food patches may lead them to areas of high predation risk and thereby they might need to invest more time being vigilant against predators (Underwood 1982, Sih 1992, Krebs and Davies 1993, Caro 1994).

High ambient temperature could place thermal stress on ungulates and may affect their daily activity patterns, and in particular, their foraging activity (Parker and Robbins 1985). Foraging increases thermal load through muscular activity and exposure to direct and indirect solar radiation. The higher the ambient temperature over body temperature, the more difficult it is to dissipate heat (Schmidt-Nielsen 1997). In ruminant ungulates, body size determines the rumen size and capacity (Demment and Van Soest 1985). The rumen capacity limits the amount of food an ungulate can ingest at any given time. Therefore, once the rumen is full, the ungulate would not be able to ingest more food until the rumen can accommodate more food. This process of rumen digestion, therefore, influences the intake rate of food in ungulates and determines the pattern in feeding activity (Arnold 1985, Bunnell and Gillingham 1985, Robbins 1993, Dove 1996, Schmidt-Nielsen 1997, Owen-Smith 2002). Food quality would greatly influence the processing efficiency of the rumen. Lower the nutritive quality, longer is the processing time. Further, mouth morphology would determine the food type (browse or graze) and food intake amount (bulk feeder or selective feeder; Jarman 1974,

Arnold 1985, Bunnell and Gillingham 1985, Spalinger and Hobbs 1992). The influences of such physiological and ecological factors, particularly that of forage quality and abundance on the activity patterns of blackbuck were yet to be studied, even descriptively. With this background, I examined the activity patterns of blackbuck and their time investment in different activities.

2.4. EFFECT OF UNGULATE GRAZING AND GRASS HARVESTING ON GRASS PRODUCTIVITY AND QUALITY

Studies on Indian semi-arid grasslands has largely been on evaluating primary productivity (Misra and Misra 1984, Shankaranarayan *et al.* 1985, Karunaichamy and Paliwal 1989, Singh *et al.* 1991). Dabadghao and Shankaranarayan (1973) gave a detailed compilation of grass cover of India, dominant grass communities and some associated ecological characteristics, such as the effects of grazing on some taxonomic groups of grasses. Singh and Joshi's (1979b) compilation of Indian grasslands, as a part of the International Biological Programme (IBP), was an important source of data on grassland productivity and protein content of grasses from different areas in India. Studies assessing the effects of ungulate grazing or grass harvesting by humans on grassland productivity and quality are few, particularly so in the semi-arid grasslands.

Most theoretical work and empirical evidence for the effect of grazing and harvesting are from studies carried out in East Africa, North America and Argentina (Day and Detling 1990, Frank and McNaughton 1992, Chaneton *et al.* 1996, Augustine and McNaughton 1998, Detling 1998, Frank 1998, Frank and Groffman 1998). Long term work in the Serengeti grassland in East Africa provided evidence that low to moderate level of grazing by wild ungulates has a positive feedback on grasslands (McNaughton 1977, 1979, 1983, 1985, 1988, McNaughton *et al.* 1996, McNaughton *et al.* 1997, Augustine and McNaughton 1998). There was increased biomass productivity and the mineralization process was accelerated. In addition, movement of nutrients from below ground parts of grasses to above-ground parts occurred. Natural rotational grazing by migratory ungulates, grazing heterogeneity (differences in parts of grasses eaten), grazing patterns and

feeding behaviour of different ungulate species had profound effects on grassland productivity, community structure and nutrient cycling (McNaughton 1977, 1983, 1984, 1985, 1988, 1990, McNaughton *et al.* 1988, Van de Koppel *et al.* 1997, Verchot *et al.* 2002). For example, selective versus non-selective grazing changed the community structure of grasslands, affected the ratios of palatable to non-palatable species, and perennial species were replaced by annual species of grasses (Detling 1988). Additionally, variability in spatial use of ungulates depositing minerals on to the soil through urine and faeces caused varying concentration of nutrients (McNaughton 1988, Day and Detling 1990).

By conducting *in situ* and *ex situ* experiments, McNaughton and his colleagues (McNaughton 1979, 1984, McNaughton *et al.* 1988, Frank and McNaughton 1992, Ruess and Seagle 1994, McNaughton *et al.* 1997, Williams *et al.* 1998), showed that low to moderate level grazing by ungulates in Serengeti enhances productivity of grasses and also has a positive effect of feedback of nutrients to the grassland. However, Milchunas and Lauenroth (1993) analysed data from 236 sites across the world and found that grazing history, consumption levels by the ungulates and productivity of the region play a significant role on the effect of grazing on productivity. When the natural productivity was low, the effect of grazing was significant and when consumption levels were high, difference in productivity between grazed and ungrazed areas was small. Additionally, harvesting the top layer of grasses also enhances productivity (Hilbert *et al.* 1981). This happens due to increased penetration of light and consequent increased photosynthetic rate and increased tillering (lateral bud) growth.

In arid high altitude moist sedge meadows (*Carex infuscata* – *Kobresia royleana* type) of the trans-himalayas in India, Mishra *et al.* (2001) found that under grazing *K. royleana* tussocks disintegrated and were replaced by members of the *Poaceae* family. The graminoid vegetation that was stimulated to grow after the top layer of sedge was removed by herbivore grazing, gets further grazed to ground level under increasing grazing pressure. Therefore, intensive grazing reduced graminoid biomass greatly as

compared to moderately grazed patches in this study. Grazing has been known to enhance productivity under a certain set of conditions, but it could also have negative impacts on rangelands, leading to their degradation. In the dry grasslands of Sahel region of northern Africa, grazing pressure has destroyed the grasslands so greatly, that sustained restoration efforts have also failed (Sinclair and Fryxell 1985, Van de Koppel *et al.* 1997). Such dry arid and semi-arid grasslands are known to be extremely vulnerable to grazing pressures (Van de Koppel *et al.* 1997, Weber *et al.* 1998, Weber and Jeltsch 2000). Theoretical simulation models also suggest that once rangelands completely degrade, restoration cannot be attained in a practical time scale (Friedel 1991, Laycock 1991).

Management of rangelands and pastures is being practiced by various methods such as rotational and deferred grazing, controlling stocking densities, and weed control in North America (Reardon and Merrill 1976, Laycock 1991, Cassels *et al.* 1995, Irby *et al.* 2002). Despite long term research and theoretical studies on the effects of ungulate use (both domestic and wild) of grasslands and rangelands, there seems to be no unanimity on the thresholds to grazing and harvesting. This is because the long-term effects of management practices and the complex interactions are still not completely understood (Friedel 1991, Laycock 1991, Glasscock *et al.* 2005). Also, comparisons of forage productivity between natural and managed rangelands was not found useful to aid management since the vegetation in natural areas respond differently to grazing than rangelands (Reardon and Merrill 1976). Different sites would have different susceptibilities to change (Friedel 1991) and therefore, any management measure has to be site specific, and should be made after detailed investigations. Although limited information was available from studies carried out within India, many studies from ecologically similar regions were referred to, for forming the working hypotheses of this study. With this background information, I examined the effect of grazing and grass harvesting on the grassland productivity and quality in VNP.

CHAPTER 3. STUDY AREA DESCRIPTION

LOCATION

Velavadar National Park (VNP) is located between N 22° 1.5', E 72 ° 1' and N 22° 5' and 72 ° 5.5' in Saurashtra region of the western Indian State of Gujarat (Fig. 3.1). It covers an area of 34.08 km² (Gujarat Forest Department Management Plan for Velavadar National Park 2002) of which about 8 km² is grassland and the remaining is comprised of patches of *Prosopis juliflora* and saline land (Plate No.1, 2a and 2b). VNP is part of an eco-region called the *Bhal*, which in Gujarati means "flat as the forehead". The *Bhal* region extends northwards up to *Dholka* (N 22° 43' and E 72° 28'), northwest up to *Limbdī* (N 22° 39' and E 71° 48'), east to Gulf of *Cambay*, and on the south up to the River *Kalubhar* and covers an area of 2590 km² (Dharmakumarsinhji 1978, Jhala 1991).

GEOMORPHOLOGY

The *Bhal* is a flat alluvium plain, its land cover is composed of a mosaic of agricultural fields, saline wastelands, grazing lands and marshy inter-tidal areas. The soil cover are considered to be silt deposits from Rivers *Narmada*, *Mahi*, *Sabarmati*, *Sukhbadar*, *Bhogavas* and rivulets like the *Kalubhar* and *Alang*. The *Bhal* region is believed to have emerged from the sea during the late Tertiary and Quaternary period, much later than the rest of the *Saurashtra* region (Raychaudhari *et al.* 1963, Jhala 1991). The soil type of the region has been described as recent coastal alluvium soil (Dabadghao and Shankaranaryanan 1973, Singh and Joshi 1979a) and that of VNP has been described as clayey loam (Ranjithsinh 1989). The soils are fine textured and heavy, have a high water holding capacity (68.6%, SE 2.2%), and are alkaline (Satyanarayana 1985, Ranjithsinh 1989, Jhala 1991). This has been attributed to the tertiary and quaternary origins of the *Bhal* region and the semi arid climate (Raychaudhari *et al.* 1963).

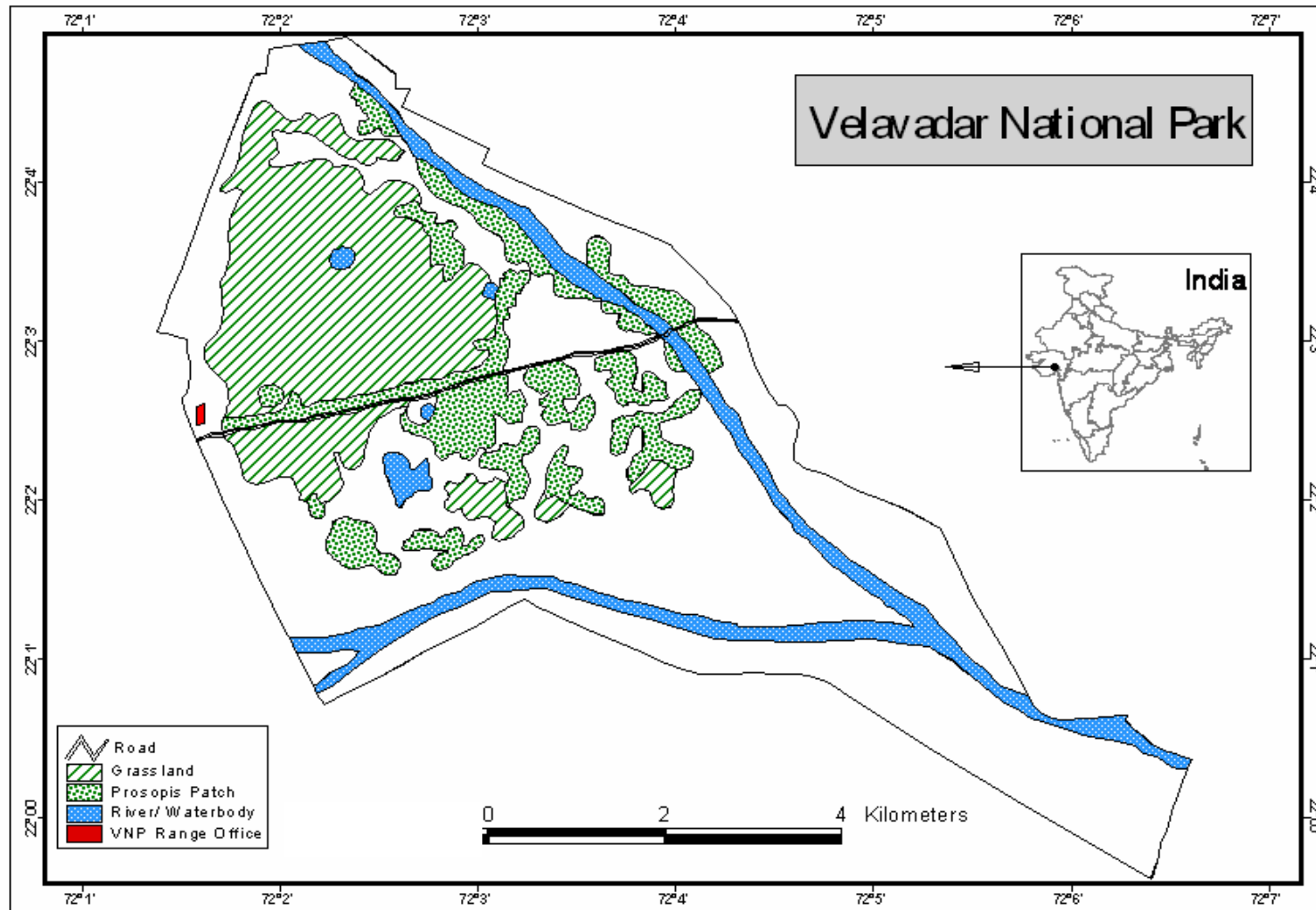


Fig. 3.1. Map of Velavadar National Park. Solid black lines mark the boundary of the Park. Black double-line marks a main road. The white space within the Park boundary is mainly comprised of barren saline land, interspersed with small patches of short grass and other shrubs. Inset map shows VNP's location in India.

Two rivers, *Alang* and *Paravalio* flow through VNP. *Alang* joins the Gulf of *Cambay* and contains inter-tidal water during a major part of the year. During the monsoon, fresh water flows in it for a short period. *Paravalio* has a check dam built by the Forest Department to prevent the fresh water collected during the monsoon to flow into the sea. Once the monsoon is over the ground salinity dissolves into the collected fresh water, and consequently, the water of *Paravalio* becomes brackish. There are no fresh water sources in VNP other than the water holes dug out to collect rainwater.

CLIMATE

Three seasons can be distinguished in the study area: Dry, Cold and Wet seasons. Dry season begins from March to May. In this season, the temperature ranges from 37 °C to 44 °C, sometimes reaching as high as 48-50 °C. Hot winds and dust storms are common in the dry season. Wet season is from July to September and almost all the precipitation occurs during the monsoon in this season. The average annual rainfall in VNP is 468 mm (Ranjithsinh 1989). During a good monsoon, most areas of the *Bhal* and a large area of VNP becomes waterlogged. Cold season begins in November and continues until January. In the cold season, temperatures range from 1 °C to 38 °C, and dew is common during this season. Months of February, June and October are transient periods occurring between the distinct seasons. The eco-climate computed for VNP by the method of Thornwaite and Mather (1955) is semi-arid (Ranjithsinh 1989).

CROPLAND CULTIVATION

Crop cultivation in the *Bhal* region is highly dependent on the monsoon rains, as the ground water in this area is saline. Cultivation is generally done just after the monsoon rains when fresh water becomes available. Main crops grown are cotton and sorghum and mainly salinity tolerant and drought resistant varieties are grown in this region. Cotton is grown during a good monsoon year or in areas where fresh water is available (from

nearby streams etc.), and in other areas, mostly sorghum is grown. Wheat is occasionally grown, in years with high rainfall.

FLORA

VNP is a densely covered grassland (Plate No.1) surrounded by areas that remain barren for most part of the year except during the wet season when crops are cultivated. VNP has patches of *P. juliflora*, an exotic woody shrub, interspersed in the grassland. *P. juliflora* has spread rapidly and invaded a large area of the *Bhal* during the recent decades. Some patches of *Acacia nilotica* trees are also found in the VNP. The dominant perennial grass species in VNP are *Dicanthium annulatum*, *Sporobolus madraspattensis* and *S. virginicus*. *S. coromandialis*, an annual grass, is found in saline areas in VNP, and in overgrazed barren patches outside VNP. The most dominant grass species in VNP is *D. annulatum*, which is known to grow successfully in such saline, semi-arid areas that are protected from grazing (Dabadghao and Shankarnarayan 1973). *Chloris barbata*, a perennial grass species is dominant in saline areas of VNP and *Aristida funiculata*, another perennial species is seen in small patches in the grassland. Most of these species are C₄ grasses, which commonly occur in such semi-arid areas (Medina 1982). *Seuda nudiflora* is a perennial halophyte that is dominant in the saline areas, and is found in association with *C. barbata*. During the wet season, many annual grass species and a few dicot plants grow in VNP (Appendix 1).

FAUNA

VNP has one of the largest populations of blackbuck in India (Rahmani 1991). Number of blackbuck reported here are greater than 1000 (Jhala 1999). This antelope is the most common of large mammals found here. Other ungulate species that are seen here are nilgai, *Bosephalus tragocamelus* and wild pig, *Sus scrofa*. The largest carnivore found in VNP is the grey wolf *Canis lupus (pallipes)*. The golden jackal, *Canis aureus*, Indian fox, *Vulpes bengalensis*, and jungle cat, *Felis chaus*, are the other wild carnivores that are found in VNP. Other small mammals

that are commonly found in VNP are desert hare, *Lepus nigricollis* (*dayanus*), grey mongoose, *Herpestes edwardsii*, five-striped palm squirrel, *Funambulus pennanti*, Indian gerbille, *Tatera indica*, and Indian porcupine, *Hystrix indica*.

VNP is also well-known for its avifauna. The endangered lesser florican, *Sypheotides indica* breeds in VNP during the wet season and the chestnut bellied sandgrouse, *Pterocles exustus* breeds here in the dry season. The short-toed snake eagle, *Circaetus gallicus* is a resident species in VNP. Other birds of prey that are commonly seen here are common kestrel, red headed merlin, black shouldered kite, steppe eagle, etc. White storks, *Ciconia ciconia*, common cranes, *Grus grus*, demoiselle cranes, *Grus virgo*, and three species of harriers, montagu *Circus pygargus*, pallid, *C. macrourus* and marsh *C. aeruginosus* are winter visitors to VNP. Several other migratory bird species, mostly water birds and grassland birds arrive in VNP after the monsoon rains.

PARK MANAGEMENT

In VNP, the Park management is mainly occupied with habitat management and protection, and does not directly manage animal populations. The Park management regulates *P. juliflora* cover by clearing the saplings and uprooting the shrub that invades into grassland areas. Some patches of *P. juliflora* are maintained, because the wolves are known to use these patches as cover (Jhala 1991). Since 1996, the Park management has been planting an indigenous tree species, *Salvadora persica* in different parts of the Park to eventually replace *P. juliflora* cover (Gujarat Forest Department Management Plan for Velavadar National Park 2002). The management also undertakes soil conservation and grassland regeneration work, and makes water conservation trenches in the barren and saline patches of the Park. In the dry season, the management provides water for animals by filling fresh water in man-made water holes (called 'guzzlers'). The Park management allows harvesting of grass by people from neighbouring villages in January and February of

every year (Gujarat Forest Department Management Plan for Velavadar National Park 2002).

HISTORICAL PROTECTION

VNP was a hunting preserve and grazing land (called *vidi*) of the erstwhile royalty of Bhavnagar and has probably been protected from use by local people for several decades (Ranjithsinh 1989). After independence, it was acquired by the Government of India and was declared a wildlife sanctuary in 1969. It was given the status of a National Park in 1976.

CONSERVATION THREATS

Most parts of the *Bhal* region are barren, except for VNP, which exists as an island of grass. VNP is surrounded by villages on all sides, where a large proportion of human population subsists on cattle rearing. The density of livestock in this region is very high (livestock population of Gujarat State and Bhavnagar District in 2003 were 14,322,591 and 648,432 respectively, stocking density for Bhavnagar district was 68 livestock head/ km²; URL: <http://www.indiastat.com, September 2004>). There is high pressure on VNP for cattle fodder, especially during the dry season, when the fodder shortage in the region becomes acute. Domestic dogs from the surrounding villages enter the Park and prey on blackbuck, and especially on calves. They also scavenge on kills made by wolves and jackals. In addition, the dogs are also potential carriers of disease to wild animals. Poaching, on a small scale, occurs in the peripheries of the Park and in other reserve forest areas in the *Bhal*. The *Bhal* is a flat landscape and most areas become waterlogged in the wet season, including a large part of VNP. There are only a few high grounds where blackbuck and other animals can take shelter when inundation occurs after the monsoon rains. During years of high rainfall, many animals are known to die by drowning.

CHAPTER 4. SEASONALITY OF CALVING IN BLACKBUCK IN THE GRASSLANDS OF VELAVADAR NATIONAL PARK

4.1. INTRODUCTION

Many mammals show seasonal variation in their reproduction. Reproduction may occur clustered during some part of the year and may even be dramatic with all the population's reproduction occurring during a distinctly short, restricted part of the year. The former type of reproduction is termed as seasonal form of reproduction and the latter is called synchronised reproduction (Sadleir 1969, Bronson 1989, Ims 1990a). Sometimes, seasonal clustering may be absent entirely and birthing might occur throughout the year. This is termed as aseasonal or continual form of reproduction. Breeding patterns, whether aseasonal, seasonal, synchronised or asynchronised, sometimes vary among populations of a species inhabiting different environments (Bronson 1989, Sinclair *et al.* 2000). Seasonal clustering of reproduction happens because certain times of the year may be better for offspring survival. This is frequently seen in environments where there are seasonal peaks in resource availability (Sadleir 1969, Field and Blankenship 1973, Iason and Guinness 1985, Rutberg 1987, Ims 1990a, 1990b, Cook *et al.* 2001). Synchronised birthing occurs when birthing is highly co-ordinated among the females in a population. Seasonal peaks in resource availability or seasonal weather patterns may often not explain synchronised breeding. Factors like predation pressure, need for migration or social behaviour (as seen, e.g., in wildebeest *Connocheates taurinus*, bank swallows *Riparia riparia*, moose *Alces alces*, African buffalo *Syncerus caffer*, musk oxen *Ovibos moschatus*) may often cause reproductive synchrony (Emlen and Demong 1975, Estes 1976, Emlen and Oring 1977, Rutberg 1987, Ims 1990a, 1990b).

Animals time their breeding during the seasonal peaks in resource availability. This timing of breeding could be an adaptive strategy of animals to increase offspring survival (Estes 1976, Rutberg 1984, 1987, Ims 1990b, Berger 1992, Krebs and Davies 1993). Theoretical biologists studying

adaptiveness of behaviour have examined the various advantages and disadvantages of various forms of seasonality and synchrony (McClintock 1978, Knowlton 1979, Rutberg 1987, Ims 1990b, Rhine 1995). Although population benefits of seasonal and synchronous birthing are known, the individual costs and benefits are still not fully understood (Berger 1992). Also, the several hypotheses that exist for explaining reproductive seasonality and synchrony, which include both ecological and socio-biological factors (such as seasonal climate, seasonal availability of food, predator swamping strategy, density-dependent effects, social foraging, maternal defence etc.), have not been tested for many species (Ims 1990a).

Ungulates, especially, show highly diverse birthing patterns, ranging from a completely aseasonal birthing, as in white-tailed deer (*Odocoileus virginianus*) in Florida keys, Burchell's zebra (*Equus burchelli*), common duiker (*Sylvicapra grimmia*) and steenbuck (*Raphiceros campestris*) (Dasmann and Mossman 1962, Bronson 1989), to a highly seasonal birthing as in nyala (*Tragelaphus angasi*, Anderson 1979, 1984), giraffe (*Giraffa camelopardalis*, Field and Blankenship 1973, Bronson 1989, Sinclair *et al.* 2000) and pygmy antelope (*Neotragus batesi*, Feer 1982). Synchronised birthing has been observed in wildebeest (*C. taurinus*) of Serengeti plains, eastern Africa (Kruuk 1972, Estes 1976), American bison (*Bison bison*, Berger 1992, Berger and Cain 1999), barren ground caribou (*Rangifer tarandus*, Dauphine and McClure 1974) and red deer in Norway (*Cervus elaphus*, Langvatn *et al.* 2004). Ecological factors such as seasonal resource availability and sociobiological factors such as offspring defence (Rutberg 1987, Ims1990a) and offspring behaviour (Geist 1981) have been stated to be some causes of birth seasonality and synchrony. Social stimulus in group-living animals on the physiological onset of oestrus has also been suggested as a cause in certain species. There is airborne communication about the onset of oestrus among females, consequent to which all females in the group may come into synchronised oestrus (McClintock 1978). The possible causes for seasonal or synchronised breeding may differ among temperate, subtropical and tropical ungulates (Rutberg 1987, Bronson 1989). In temperate areas, winter survival of calves, in addition to good forage

availability have been cited as causes (Festa-Bianchet 1988, Bowyer 1991, Rachlow and Bowyer 1991, Linnell and Andersen 1998, Cook *et al.* 2001, Langvatn *et al.* 2004). High predation pressure has been found to be a cause of synchrony in births among ungulates in both tropics and temperates (Estes 1976, Rutberg 1987, Ims 1990b, Gregg *et al.* 2001). In the tropics, wildebeest of the Serengeti plains synchronise birthing (to a 2-week period) to swamp and satiate the predators with prey. This is considered as an anti-predatory strategy adopted by this population to increase offspring survival (Estes 1976, Sinclair *et al.* 2000).

In many tropical ungulates, seasonality of forage quality has been found to be a main cause of seasonal reproduction (Bell 1971, Field and Blankenship 1973, Rutberg 1987, Sinclair *et al.* 2000). Seasonal factors such as rainfall affect habitat quality and productivity, which in turn affect herbivore population dynamics and reproductive success (Sinclair 1977a, Huntley and Walker 1982, McNaughton 1983, Sinclair *et al.* 2000). Nutrition plays a very important role in animal reproduction, since reproductive costs are high and consequently, the nutrient requirements are high. Females giving birth would need high quality forage, with sufficient energy and protein content, since gestation and lactation are energy and protein demanding physiological processes (Oftedal 1985, Robbins 1993, Schmidt-Nielsen 1997, Cook *et al.* 2001). Many ungulates are known to tune their reproductive and other energy and protein demanding activities to peaks in forage quality (Robbins 1993). Newborn offspring would need good quality nutrition, in particular, protein, for survival and growth. Also, protein requirement for weanling animals is known to be much higher as compared to nursing animals (Robbins 1993). This is because the dry matter protein in mothers' milk meets the requirements of the nursing young, whereas, the weaned young would have to obtain the required protein by foraging. The adult animals require much less protein as compared to the growing young, but a minimum amount is still required to meet the maintenance and activity costs (Robbins 1993, Schmidt-Nielsen 1997). There are seasonal differences in body condition of ungulates that are influenced by changes in forage quantity and quality (Fryxell 1987, Bronson 1989, Berger 1992, Robbins 1993, Parker *et al.* 1999, Sinclair *et al.* 2000, Cook *et al.*

2001). Thus, many aspects of physiology and ecology of ungulates seem to be greatly affected by changes in availability and quality of forage (Bunnell and Gillingham 1985, Hudson and White 1985, Robbins 1993, White 1993, Dove 1996, Schmidt-Nielsen 1997, Sinclair *et al.* 2000, Cook *et al.* 2001, Langvatn *et al.* 2004). However, in some species, seasonal reproduction has been found to be absent despite peaks in resource availability (Dasmann and Mossman 1962, Bronson 1989, Sinclair *et al.* 2000). Therefore, the determinants of seasonal or synchronised breeding pattern may be various and are still not fully identified for many ungulates (Rutberg 1987, Ims 1990a). In the Indian sub-continent, a variety of ungulate species occur and there is a possibility of reproductive seasonality in many of them, driven by seasonal resource variability caused by the monsoonal climate. However, only a few ungulate species in a few areas have been studied and their reproductive patterns and causal factors assessed (Rice 1988, Shankar Raman 1998).

Blackbuck, inhabits arid and semi-arid areas, which are characterised by seasonal, low and annually highly variable rainfall (Singh and Joshi 1979a). Consequently, there may be a marked seasonality in forage growth and quality in these habitats. VNP, a semi-arid grassland holds a large population (approximately 1200) of wild blackbuck (Ranjithsinh 1989, Jhala 1991, Rahmani 1991). Grass growth in VNP may be highly dependent on monsoon rains and consequently the forage availability and quality may have a marked seasonality. For instance, Jhala (1997) reported seasonal lows (dry as compared to wet season) in forage quality (crude protein content) in VNP and suggested that this caused low forage consumption and nutrient digestibility of blackbuck in that season of low forage quality. Seasonal birthing has been observed in blackbuck (Prakash 1960, Schaller 1967, Mungall 1978, Ranjithsinh 1989, Jhala 1991), however, it has not been studied in detail and the patterns and causes of it have not been examined. Inhabiting an area that is semi-arid, drought prone and a climate that is highly seasonal, blackbuck reproduction in VNP might be strongly influenced by the seasonal quality of nutrition. I further expected that calving in blackbuck might be synchronised because forage availability and quality would be higher for a short period of the year, coinciding with the monsoon rains. The known

blackbuck predators in VNP are wolves, jackals, semi-feral domestic dogs and jungle cats, of which the latter three predate mostly on calves. The blackbuck calves have a “lying out” period and are well camouflaged, but also follow their mothers for short durations (Mungall 1991). This behaviour of the calves falls in the “hider” category described by Geist (1981).

I studied the seasonality of blackbuck calving in VNP and examined whether birth synchrony exists for this species in the study area. I assessed the seasonal patterns in forage availability and quality, and body condition of blackbuck females, and examined if calving seasonality was influenced by changes in forage availability, quality and body condition of females. Since, this is an initial study on these aspects of reproductive ecology of blackbuck and on seasonality of the habitat, it is generally exploratory in nature.

The hypotheses that I tested are:

- Calving frequency would be positively related to forage availability (above-ground biomass) and quality (specifically, crude protein content) and would be negatively related to indigestible matter in forage.
- Body condition of blackbuck females would be higher during seasons of high forage quality.
- Calving frequency would be positively related to body condition of females.

4.2. METHODS

Rainfall

Rainfall was measured using a graduated rain gauge (Tru-check, Edwards Mfg. Co., Minnesota, U. S. A.). This gauge was mounted on a 6 feet high pole, placed in the open grassland of VNP. It was monitored every rainy day during 2001 and 2002 and the rainfall was directly read from the scale on the gauge.

Seasons in VNP

I classified the seasons in VNP as dry (March to May), wet (July to September) and cold (November to January) seasons. The months of February, June and October are transitional months with high variability in climatic factors that influence the seasons (e.g. the date of onset of monsoonal rains varies) and so were not used in the analysis of seasonal effects. But data from these transitional months were used in other analyses of relationships. The amounts of moisture content in the grasses of VNP were used as an aid to classify seasons in this biologically appropriate way.

Forage availability and quality

The forage availability for blackbuck in VNP was measured in terms of above-ground grass biomass and quality in terms of crude protein content and indigestible matter (acid detergent fibre, lignins and silica) content in the grasses. Biomass was estimated for grass and browse, forage quality variables only for grass, as it was the predominant food. These measurements were done from August 2000 to December 2002 in VNP.

The grassland area of VNP (about 8 km²) was divided into 12 equal-sized blocks (approximately 0.64 km² each). Above-ground biomass was estimated by harvesting the grass inside two randomly laid plots (size 0.5m x 0.5m) within each block, totalling 24 plots harvested for each month. The wet (fresh) biomass was weighed with a Pesola spring balance (PESOLA, Pesola AG, Baar, Switzerland) or an electronic balance, with a readability of 1 g

(OHAUS, Ohaus Corp., New Jersey, U. S. A.). The grass samples were then oven-dried to a constant weight, at less than 60°C, and the dry weights were measured. The moisture content of the grasses was calculated from the fresh and dry weights and reported as % moisture (g moisture per 100 g of fresh grass). The dried samples were ground and stored in airtight bags in the field. In the laboratory, these samples were made to pass through a 1mm mesh screen of a Wiley mill and further chemical analyses were conducted on them.

Samples from three random plots out of the 24 harvested plots each month were analysed for estimating crude protein and samples from two plots were analysed for acid detergent fibre, lignins and silica, because of the cost limitations of analysing more samples. The samples were analysed using a semi-automated method using the Kjeltex equipment (at the Central Arid Zone Research Institute, Jodhpur, India) to estimate crude protein content (AOAC 1990). Samples were digested via a modification of the Aluminium block digestion procedure. The digestive mix contained 1.5 g of 9:1 K₂SO₄:CuSO₄ and digestion proceeded for ≥ 4hours at 375° C in 6 ml of H₂SO₄ and 2 ml of H₂O₂. Nitrogen content was determined in the digestate by semi-automated colorimetry and Nitrogen x 6.25 was used as a measure of crude protein (AOAC 1990, Hudson and White 1985, Robbins 1993).

The Van Soest (1963) method, later modified by Goering and Van Soest (1970) and Robertson and Van Soest (1980) was used to estimate the fibre content of grasses by measuring the acid detergent fibre (ADF), lignins and silica (acid insoluble ash). ADF is a measure of cell-wall cellulose and hemi-cellulose that can be digested by ruminants such as the blackbuck. ADF is fermentable, while lignins are not. Lignins are indigestible fibre for ruminants and their content was estimated after further digestion of the remaining sample with alkali (Van Soest 1982). Silica was estimated by burning the remaining sample after lignin estimation, in a muffle furnace at 600°C for five hours. All these were estimated as dry weight of grass sample (AOAC 1990).

The browse for blackbuck in VNP was found to be mainly from the ripe pods of *Prosopis juliflora* trees (Jhala 1997). To measure browse availability, I marked 5-15 *P. juliflora* trees randomly within each *P. juliflora* patch in VNP and thus covered all the patches in VNP. The number of trees marked in each patch was kept proportional to the area of the patch and a total of 55 trees were marked. The ripe pods on these marked trees were to be counted every three months from November 2000 to December 2002. However, no fruiting of these trees occurred during the study period.

Body condition of blackbuck females

The physical body condition of blackbuck females in VNP was assessed by visually ranking, on a scale of 1 to 5, five parts of the body, namely rump, pelvic girdle, tailbone depression, pectoral girdle and ribs (Plate No.3a & 3b). Fat deposition occurs in these five body parts and so these parts were considered to be indicators of body condition (Kistner *et al.* 1980). The high the roundness of rump, the less the depth of tailbone depression, the less prominent the pelvic and pectoral girdles and the near indistinguishability of ribcage and backbone indicated a very good condition and were given ranks of 5. The other extremes indicated a very poor condition and were given ranks of 1. Depending on intermediate conditions, ranks of 4, 3 and 2 were given. The body condition assessment was done simultaneously while assessing lactation status of females, following the same sampling scheme (described below).

As the conditions of the five body parts were not likely to be independent, a principal component analysis (PCA) was done to extract a smaller set of components that would explain the original variables (McGarigal *et al.* 2000). The body condition factor scores obtained from PCA were used to assess the effect of seasons on the body condition of females and were also used in the analyses of relationships with other variables.

Calving frequency

I used the number of females lactating as a proportional index of number of females with newborn calves (i.e., no. of females calving). Directly observing if a female had calved is difficult, since the calves have a “lying out” period of 10 days to two weeks (Mungall 1978, 1991). During this period the calves are well-camouflaged and so are difficult to sight (Plate No.4a & 4b). However, udders of females can be easily seen, when they are lactating (Mungall 1978). It is easy to confirm lactation in females when viewed from behind, even in a brief sighting in the field, since the teats are a contrasting black against a white rump (Plate no.5). The teats are visible from parturition until the time the females are lactating, and they retract afterwards (Mungall 1978). I considered that the births had occurred if teats were clearly visible.

The study area was divided into eight blocks. All the blocks were searched systematically to locate blackbuck herds and females in the herds were sampled to estimate the proportion of females calving. A set of 15 females (of reproductive age; Mungall 1978) was sampled in a block, but when the herds were large (size > 200), one set of 15 females was picked for approximately every 100 blackbuck. The sampling was repeated every week during the sampling period and was with replacement. Sampling was done throughout the year in 2000, but in 2001 and 2002, intensive sampling was restricted to calving seasons that were identified from 2000 data. Blackbuck females of reproductive age were sampled (Mungall 1978). Although I sampled outside the calving seasons too in 2001 and 2002, the sampling effort was considerably less as compared to 2000. The proportion calculated from each set of 15 sampled females was averaged over weeks and months. The calving seasons were determined from the mean proportion of blackbuck females calving each month. A sequence of months, when the monthly proportion calving was greater than 20% was termed as a calving season. For each year, the lengths of calving seasons (as no. of weeks) were determined using plots of cumulative weekly proportion of females calving by measuring the difference between the points of inflection (an example of such a plot is given in Fig. 4.1).

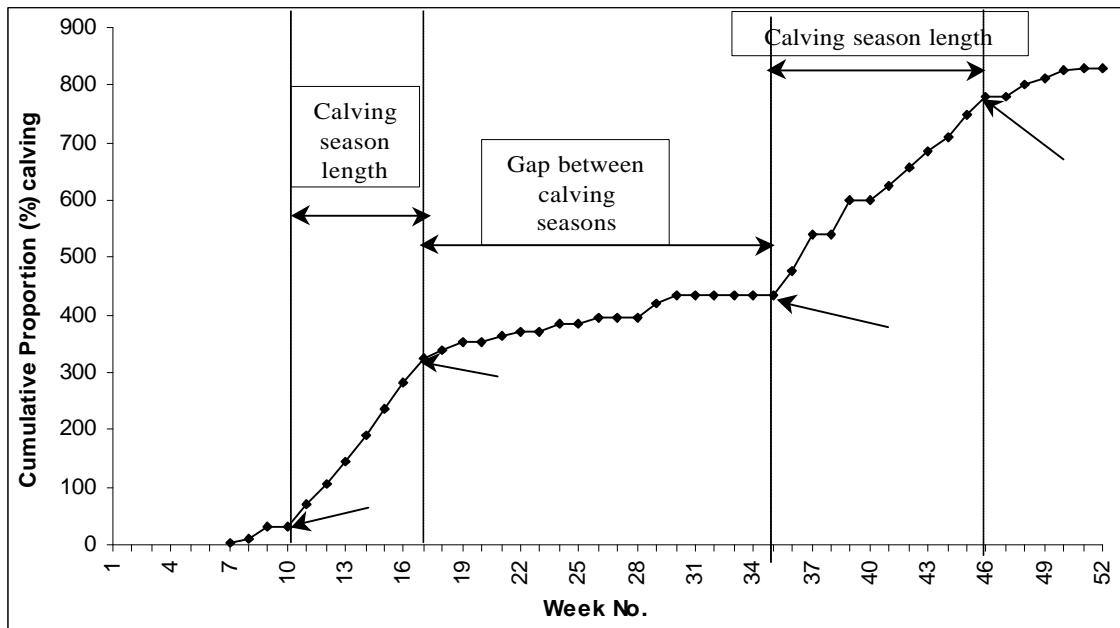


Fig. 4.1. A plot of cumulative weekly proportion of blackbuck female calving (lactating) in year 2000. Arrows mark the points of inflection, which were used for measuring the calving season lengths and gaps between calving seasons.

Relationships between calving frequency, forage quality and body condition

To examine the relationship of proportion of females calving with predictor variables, the proportion data was arcsine transformed ($\theta = \arcsine(\sqrt{\text{proportion calving}})$; Sokal and Rohlf 1995). Linear regression analysis was done to assess the relationship between arcsine proportion calving and each of the possible predictor variables (grass biomass, moisture, crude protein, ADF, lignins and silica content in grass and body condition of females). Stepwise multiple regression analysis was used to further identify the smallest set of predictor variables that would best explain the variation in (has the strongest relationship with) calving frequency. A stepwise multiple regression model, with $P(F) \leq 0.05$ for entry and $P(F) \geq 0.1$ for removal, was used. Collinearity among predictor variables was assessed from tolerance values.

Dichotomous logistic regression analysis was used to examine if lactation status of females was influenced by body condition of the females. Logistic regression was used because the response variable – lactation

status, was dichotomous (lactating or non-lactating). To examine the influence of season on the relationship between body condition and lactation status of females, a logistic regression model with two predictor variables was used and season, a categorical variable, was coded as a dummy variable.

Statistical models used

All the data that were analysed with parametric models were examined for adherence to normality assumption by graphically checking for symmetry of samples, using boxplots and scatter plots. If the data were highly skewed or relationship appeared non-linear, appropriate transformations were made or non-parametric tests were used. To examine the effect of seasons on different forage quality variables, an Analysis of Variance (ANOVA) model was used. When the values of variables that were measured for multiple years were different among years (e.g. biomass of wet season in 2000-01 and 2001-02 were very different), the data were not combined to assess the effect of seasons by ANOVA, but seasonal differences were analysed separately for each year. For ANOVA, when group variances were unequal, box-cox family of power transformations (Sokal and Rohlf 1995) were applied manually (with λ ranging from -2 to 2 , with an interval of 0.5) and the equality of variance was assessed by box plots. When the transformations were not helpful, a weighted least-squares ANOVA was used, where the group values were weighted by the reciprocal of estimated group variances (Neter *et al.* 1996). For comparison of two groups with unequal variances, a t-test for unequal variance was used (Sokal and Rohlf 1995). Post-hoc pair-wise comparisons were made with Tukey's HSD test (Sokal and Rohlf 1995). For all analysis comparing intra-year seasonal values, years were defined such that a year starts from June (with the beginning of the rainy season) and ends in May of the next calendar year (e.g. year 2000-01 begins with June 2000 and ends with May 2001).

Relationships between variables were assessed with regression or correlation analysis. Residual plots were used to check for homogeneity of variance and non-linear relationships in regression models. All analyses were

done using SPSS v. 8.0 software (SPSS Inc., Chicago, Illinois, U.S.A.). To plot the different forage quality variables together on the same scale, the values were standardised so as to range from 0 (minimum) to 1 (maximum). This range transformation (termed “ranging”) was done as

$$y_i = (y_i - y_{\min}) / (y_{\max} - y_{\min}) \text{ (Legendre and Legendre 1998).}$$

Statistical hypothesis testing and effect sizes

For all statistical hypothesis testing, type-I error rate of 5% ($\alpha = 0.05$) was used. Two-tailed tests were used generally. However, when the direction of change was known *a-priori*, one-tailed *P* values were used. Values in parenthesis given alongside means in the Results section are 1 standard error, if not specified otherwise. Considering that the statistical significance often depends purely on sample size (rather than on effect size) and does not necessarily mean biological significance (Yoccoz 1991, Johnson 1999), I have also calculated the effect sizes and their confidence intervals and used them as complementary to significance tests, to examine and interpret the results.

4.3. RESULTS

Rainfall

There was negligible rainfall in VNP during 2000. It was the third consecutive year of drought in that region (Mr. V. A. Rathod, Range Officer, VNP, *personal communication*). In 2001, the first rain fell on 30th May. The rains continued intermittently until September and the last rain was recorded on 20th September (Fig. 4.2). There was rainfall during nine weeks in that year and the maximum weekly rainfall recorded was 90 mm. Total rainfall in 2001 was 309.2 mm. The first rainfall in 2002 was on 20th June. The rains continued until the first week of September (last day of rain was 4th September). There was rainfall during six weeks and the maximum weekly rainfall was 195 mm. The total rainfall for 2002 was 384.3 mm.

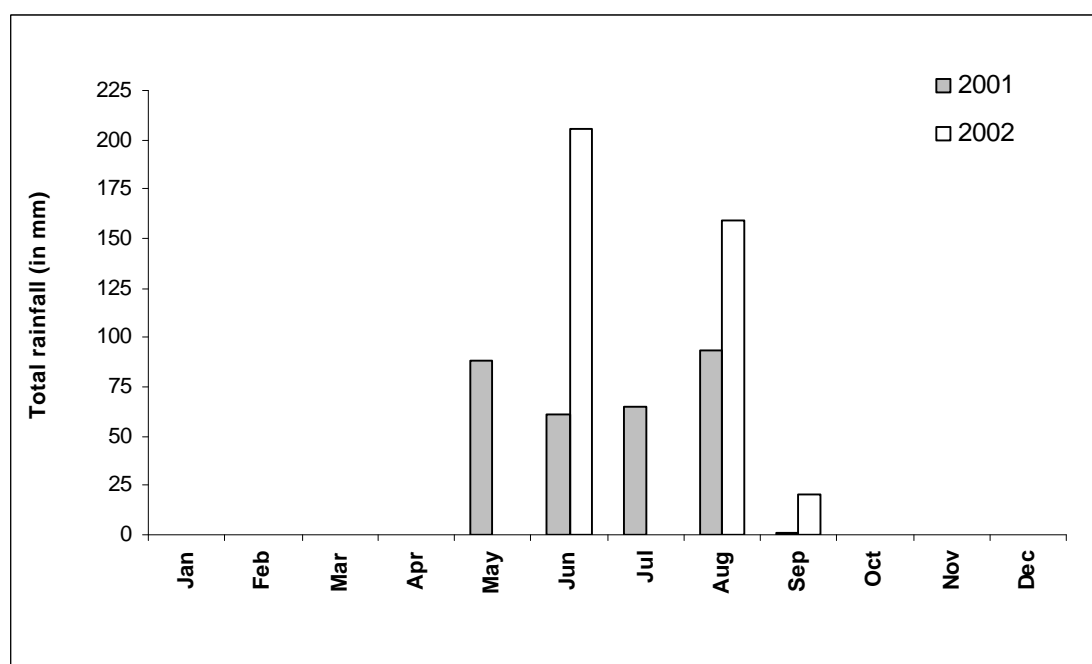


Fig. 4.2. Total monthly rainfall recorded in the grassland of Velavadar National Park. There was negligible rainfall in the year 2000.

Forage availability and quality

The mean of monthly above-ground dry biomass of grasses in VNP was $160.5(\pm 3.7)$ g/m² and the monthly means ranged from 60.2 g/m² to 359.3 g/m² during August 2000 to December 2002 (Fig. 4.3). Biomass levels were generally highest from September to February and lowest from March to July. However, for any month there was considerable variability in biomass among

years, seemingly related to rainfall conditions of those years. When the data were pooled into seasons, the differences among years were more clearly seen (Fig. 4. 4). Differences in mean above-ground biomass among seasons was significant in the years 2000-01 and 2001-02 (Table 4.1). For the sampling year 2002, difference between wet and cold seasons (for which seasons data were available) was not statistically significant. Post-hoc multiple comparison tests showed that the differences in biomass for all pairs of seasons were significant for year 2000-01, and between dry and the other two seasons were significant for year 2001-02 (Table 4.1). Dry season biomass were consistently lower than the other two seasons and the differences in mean effect sizes of dry and the other two seasons were large and the 95% Confidence Interval (CI) of effect sizes were not very wide, indicating that the true differences in biomass between these seasons were large and perhaps biologically significant. In contrast, the differences between wet and cold seasons were small (except in 2000-01), inconsistent, and very variable. The wide CI of effect sizes makes the true difference in biomass between these two seasons uncertain.

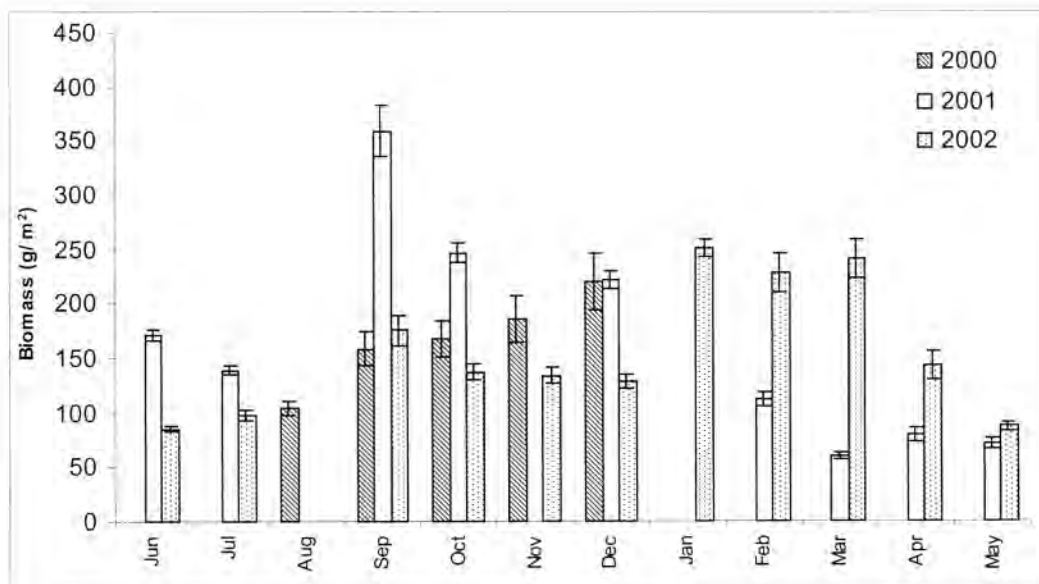


Fig. 4.3. Monthly means of dry biomass of grasses (g/m^2) in Velavadar National Park (error bars represent 1 SE).

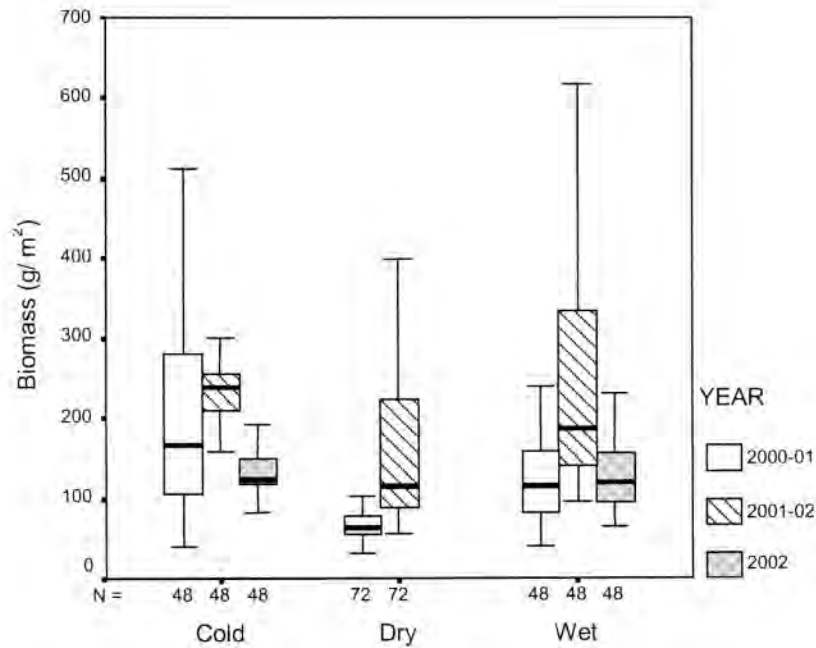


Fig. 4.4. Seasonal differences in grass biomass during the sampled years in Velavadar National Park. The line across the box indicates the median value; the hinges of the box give the range containing 50% of values and the whiskers, the minimum and maximum values.

Monthly mean moisture content of grasses ranged from 2.9% in May 2001 to 52.7% in July 2001 (Fig. 4.5). Moisture content peaked during rainy months and dropped rapidly after the rainy months and was the lowest in the dry season months. Within seasons, moisture content was variable among years and it was also generally more variable in wet season as compared to cold and dry seasons (Fig. 4.6). Seasonal means of moisture content were significantly different in all the sampled years (Table 4.1). Post-hoc multiple comparison tests showed statistically significant differences in moisture content between all pairs of seasons except dry and cold seasons of 2001-02. The differences in means were large between wet and the other two seasons and the 95% CI on the differences too were narrow, indicating that the actual differences were large. Differences in moisture content between cold and dry seasons were small and the CI were wide, rendering the actual magnitude of difference uncertain.

Table 4.1. Seasonal differences in the means of above-ground biomass (g/m²), moisture content (%), crude protein, ADF, lignins, silica content of grass (g/100g dry weight), and body condition factor scores of blackbuck females in Velavadar National Park. Weighted least-squares ANOVA was used for comparisons among 3 groups, and unequal variances t-test was used for 2 groups (except for body condition scores). Tukey's HSD test was used for post-hoc pair-wise comparisons.

Variable and Year	Seasonal comparisons ^a	Effect Size (difference in means) ± 1 SE	P value	95% Confidence Interval of effect size	
				Low	High
Biomass (2000-01) $F_{(2,165)} = 49.26,$ $P < 0.001$	Cold - Wet (203.16 - 132.0)	71.17 (±19)	0.001	24.65	115.68
	Wet - Dry (132.0 - 70.78)	61.22 (±9.3)	< 0.001	39.41	83.02
	Cold - Dry (203.16 - 70.78)	132.39 (±17.05)	< 0.001	92.42	172.35
Biomass (2001-02) $F_{(2,165)} = 22.34,$ $P < 0.001$	Wet - Cold (250.08 - 236.58)	13.5 (±20.62)	0.79	-34.82	61.82
	Wet - Dry (250.08 - 157.39)	92.64 (±22.39)	< 0.001	40.22	145.16
	Cold - Dry (236.58 - 157.39)	79.19 (±12.2)	< 0.001	50.58	107.8
Biomass (2002) $T = 0.5, df = 68.6$	Wet - Cold (136.8 - 131.75)	5.08 (± 10.2)	0.62	-15.17	25.34
Moisture (2000-01) $F_{(2,165)} = 65.78,$ $P < 0.001$	Wet - Cold (35.4 - 14.05)	21.34 (±2.85)	< 0.001	14.66	28.01
	Wet - Dry (35.39 - 7.15)	28.24 (±2.46)	< 0.001	22.47	34.01
	Cold - Dry (14.05 - 7.15)	6.9 (±2.2)	0.005	1.73	12.07
Moisture (2001-02) $F_{(2,165)} = 361,$ $P < 0.001$	Wet - Cold (49.4 - 10.4)	39 (±1.57)	< 0.001	35.31	42.7
	Wet - Dry (49.4 - 10.52)	38.95 (±1.8)	< 0.001	34.63	43.28
	Dry - Cold (10.52 - 10.40)	0.048 (±1.75)	1	-4.15	4.05
Moisture (2002) $T = 4.6, df = 59.23$	Wet - Cold (25.55 - 14.9)	10.67 (±2.31)	< 0.001	6.07	15.28
Crude-protein (2000-01) $F_{(2,16)} = 12.29,$ $P = 0.001$	Wet - Cold (4.26 - 2.74)	1.52 (±0.37)	0.003	0.55	2.48
	Wet - Dry (4.26 - 2.35)	1.9 (±0.44)	0.001	0.77	3.03
	Cold - Dry (2.87 - 2.35)	0.38 (±0.43)	0.652	-0.73	1.5
Crude-protein (2001-02) $F_{(2,18)} = 6.96,$ $P = 0.006$	Wet - Cold (4.13 - 2.75)	1.38 (±0.92)	0.320	-0.99	3.75
	Wet - Dry (4.13 - 1.83)	2.3 (±0.64)	0.006	0.665	3.92
	Cold - Dry (2.75 - 1.83)	0.91 (±0.72)	0.431	-0.93	2.75
ADF (2000-01) $F_{(2,11)} = 0.25, P = 0.78$					
ADF (2001-02) $F_{(2,11)} = 0.49, P = 0.62$					
Lignins (2000-01) $F_{(2,11)} = 5.45,$ $P = 0.023$	Cold - Wet (6.15 - 5.65)	0.5 (±0.58)	0.676	-1.07	2.06
	Dry - Wet (8.05 - 5.65)	2.4 (±0.73)	0.018	0.435	4.36
	Dry - Cold (8.05 - 6.15)	1.9 (±0.78)	0.08	-0.22	4.02
Lignins (2001-02) $F_{(2,11)} = 0.10, P = 0.9$					
Silica (2000-01) $F_{(2,11)} = 0.05, P = 0.95$					
Silica (2001-02) $F_{(2,11)} = 0.2, P = 0.82$					
Body condition (2000-01) $F_{(2,549)} = 104.65,$ $P < 0.001$	Wet - Cold (0.66 - (-0.145))	0.8 (±0.11)	< 0.001	0.541	1.07
	Wet - Dry (0.66 - (-0.774))	1.43 (±0.01)	< 0.001	1.2	1.7
	Cold - Dry ((-0.145) - (-0.774))	0.63 (±0.09)	< 0.001	0.427	0.84
Body condition (2001-02) $T = 6.6, df = 709$	Wet - Dry (0.26 - (-0.224))	0.48 (±0.07)	< 0.001	0.34	0.627

^a Seasonal means are given in parentheses

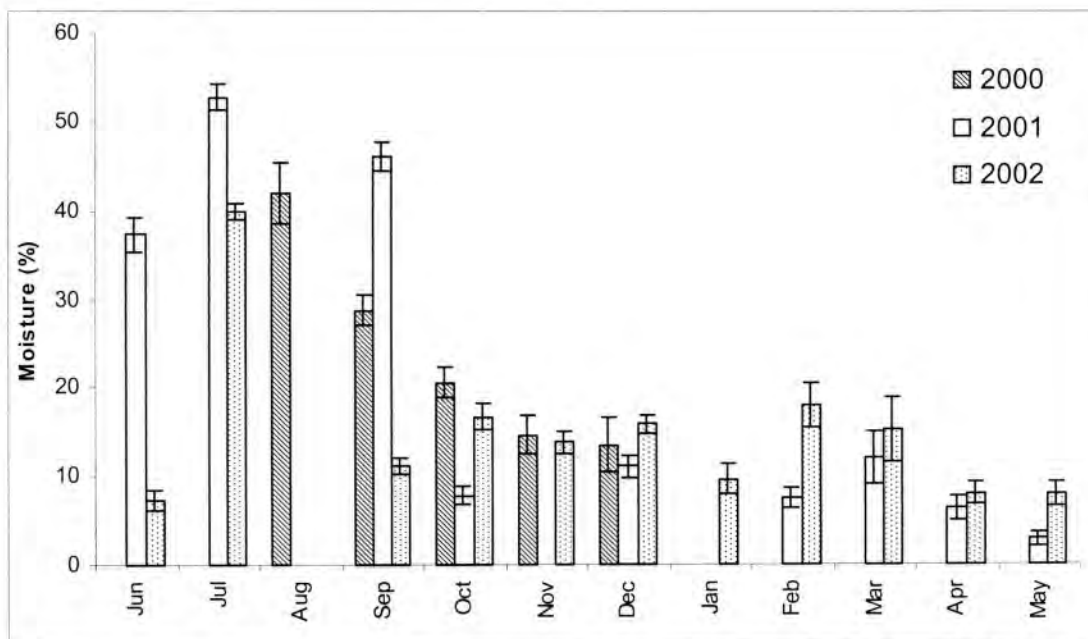


Fig. 4.5. Monthly means of moisture content (%) of grasses in Velavadar National Park (error bars represent 1 SE).

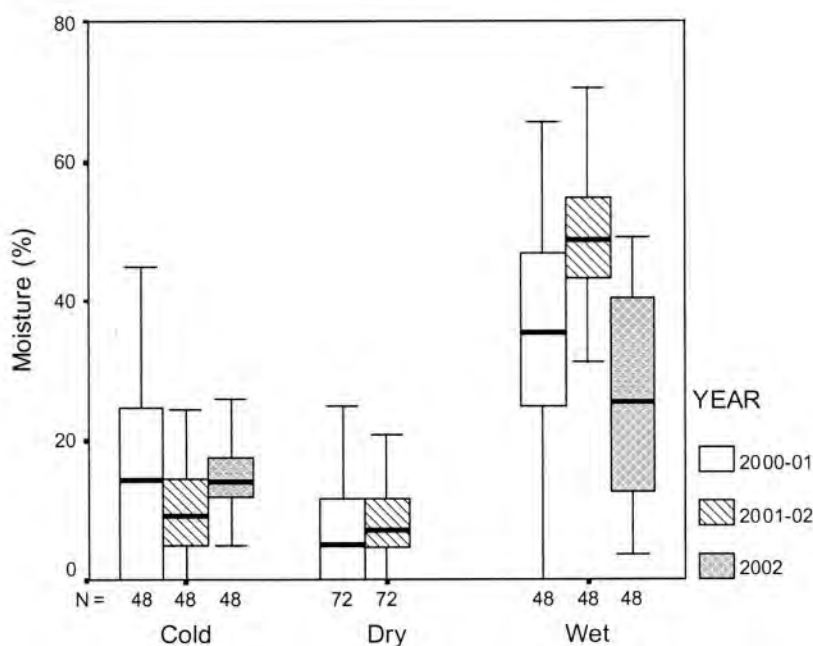


Fig. 4.6. Seasonal differences in moisture content of grasses in Velavadar National Park. The line across the box indicates the median value; the hinges of the box give the range containing 50% of values and the whiskers, the minimum and maximum values.

Monthly means of crude protein content of grasses was substantially variable among months within years. It ranged from 1.2 g/100g dry weight in December 2001 to 5 g/100g dry weight in July 2001 (Fig. 4.7). When grouped

into seasons, wet season mean crude protein content was the highest among seasons in both the sampled years, followed by cold and dry seasons (Fig. 4.8). Two outliers were found in the dry season of 2000-01, which might have been due to labelling errors during laboratory analysis. These outliers were excluded from all further analysis. Crude protein content showed significant seasonal differences in the sampled years (Table 4.1). Differences in means of crude protein content between wet and dry seasons in both years were statistically significant and the differences in means were considerably large. But the 95% CI were wide, indicating that the true magnitude of difference is likely to be large, but is uncertain. Differences in crude protein content between wet and cold seasons were smaller, and in the year 2001-02, the variability was high making it statistically not significant. Differences in crude protein between cold and dry seasons were much smaller, with very wide CI, for both years, indicating that the true difference is uncertain and not statistically significant.

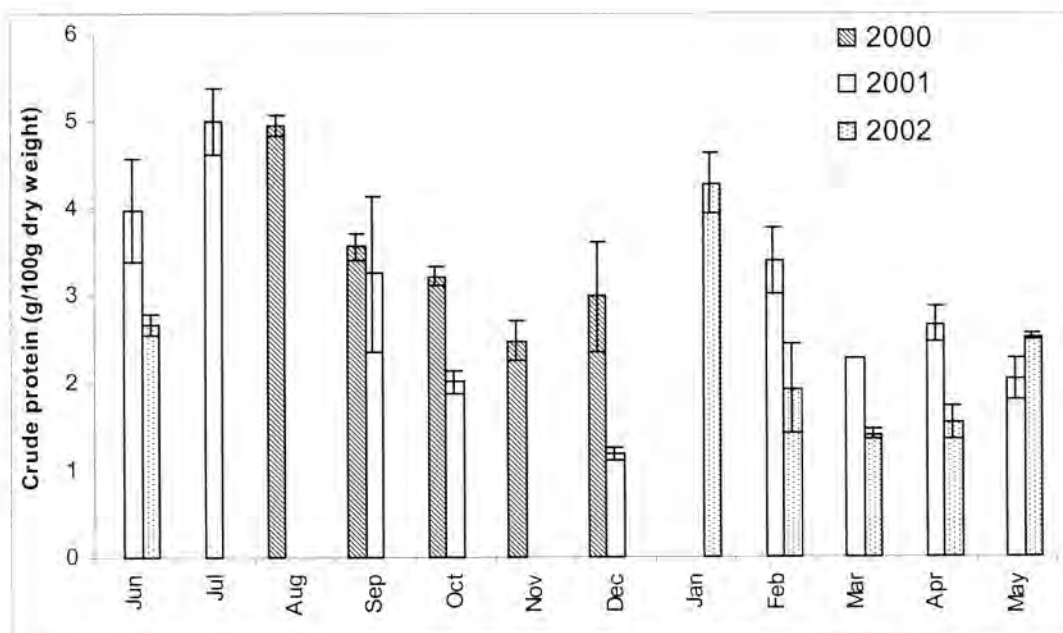


Fig. 4.7. Monthly means of crude protein content (g/100g dry weight) of grasses in Velavadar National Park (error bars represent 1 SE).

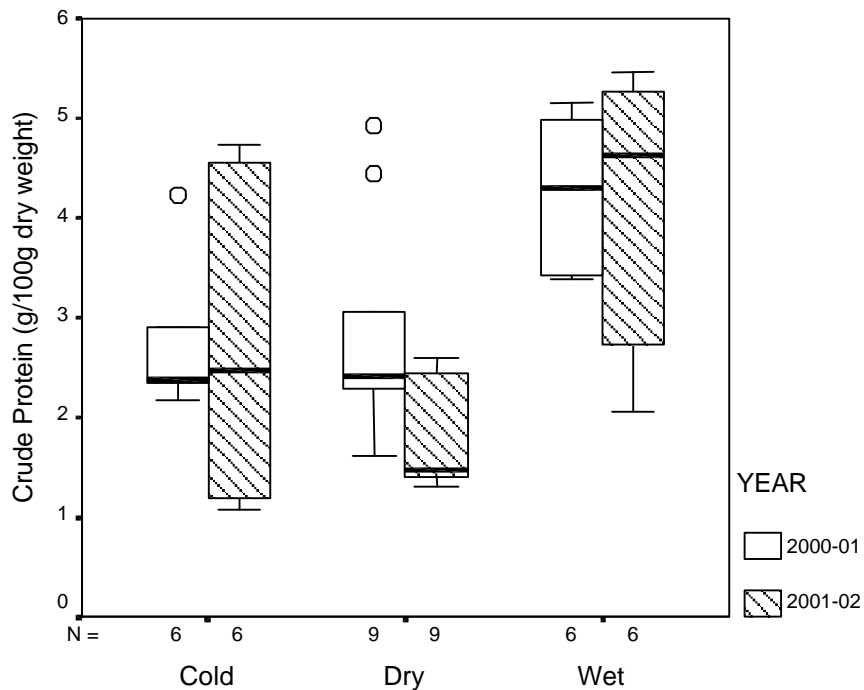


Fig. 4.8. Seasonal differences in crude protein content (g/100g dry weight) of grasses in Velavadar National Park. The line across the box indicates the median value; the hinges of the box give the range containing 50% of values and the whiskers, the minimum and maximum values. Circles denote outliers.

Monthly means of ADF in grasses did not vary much among months (Fig. 4.9), while that of lignins were relatively lower from August to January and higher from February to June (Fig. 4.10). Variability in monthly means of silica was considerable, but did not show a consistent pattern (Fig. 4.11). In general, ADF, lignins and silica levels in grasses do not seem to vary much through the year. However, small sample sizes limit the inferences that could be drawn here. When data were grouped into seasons, ADF did not show any substantial or statistically significant seasonal difference in both the sampled years (Fig. 4.12; Table 4.1). Lignins content was not statistically different among seasons in year 2001-02, but in year 2000-01, a statistically significant difference was seen (Fig. 4.13; Table 4.1). In that year, dry season lignins content was substantially higher than cold and wet seasons. The difference between dry and wet seasons was statistically significant, considerably large, but the 95% CI of difference of means was wide, making the actual magnitude of difference uncertain. This uncertainty was perhaps caused by an outlier sample, and if that sample is excluded, the difference

would be substantial. There were no significant seasonal differences found in silica content in both the years (Fig. 4.14; Table 4.1).

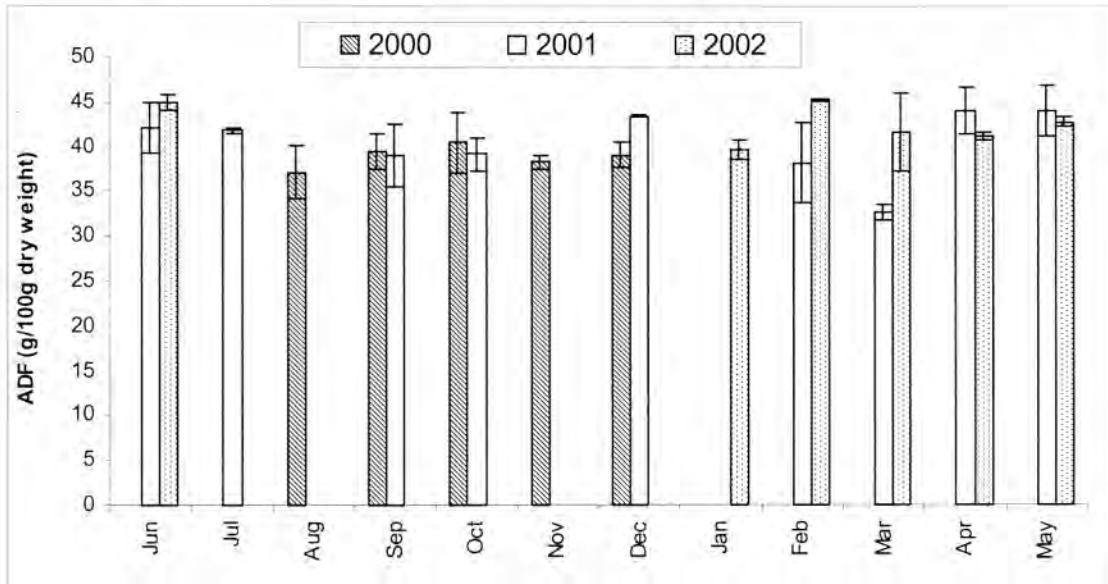


Fig. 4.9. Monthly means of Acid Detergent Fibre (ADF; g/100g dry weight) in the grasses in Velavadar National Park (error bars represent 1SE).

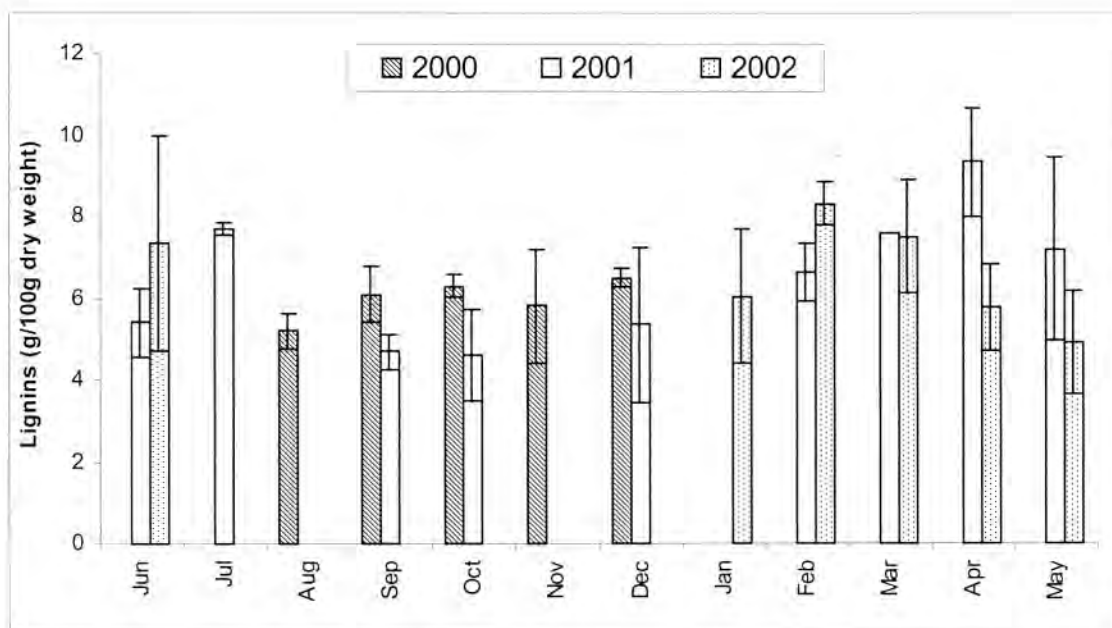


Fig. 4.10. Monthly means of lignins (g/100g dry weight) in grasses in Velavadar National Park (error bars represent 1SE).

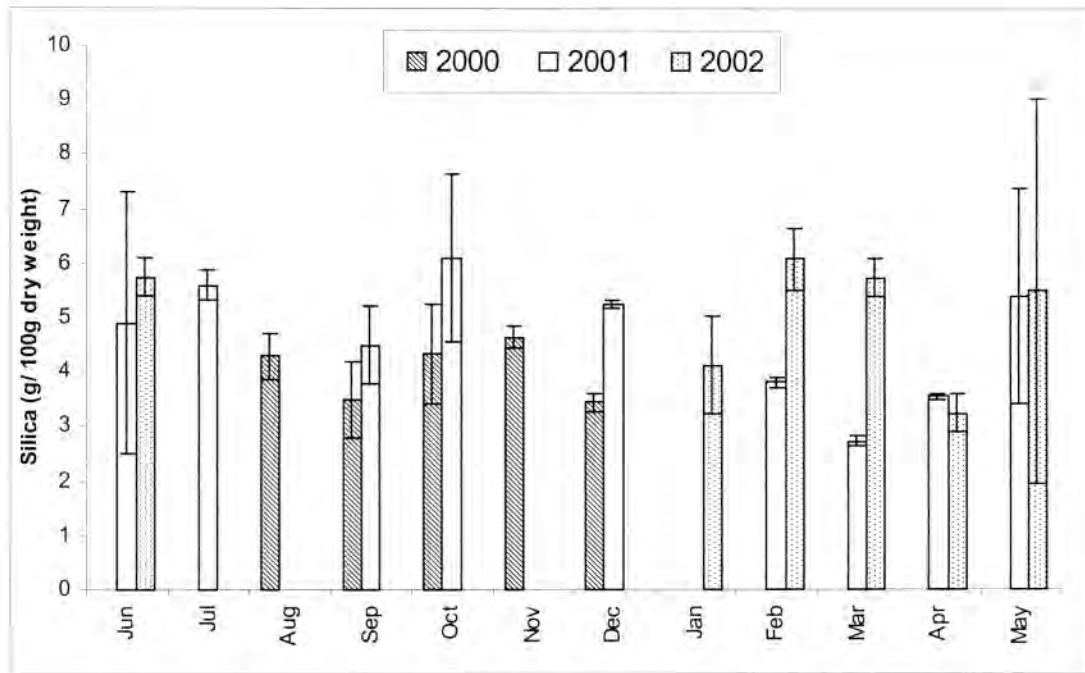


Fig. 4.11. Monthly means of silica (g/100g dry weight) in grasses in Velavadar National Park (error bars represent 1 SE).

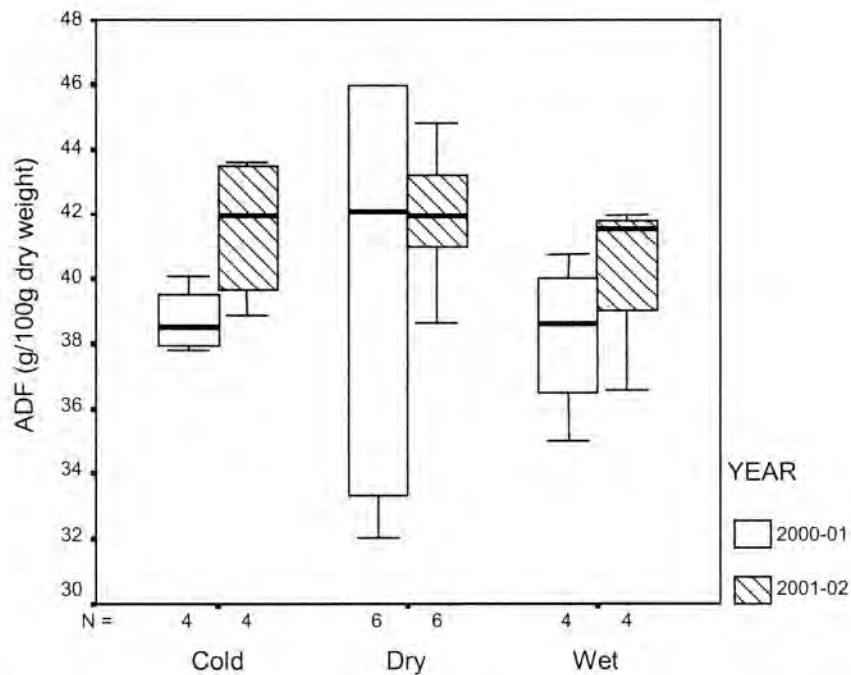


Fig. 4.12. Seasonal differences in the ADF content (g/100g dry weight) of grasses in Velavadar National Park. The line across the box indicates the median value; the hinges of the box give the range containing 50% of values and the whiskers, the minimum and maximum values.

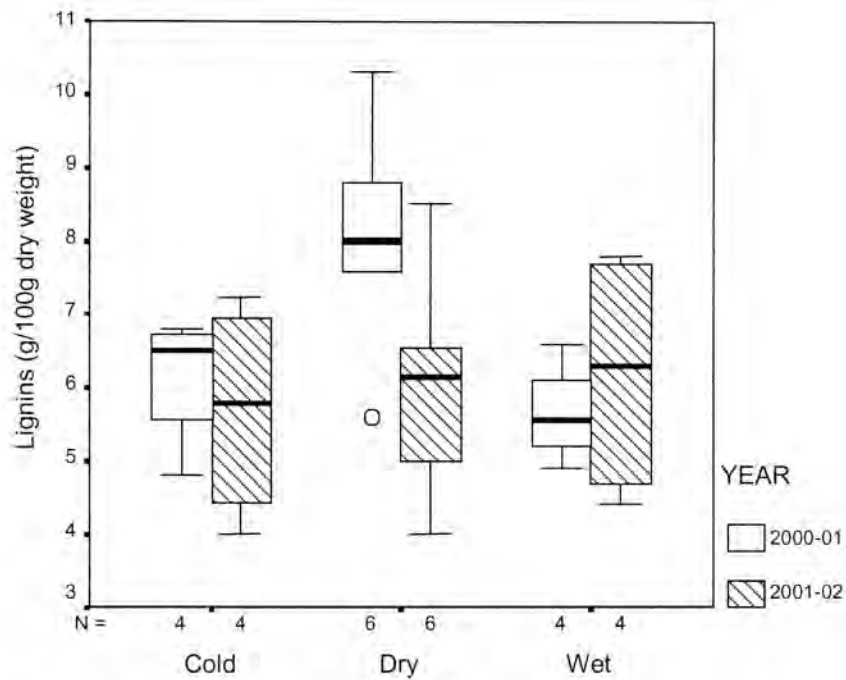


Fig. 4.13. Seasonal differences in the lignins content (g/100g dry weight) of grasses in Velavadar National Park. The line across the box indicates the median value; the hinges of the box give the range containing 50% of values and the whiskers, the minimum and maximum values. Circle denotes an outlier.

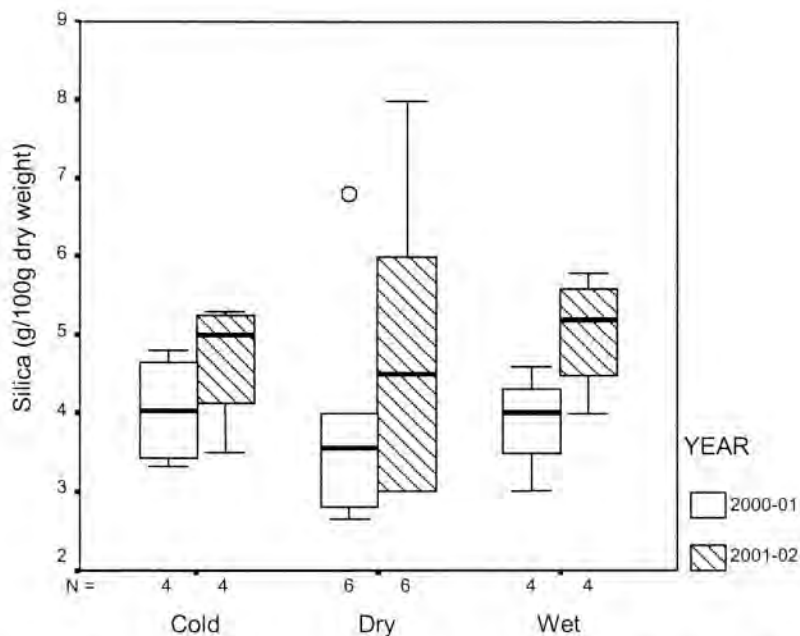


Fig. 4.14. Seasonal differences in silica content (g/100g dry weight) of grasses in Velavadar National Park. The line across the box indicates the median value; the hinges of the box give the range containing 50% of values and the whiskers, the minimum and maximum values. Circle denotes an outlier.

Relationship among forage quality variables

Linear correlation analysis of forage quality variables – biomass, moisture, crude protein, ADF, lignins and silica showed that crude protein and moisture values were positively correlated (Pearson's $r = 0.5$, $P < 0.001$) and ADF and crude protein showed a significant negative relationship (Pearson's $r = -0.437$, $P = 0.006$). A few other relationships were statistically significant, but were not strongly correlated ($-0.4 < r < 0.4$, Table 4.2).

Table 4.2. Relationships (Pearson's r) among various forage quality variables in Velavadar National Park, sampled monthly from August 2000 to December 2002. Number of months sampled and samples in a month vary among variables (see Text).

	Pearson's r , P and n	Biomass	Moisture	Crude protein	ADF	Lignins	Silica
Biomass	r P n	1.00 - -					
Moisture	r P n	0.128 ^a 0.002 600	1.00 - -				
Crude protein	r P n	-0.159 0.233 58	0.500 ^a <0.001 58	1.00 - -			
ADF	r P n	0.039 0.812 40	0.025 0.876 40	-0.437 ^a 0.006 40	1.00 - -		
Lignins	r P n	-0.128 0.431 40	-0.033 0.840 40	-0.178 0.286 40	0.317 ^a 0.046 40	1.00 - -	
Silica	r P n	0.229 0.154 40	0.067 0.679 40	-0.282 0.086 40	0.316 ^a 0.047 40	0.048 0.769 40	1.00 - -

^aCorrelations are significant at $\alpha = 0.05$

Body condition of blackbuck females

Body condition ranks of all the five body parts were strongly correlated with each other (Table 4.3). A PCA extracted only one component (with Eigenvalue = 4.636) that explained 92.7% of variation in the data. Component loadings of

all original variables were > 0.93 (Table 4.3), indicating that the original variables were strongly correlated with the extracted component.

Table 4.3. Correlations (Pearson's r) among the body condition ranks (visually ranked in the field) of five body parts of blackbuck females in Velavadar National Park. Component loadings give the correlations of the original body condition variables on the extracted PCA component.

Correlations (all $P < 0.001$)	Rump (B)	Pelvic Girdle (PG)	Pectoral Girdle (PECG)	Ribs (R)	Tail-Bone Depression (TBDEPN)	Component loadings
B	1.000					0.962
PG	0.920	1.000				0.979
PECG	0.917	0.989	1.000			0.977
R	0.882	0.870	0.867	1.000		0.931
TBDEPN	0.912	0.931	0.930	0.868	1.000	0.964

Blackbuck females were found to be in good body condition from June to October and in poor condition from March to May (Fig. 4.15). Overall, females were found to be in the best body condition in wet season and the worst in dry season (Fig. 4.16). However, within seasons, considerable variability in mean values among years was seen. The differences in mean body condition factor scores among seasons were statistically significant in both the years (Table 4.1). In the year 2000-01, a post-hoc pair-wise comparison showed that the difference in body condition was significant for all pairs of seasons. In 2001-02 too, the difference between wet and dry seasons was significant. The differences in means for all pairs of seasons were large, 95% CI were relatively narrow, suggesting that the true difference was large, and could be of biological significance. Mean body condition scores in the dry season of 2000-01, which followed a low (negligible) rainfall wet season, was the lowest. Also, the seasonal differences in body condition in that year were particularly large.

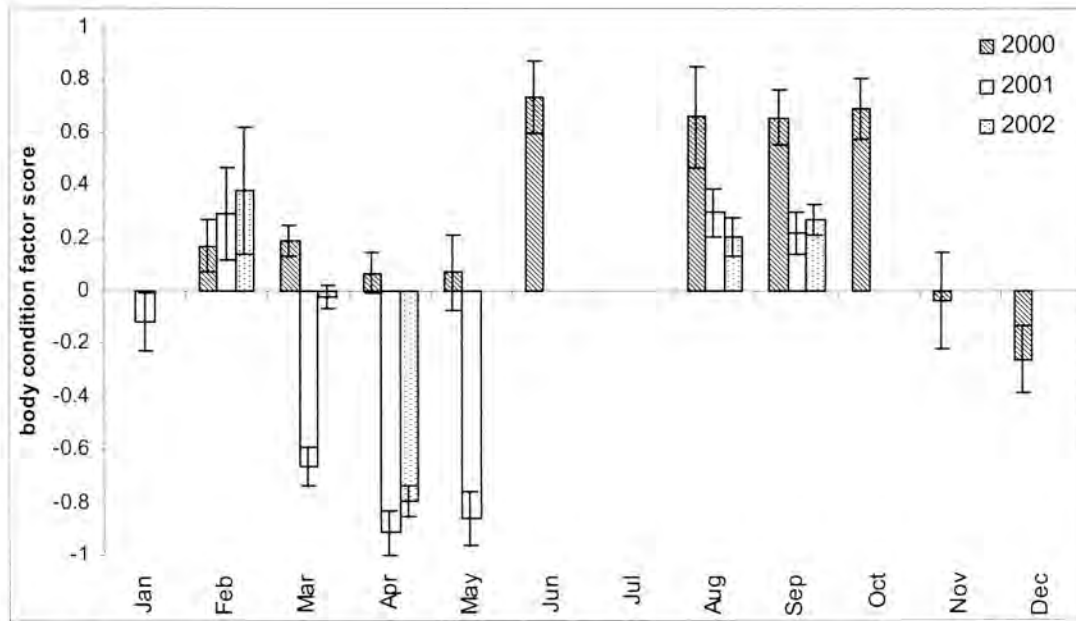


Fig. 4.15. Monthly means of body condition factor scores (from PCA) of blackbuck females in Velavadar National Park from 2000 to 2002 (error bars represent 1 SE).

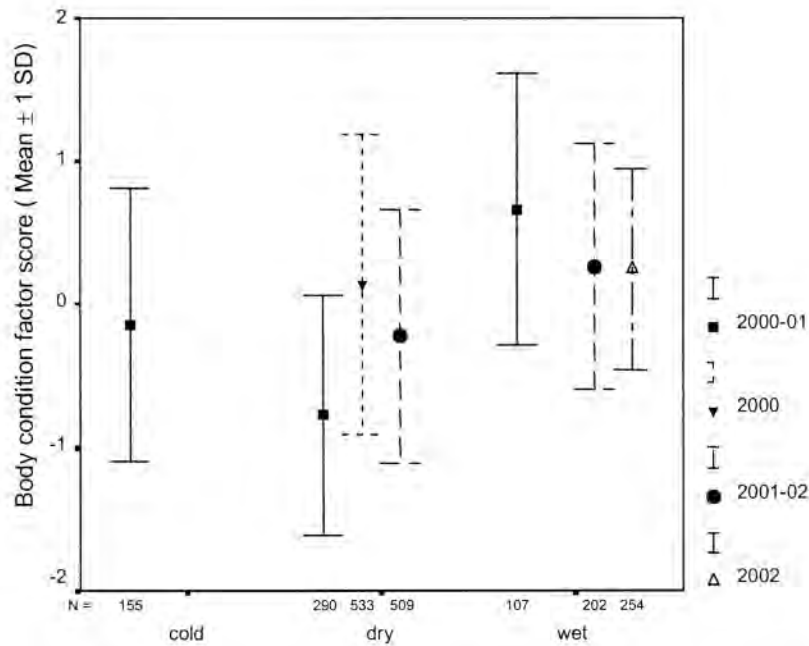


Fig. 4.16. Seasonal differences in body condition of blackbuck females in Velavadar National Park. Body condition is given as PCA factor scores derived from visual ranking of 5 body parts. Mean values are denoted by markers and 1 standard deviation by error bars.

Relationship between body condition and forage quality variables

Monthly means of body condition factor scores of blackbuck females were positively correlated to monthly means of moisture (Pearson's $r = 0.641$, $P = 0.01$) and crude protein (Pearson's $r = 0.609$, $P = 0.03$), among the various forage quality variables (Table 4.4). Relationships with other variables were neither strong nor statistically significant.

Table 4.4. Relationships between monthly means of body condition factor scores of blackbuck females and various forage quality variables in Velavadar National Park.

	Pearson's r	P	n
Biomass	0.392	0.166	14
Moisture	0.641 ^a	0.014	14
Crude protein	0.609 ^a	0.027	13
ADF	-0.153	0.617	13
Lignins	-0.447	0.126	13
Silica	0.253	0.404	13

^a Correlations are significant at $\alpha = 0.05$

Calving frequency

Calving was clustered during two separate periods of the year and this was consistent for all three years of study (Fig. 4.17). Higher proportion of females (> 20%) were calving during these two peak periods (termed "calving seasons"), however, a basal level of calving (5-15%) was happening throughout the year. These calving seasons appear to be cyclical, occurring with a gap of 11-18 weeks between the seasons and an interval of 23-28 weeks between peak-points. The calving seasons themselves were not narrow, but considerably spread out with season lengths ranging from 7-15 weeks during the three years (Table 4.5). The calving season that occurred following the rains (wet season calving peak) was wider (by 4 weeks and 5 weeks in years 2000 and 2001 respectively, Table 4.5) than the season before the rains (dry season calving peak). Maximum weekly mean proportion of females calving was over 50% for a few weeks during both the seasons, but the proportion was generally between 20-50% during the seasons. Dry season calving ended just before the rains started and wet season peak started as the rains were getting over (Fig. 4.17). Monthly mean

proportion of females calving depicts the same bimodal pattern in calving as weekly data, but it additionally shows the variability within months and among years more clearly (Fig. 4.18). It also depicts the wet season calving peak as much wider than the dry season peak. Maximum calving occurred in the months of March, April, August and September during the study.

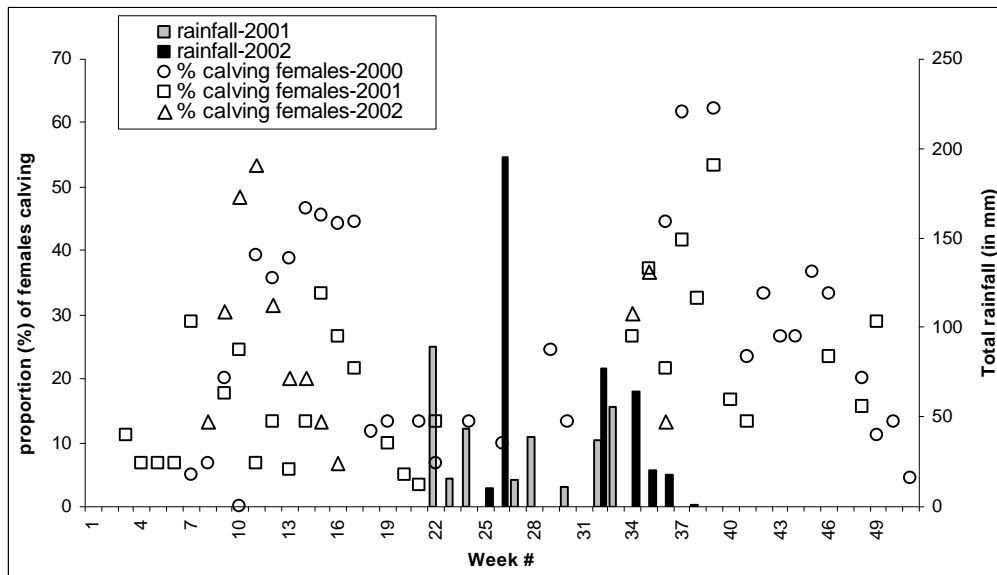


Fig. 4.17. Weekly mean proportion (%) of females calving (lactating) and weekly total rainfall (in mm) during 2000 to 2002 in Velavadar National Park.

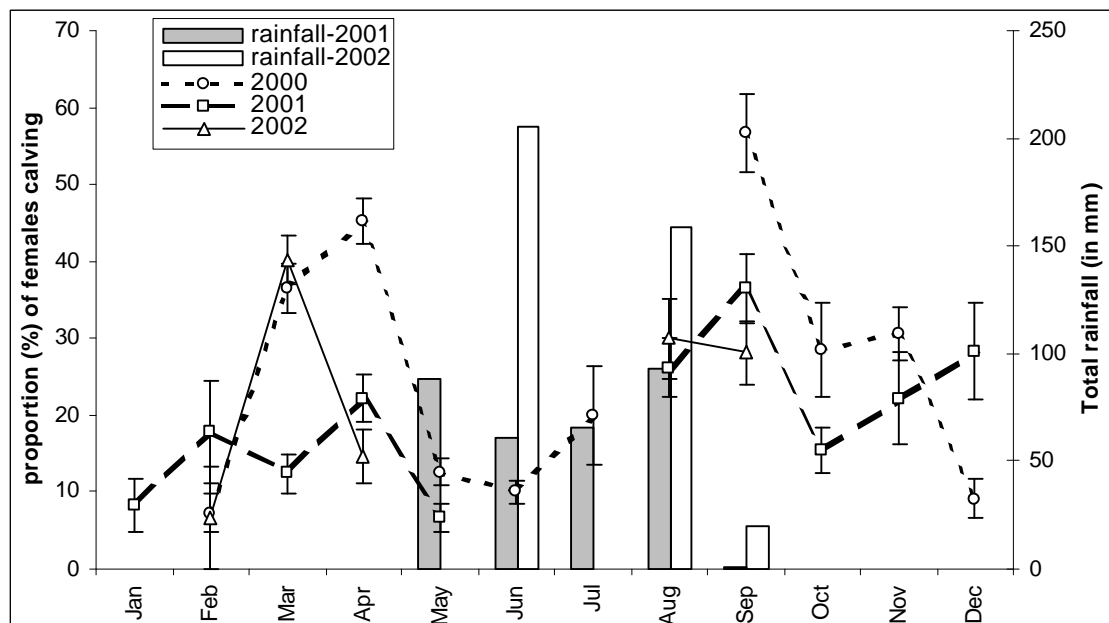


Fig. 4.18. Monthly mean proportion (%) of females calving (lactating) and monthly total rainfall from 2000 to 2002 in Velavadar National Park (error bars represent 1 SE).

Table 4.5. Length and other characteristics of calving seasons in Velavadar National Park. The lengths of seasons were determined for each year from plots of cumulative weekly proportion of females calving (see Fig. 4.1), by measuring the difference between points of inflection.

Year	Season	Calving season length	Compared calving seasons	Gap between calving seasons	Interval between successive calving peak-points
2000	Dry	7 weeks	--	--	--
2000	Wet	11 weeks	2000 dry – 2000 wet	18 weeks	23 weeks
2001	Dry	10 weeks	2000 wet – 2001 dry	11 weeks	28 weeks
2001	Wet	15 weeks	2001 dry – 2001 wet	17 weeks	24 weeks
2002	Dry	7 weeks	2001 wet – 2002 dry	12 weeks	24 weeks
2002	Wet	^a	2002 dry – 2002 wet	16 weeks	^a

^a Length and interval not calculated due to limited sampling.

Relationships between calving frequency, body condition and forage quality variables

Logistic regression analysis of relationship between lactation status (lactating or non-lactating) and body condition factor scores of females showed that the probability (odds) that females were lactating does not have a relationship with the body condition of females ($-2 \log \text{likelihood} = 2794.06$, Model chi-square = 0.106, $df = 1$, $P = 0.745$, $B = -0.015 (\pm 0.046)$, $\exp(B) = 0.985$). Since body condition of females differed between seasons (Table 4.1), there was a possibility that season might interact with body condition and consequently improve its relationship with the probability of lactation. To assess such an influence, a multiple logistic regression model including season (coded as a dummy variable) and interaction terms for season and body condition was built and parameters were estimated. This analysis showed that the model, although had a good fit overall ($-2 \log \text{likelihood} = 2761.32$, Model chi-square = 32.85, $df = 5$, $P < 0.001$), the predicted values from the model and the observed data were significantly different (Hosmer and Lemeshow Goodness-of-fit-test: $\text{chi-square} = 18.79$, $df = 8$, $P = 0.016$). Further, the body condition was not related to lactation status ($B = -0.174 (\pm 0.18)$, Wald statistic = 0.94, $df = 1$, $P = 0.33$, $\exp(B) = 0.84$). The interaction terms too were not significant. The categorical predictor, season, however was significantly related to lactation status (dry season with

reference to cold: $B = 0.655(\pm 0.19)$, Wald statistic = 11.94, $P < 0.001$, $\exp(B) = 1.93$, 95% CI for $\exp(B) = 1.33$ to 2.79; wet season with reference to cold: $B = 1.04 (\pm 0.2)$, Wald statistic = 26.33, $P < 0.001$, $\exp(B) = 2.83$, 95% CI for $\exp(B) = 1.9$ to 4.2). On the whole, this indicated that season was related to probability of lactation, while body condition was not. The odds that females were lactating was higher in wet and dry seasons as compared to cold season, independent of body condition of females. This significant effect of season ($H_a: \beta_2 \neq 0$) has influenced the test of overall model fit, even though the model predicted poorly.

Bivariate linear regression analysis of relationships between arcsine transformed monthly mean proportion of females calving and the different forage quality variables and body condition factor scores showed that only moisture content in grasses was significantly related, although it explained only about 34% variation in proportion calving ($r^2 = 0.34$, $F_{(1,13)} = 6.627$, $P = 0.023$, $B = 0.0091(\pm 0.004)$). Also, the effect size (B) had a wide 95% CI, making its true value uncertain. None of the other variables had any bivariate relationship with calving frequency (Table 4.6). To develop a better model including multiple predictor variables that might explain more variation in calving frequency, a stepwise multiple linear regression analysis was done. However, moisture was the only variable included, and therefore did not result in a better model ($Adjusted R^2 = 0.29$, $F_{(1,10)} = 5.499$, $P = 0.04$, $B = 0.0094 (\pm 0.004)$). No other predictor variable explained more variation in calving frequency than had already been explained by moisture. Even when moisture was removed from the model, other variables did not show a relationship with calving frequency. However, small samples may have been a limitation here. A graphical representation (Fig. 4.19) of monthly means of proportion of females calving and the main forage quality variables and body condition factor scores (all predictor variables were standardised, by range transformation, so as to vary from 0 (minimum value on the original scale) to 1 (maximum value on the original scale)) depicted the pattern of relationships more clearly and provided some insights on the underlying processes. The

Table 4.6. Summary of relationships between (arcsine transformed) monthly mean proportion of blackbuck females calving and the different predictor variables in Velavadar National Park, based on linear regression analysis.

Predictor variable	r^2	Adj r^2	F statistic ^a	P value	Effect size (B) and the Standard Error of B ^b	t statistic	95% Confidence Interval of B ^b	
							Low	High
Biomass	0.099	0.029	$F_{(1,13)} = 1.422$	0.254	$6.631 \times 10^{-4} (\pm 0.001)$	1.193	-0.001	0.002
Moisture	0.338	0.287	$F_{(1,13)} = 6.627$	0.023	$9.045 \times 10^{-3} (\pm 0.004)$	2.574	0.001	0.017
Crude protein	0.083	0.007	$F_{(1,12)} = 1.089$	0.317	$6.44 \times 10^{-2} (\pm 0.062)$	1.043	-0.070	0.199
ADF	0.014	-0.069	$F_{(1,12)} = 0.166$	0.691	$-6.2 \times 10^{-3} (\pm 0.015)$	-0.408	-0.039	0.027
Lignins	0.084	0.008	$F_{(1,12)} = 1.101$	0.315	$-3.73 \times 10^{-2} (\pm 0.036)$	-1.049	-0.115	0.040
Silica	0.005	-0.077	$F_{(1,12)} = 0.066$	0.801	$-1.15 \times 10^{-2} (\pm 0.045)$	-0.258	-0.109	0.086
Body condition factor	0.116	0.070	$F_{(1,19)} = 2.495$	0.131	$0.122 (\pm 0.077)$	1.579	-0.040	0.284

^a Degrees of freedom are given inside the parentheses

^b The values of B, it's Standard Error and confidence intervals reported here have not been back transformed.

dry and wet season calving peaks seem to have different relationships with the predictor variables, and both peaks seem to be out-of-synchrony with the changes in predictor variables. Wet season calving peaked after moisture and crude protein levels peaked and started declining, whereas, dry season calving peaked and declined before the crude protein peaked. Biomass and body condition were generally high during the wet season calving peak, but relatively low during the dry season calving peak. Crude protein and moisture levels were also low during the dry season calving peak.

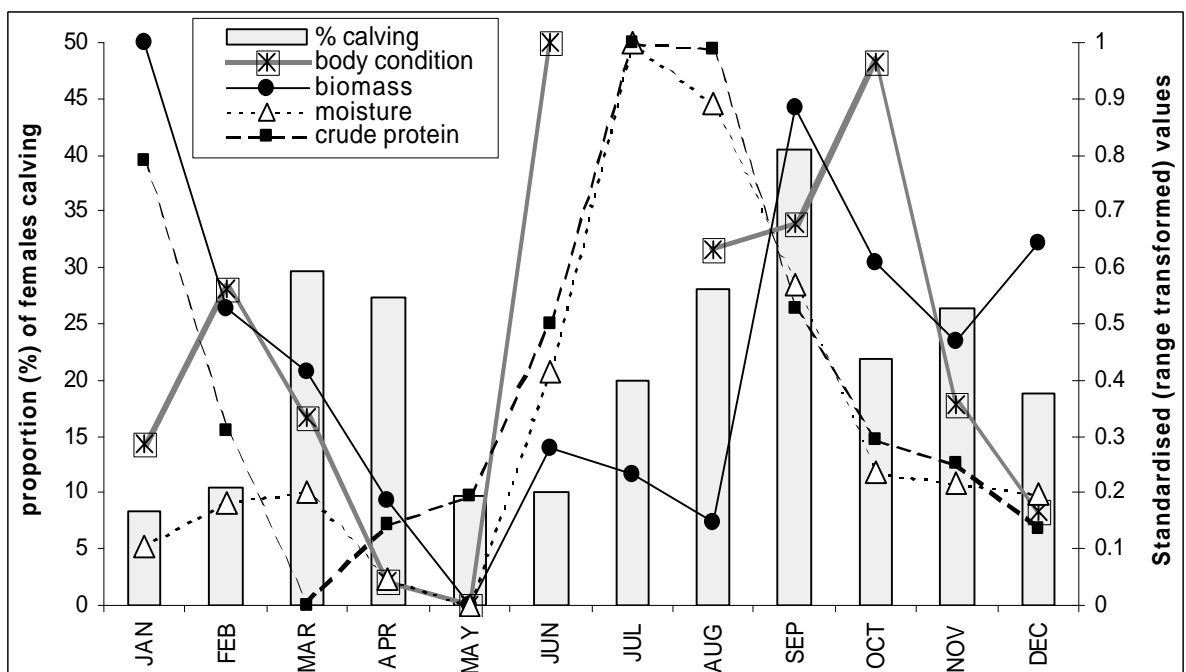


Fig. 4.19. Monthly mean proportion (%) of blackbuck females calving (bars; primary y-axis), standardised (range transformed so as to vary from 0 to 1) values of monthly means of body condition factor scores of females (not measured in July) and main forage quality variables (lines; secondary y-axis) during 2000 to 2002 in Velavadar National Park.

4.4. DISCUSSION

Effect of season on forage quality

Rainfall is locally highly variable in the *Bhal* region of Gujarat, of which VNP is a part. The first year (2000) of this study was the final year of a three-year consecutive drought in VNP, although there had been rains in other parts of the region. Drought is a frequent phenomenon in that region (data from URL: <http://www.indiastat.com, September 2004>). No rainfall data from VNP, apart from the three years data of this study is available for comparison. However, if the regional rainfall is considered, rainfall in VNP was less than the regional average in 2000, 2001, and 2002 (regional rainfall data from URL: <http://www.indiastat.com, September 2004>). In spite of frequent local failures in rainfall, the regional-scale air moisture during the monsoon season is generally high, and this might be influencing the seasonal vegetation growth and chemical changes. This is evident from the changes in above-ground biomass, moisture and protein content of grasses in 2000 wet season, despite the negligible rainfall in VNP.

The unimodal pattern of rainfall in VNP may cause the pronounced seasonality of forage abundance and quality in VNP. Monsoon rains commenced usually by the end of May or June but was variable among years. Fresh growth in grass, flowering and seeding happened during the wet season. Above ground biomass increased in the wet season, it's rate of growth declined by the end of that season and was at the highest levels in the late wet or cold season (Fig. 4.3). Grasses continued to grow even after seeding, but at a slower rate, in the presence of moisture in soil and air, and matured as the seasons progressed from wet to cold. There was some above ground growth in grasses until late winter. The grass blades started to senesce as moisture content declined in the early part of dry season. In the dry season, biomass declined because removal was not compensated by biomass addition. Biomass removal may have been due to herbivory, physical damage by either wind or animals or just litterfall. Grasses found in VNP are C₄ grasses and the productivity and Nitrogen content of these

grasses are comparable to semi-arid areas elsewhere in India (Singh and Joshi 1979a).

Grasses in VNP had higher moisture and crude protein content in the earlier part of wet season. Although a relatively pronounced protein peak was seen in wet season (Fig. 4.5), the change in mean values was only relatively, not absolutely large (i.e. only about 1.3 to 2.3% change) and also the actual magnitudes of differences were uncertain (95% CI were wide). However, although the crude protein level did not increase a lot, its digestibility in blackbuck may have increased in the wet season (Jhala 1997). In contrast, in dry season, a negative crude protein digestibility was found by Jhala (1997). In ruminants, forage must contain at least 3.13% crude protein (31.3g/kg of forage) for just the maintenance requirements and the necessary dietary requirement may be higher (Robbins 1993). Therefore, even though some crude protein was available to blackbuck in dry season in VNP, it just may not have been digestible. Similar to VNP, in Gir forests, protein in grasses (*Apluda mutica* and *Sehima nervosum* dominated communities) changed only marginally, from 2 – 4%, from dry to wet season (Berwick 1974). The crude protein levels in VNP (N ranges from 0.24 g/m² in May 2001 to 1.87 g/m² in September 2001) were, in general, comparable to other western Indian semi-arid grasslands (Singh and Joshi 1979b). The low levels of protein in VNP may have been due to the nitrogen-poor soil quality there (Singh and Joshi 1979a, Satyanarayana 1985), but soil quality was not assessed in this study. Crude protein level was found to be positively related to moisture content of grasses (Table 4.2). There may have been high moisture available during the wet season for protein synthesis to occur and for translocation of minerals from soil to grass (McNaughton 1985). Various studies suggest that plant growth in semi-arid areas is limited by water availability, which simultaneously restricts acquisition of nutrients like Nitrogen and Phosphorus (Johnson and Asay 1993).

Acid detergent fibre, lignins and silica content of grasses in VNP did not show much change among the three seasons, except that lignins content was higher in dry season than wet season in one year. Fibre (ADF and

lignins) content is expected to be low only during growth phase or in fresh green shoots (McNaughton 1985). However, in VNP, grasses were perennial and so clumps were mostly mature. In addition, there was no annual fire or heavy grazing by cattle to create space for fresh growth to happen in the wet season. A limited harvesting of grass by villagers was being allowed as part of an eco-development programme. So, grazing by wild herbivores (ungulates, other vertebrate and invertebrate fauna) was the main means of grass removal. Therefore, there may have been limited space for grass to grow or regrow and a consequent limited scope for overall change in fibre level in grasses in VNP. Fibre content generally reduces the digestibility of forage in ungulates. However, in ruminants, ADF is digestible by microbial fermentation in the rumen, but lignins and silica are indigestible (Van Soest 1982, Robbins 1993, Schmidt-Nielsen 1997). Therefore, high ADF levels may not affect blackbuck as much as lignins and silica. However, high ADF may mean higher retention time and therefore, high digestive costs (Bunnell and Gillingham 1985, Robbins 1993). How much these fibre levels affect forage consumption by blackbuck is not known. Seasonal changes in forage consumption by blackbuck in VNP has been found (Jhala 1997), but the role of fibre in that is unclear. A caution that I add here is that the results may have been influenced to some extent by small sample sizes available for these variables.

Limited data on seasonal changes in forage quality is available from Indian habitats. The available studies suggest that biomass and grass growth in drier parts of India are highly dependent on monsoon rains, its periodicity, and the quantum of rainfall (Singh and Joshi 1979a, Misra and Misra 1984, Shankarnarayan *et al.* 1985, Karunaichamy and Paliwal 1989, Jhala 1997). In Serengeti plains of eastern Africa, a similar kind of seasonality in forage abundance and quality is seen as a consequence of rainfall (Field and Blankenship 1973, Sinclair 1977a, McNaughton 1979, 1985, Sinclair *et al.* 2000). In higher latitudes too, forage availability and quality are affected by seasonal climate, where high quality forage is available in spring, but lasts only for a short period (Festa-Bianchet 1988, Berteaux *et al.* 1998, Cook *et al.* 2001, Langvatn *et al.* 2004).

Effect of forage quality on body condition of blackbuck females

Body condition scores of blackbuck females in VNP was found to be better in wet season and worse in dry season (Fig. 4.15). This corresponded with the availability of higher quality forage to females in wet season, as compared to dry season. However, the body condition scores of females in VNP, even in wet season may not be considered high on an absolute scale. The pectoral and pelvic girdles and tailbone depression were visible in the wet season too in VNP during the study period and this did not indicate a high body condition. In contrast, body condition scores of females from other populations such as Sawainagar, Madia (*Bhal* region, Gujarat) and Katuda (Surendranagar district, Gujarat), which largely subsist on croplands or on browse, were much higher than VNP, in the same seasons (unpublished data). Body condition score of females in VNP was positively correlated with moisture and crude protein content of grasses (Table 4.4). Moisture, although would not affect body condition directly, may have an indirect effect by increasing the forage quality of grasses. Energy and protein levels of forage affect the nutritional status of adult females, as these are essential physiological requirements for maintenance, and for other reproductive activities such as pregnancy and lactation (Sinclair 1977b, Oftedal 1985, Price and White 1985, Robbins 1993, Schmidt-Nielsen 1997, Parker *et al.* 1999). Tropical ungulates show changes in body condition as forage quantity and quality changes with seasons, and in particular with rainfall patterns (Sadleir 1969, Sinclair 1977b, Fryxell 1987, Sinclair *et al.* 2000). In northern latitudes, period of high energy and protein availability to animals is short, and animals respond by changes in body condition. Animals synchronise most high energy and protein demanding activities to that period. They reproduce, wean their young and put on body reserves during the short spring season to tide them over harsh winters (Festa-Bianchet 1988, Berteaux *et al.* 1998, Cook *et al.* 2001, Langvatn *et al.* 2004).

Seasonality of calving in blackbuck

There was pronounced seasonality of calving in blackbuck in VNP, although a basal calving of 5-15% was seen throughout the year (Figs. 4.17 and 4.18).

Calving seasonality was bimodal and appeared to be cyclical with an interval between successive calving peak points of about 23-28 weeks (Table 4.5). Blackbuck females in VNP appeared to calve twice in a year with a calving interval of 6 months, as had been observed in Texas ranches (Mungall 1978). A bimodal pattern of reproduction, with two seasonal peaks in calving and two births in a year, is common in several other tropical and subtropical ungulates (Dasmann and Mossman 1962, Sadleir 1969, Field and Blankenship 1973, Anderson 1979, Geist 1981, Kingdon 1982, Murray 1982, Rutberg 1987, Rice 1988, Bronson 1989, Sinclair *et al.* 2000). In the monsoon tropics, rainfall plays an important role in defining seasons by its effect on forage quality and quantity (Sadleir 1969, Field and Blankenship 1973, Fryxell 1987, Sinclair 1977a, Bronson 1989, Sinclair *et al.* 2000). Whereas, in the temperate areas, photoperiod and extreme seasonality defines the birthing seasons (Clutton-Brock *et al.* 1983, Festa-Bianchet 1988, Bronson 1989, Langvatn *et al.* 2004).

A weekly maximum of 62% of females in 2000 and 53% of females in 2001 and 2002 had calved in VNP. This is much lower as compared to the proportions that were reported for some ungulate species. The percentage of females that reproduced in a year was up to 90% in white-tailed deer, red deer, caribou, Dall's sheep and bison (Dauphine and McClure 1974, Richter and Labisky 1985, Rachlow and Bowyer 1991, Berger 1992, Langvatn *et al.* 2004, Keyser *et al.* 2005). These were observed when the forage conditions were good (e.g., the forage was abundant and quality was good) and in addition, population density was low (Richter and Labisky 1985, Langvatn *et al.* 2004, Keyser *et al.* 2005). Even in tropical ungulates of Africa, the percentage of females having given birth in a year has been reported to be as high as 85% (Field and Blankenship 1973, Estes 1976). The blackbuck population in VNP is considered to be a high-density population (approximately 30 blackbuck/km² for the whole area of VNP; Ranjithsinh 1989, Jhala 1999, Gujarat Forest Dept. Management Plan for Velavadar National Park 2002). Within the suitable grassland habitat of about 10km², the density could be over 100/ km². The forage quality, in terms of crude protein, can not be considered high in VNP. The lower reproduction percentage in VNP could have been influenced by these factors.

The calving seasons in VNP were considerably spread out, with lengths ranging from 7-15 weeks. These were too long to be classified as synchronised calving. Most other ungulates that have synchronised birthing, such as wildebeest (Estes 1976), American bison (Berger 1992, Berger and Cain 1999), barren ground caribou (Dauphine and McClure 1974), bighorn sheep (Festa-Bianchet 1988), mountain sheep (Bunnell 1982) and red deer (Langvatn *et al.* 2004) have birthing seasons that are extremely short (ranging from 10 days to 3 weeks). Even in the range of taxonomic groups that show synchrony, including plants (Janzen 1976, Kelly and Sork 2002), brachyuran crabs (Morgan and Christy 1994), insects (Karban 1982), marine reptiles (Rubenstein and Wikelski 2003), birds (Emlen and Demong 1975, Hatchwell 1991, Westneat 1992, Amundsen and Slagsvold 1998) and bats (Heideman and Utzurrum 2003), the birthing season is extremely short. Moreover, all species that show synchronised birthing breed only once a year, as the factors that cause such acute synchrony is more likely to occur once in a year. In ungulates, two reasons have been most frequently cited as causes for synchronised birthing. One is seasonal availability of high quality forage (Sadleir 1969, Festa-Bianchet 1988, Bronson 1989, Fournier *et al.* 1999, Langvatn *et al.* 2004) and second is predator satiation (Kruuk 1970, 1972, Estes 1976, Rutberg 1987, Bronson 1989, Ims 1990a, b). Although there is a seasonal peak in forage quality in VNP, this does not seem to cause any synchrony in calving. In ungulates where predator satiation (or in other words, predator swamping), is a strategy the young follow their mother immediately after birth, i. e., they are precocial and are also highly conspicuous (Estes 1976, Geist 1981, Kingdon 1982, Rutberg 1987, Ims 1990a). Blackbuck have hiding young that are inconspicuous and predation is avoided mainly by concealment (Fitzgibbon 1990, Mungall 1991). Therefore, predator swamping does not seem to operate in blackbuck in VNP. Further, Emlen and Oring (1977) suggested that the species that lek tend to have a longer breeding period and synchrony is rare. One of the main reasons that is forwarded by them for this pattern is the long period of food availability. The male blackbuck in VNP exhibit lekking behaviour and year round rutting, although with seasonal peaks (Mungall 1978, Isvaran and Jhala 2000, Isvaran 2003, *personal observation*). All these characteristics – 2 calving peaks, wide

calving seasons, year round basal level of calving, calf hiding behaviour and male rutting behaviour, point to an absence of acute birth synchrony in this population. However, one caveat needs to be added to these results here. I have used lactation as an index to calving. So, the season of calving here is not the season of births alone, but is confounded by the nursing period. The season of actual births might be shorter than what was measured in this study. Unless the actual births are followed, it would not be possible to measure the length of actual calving seasons. However, since the lactation season lengths were measured from cumulative distributions of lactation, it is likely to reflect the actual calving season lengths.

There was no strong relationship between the body condition scores of females and their lactation status. This is contrary to what has been reported in many studies (Price and White 1985, Robbins 1993, Parker *et al.* 1999, Cook *et al.* 2001). Ungulate body condition greatly influences reproduction and lactation. Females with bad body condition either do not conceive or are unable to successfully reproduce (Sinclair 1977b, White and Price 1985, Robbins 1993). In this study, although seasonal changes in body condition of females were found, body condition differences between lactating and non-lactating females was not found, in any season. This shows that there may have been stronger factors than body condition that were influencing lactation and were probably overriding the possible influence of body condition. Or, although there were relative seasonal differences, the females were in (an absolute) condition sufficient for reproduction in all seasons. During my study period, I have not seen many females in absolutely poor condition in any season and probably the minimum nutritional requirements were being met. Also, I sampled lactating females and the phase of lactation could not be determined. Therefore, the sampled females could have calved much before sampling and had lost condition already due to lactation costs. Animals are known to lose body condition rapidly during lactation (Sadleir 1969, Robbins 1993). Further, for determining fine-grade changes in body condition, an indirect method of visual estimation such as the one I followed may not be appropriate, and better techniques (such as body size measurements, bone-marrow fat or kidney fat index; Sinclair 1977b, Robbins 1993) need to be

adopted. Also, the influence of body condition may have to be measured in terms of offspring survival, rather than birthing alone. Females in poor condition may give birth, but survival of their offspring may be low. Therefore, measuring calf survival rates would be more appropriate for assessing the influence of body condition on blackbuck reproduction. Although body condition did not seem to influence lactation, season had a strong effect. Females, irrespective of body condition, were more likely to calve in the appropriate seasons (wet and dry) when they probably experience high calf survival rates.

The dry season calving peak declined before protein content of grasses started to increase (Fig. 4.19). Although dry season calving occurred during period of low forage availability and quality, calves born during this peak weaned (after 2 months) at a time of higher quality (high in protein) forage. Protein requirement for early growth, especially in weanling calves may be relatively much higher as compared to nursing young or adults (White and Price 1985, Robbins 1993). In white-tailed deer, protein requirement for weanlings is 13 – 20 % protein in forage intake. For nursing young, protein requirement may be met from protein in mothers' milk, but the weaned calves would have to obtain protein from forage. For adult wild ruminants, protein requirements for maintenance and daily activity can be as low as 5% of forage intake (Robbins 1993). Ruminants do not require high protein from forage, except may be for the growth of young ones (White and Price 1985, Robbins 1993, Dove 1996). So, for blackbuck in VNP, protein may be a limiting factor only during the seasons when the young are growing. Therefore, dry season calving peak may have been timed to precede the peak in quality of forage that would be available for young when they weaned, so as to meet their energy and protein requirements for growth and survival. Similar results were found in Grant's and Thompson's gazelle in Kenya's rift valley and in white-eared kob in southern Sudan, which calved during suboptimal forage availability, but the calves weaned when forage quality was at its peak (Field and Blankenship 1973, Fryxell 1987). Reproduction in many tropical ungulates tends to track seasonal highs in forage quality to maximise reproductive output (Geist 1981). Lactation probably provides a buffer for

calves against poor forage quality present through the dry season. The dry season calving peaks were also shorter than the wet season peaks, by 1 – 8 weeks (Table 4.5). As lactation costs for the females would be high, they perhaps invested a shorter time in lactation during the dry season. Consequently, the calves would have weaned earlier as compared to wet season. The nutritional requirements of lactation probably would not be met from the dry season forage and the females in VNP may depend, to a large extent, on catabolization of body reserves (Sadleir 1969, Parker *et al.* 1999). Blackbuck populations that have browse available may shift to feeding on browse in the dry season (Berwick 1974, Chattopadhyay and Bhattacharya 1986, Jhala 1997).

Wet season calving frequency started increasing just as the protein level peaked and the calving peaked as the protein level started to decline. The wet season calving peak occurred after a gap of 23-24 weeks (Table 4.5), which roughly corresponds to the calving interval (5 months gestation period + 1 month post-parturition, pre-oestrus interval) in blackbuck (Mungall 1978). In the later part of the wet season, although protein levels were lower, there was high biomass available until the onset of dry season. In addition, higher protein levels in the earlier part of the wet season may have helped pregnant females and the ones that had recently calved in investing more in foetus and in body reserves. Thus, both the energy and protein needs of lactating females could be met in that season. Also, the body condition of females was high during that season, and this perhaps enabled them to invest more in offspring (e.g., offspring body mass may have been higher in the wet season calving as compared to dry season calving), or lactated longer. During gestation and lactation, adult females may not need protein-rich, but would need energy-rich forage. However, their protein requirements would be relatively higher than non-gestating or non-lactating females (Robbins 1993, Schmidt-Nielsen 1997). In the wet season, the protein digestibility in blackbuck in VNP increased as compared to dry season (Jhala 1997). Therefore, higher protein digestibility, in addition to higher protein content in grass in wet season may have combined to cause a greater increase in forage quality during wet season. Also, intake of digestible energy may be a

greater nutrient limitation than intake of digestible protein, annually, for ruminant ungulates (Robbins 1993, Berteaux *et al.* 1998, Parker *et al.* 1999). Since there was higher biomass available to meet the energy demands of females giving birth in the wet season, and given the higher body condition in that season, those females might have lactated for a longer period. Thus, they may have provided a greater investment in the calves, which might have compensated for the lower quality forage that was available when the calves weaned. This probably has caused the observed longer wet calving season (11 to 15 weeks) as compared to dry calving season (7 to 10 weeks). Note that the length of calving season that I measured was that of nursing rather than birthing season.

The observed cyclical calving pattern, with the wet season calving peak following the dry season calving peak (which precedes the seasonal peak in forage quality and digestibility) after an interval equivalent to the inter-calving period in blackbuck, may be related to the oestrus cycle characteristic of blackbuck. In blackbuck, post-partum oestrus has been observed and lactation and development of a new embryo can occur simultaneously (Mungall 1978). In other tropical and subtropical ungulates too, females tend to come into oestrus shortly after giving birth (Geist 1981, Rice 1988). The observations that blackbuck males in VNP lek more frequently during both the calving peaks (Schaller 1967, Mungall 1978, Ranjithsinh 1989, *personal observations*) also supports this viewpoint.

The basal level calving that occurred throughout the year was maintained probably due to individual genotypic variations, or individual's nutritional status related reproduction, first time calving of young females, or loss of neonate and subsequent post-partum oestrus. Even moderate survival chances of young might maintain both the peaks and the biannual calving might increase the lifetime reproductive output of blackbuck females. Offspring survival is probably enhanced by females that calved in the dry season by having timed their calf weaning to the impending peak in forage quality. The females that calved in the wet season, perhaps compensated for forage quality by greater maternal nutritional investment into the young. In

addition, limited space for new flush to grow and limited scope for increase in forage quality in VNP (due to perennial, matured grass) may have limited the increase in calving frequency (proportion of females calving) in the apparently better (for the growth and survival of weaned-calf) dry season peak. Therefore, both the calving peaks may be maintained over time. However, the limitations to an increase in the proportion of females calving in the wet season are not clear. Data on survival rates of young in both the calving seasons and individual female reproductive rates are required to verify these hypotheses and to better understand the factors limiting blackbuck calving.

4.5. SUMMARY

- I studied the seasonality of blackbuck calving in VNP and examined whether birth synchrony exists in this population. I assessed the seasonal patterns in forage availability, quality, and body condition of blackbuck females, and examined if changes in forage availability, quality and body condition of females influenced calving seasonality.
- Forage variables that were measured are, aboveground grass biomass, moisture, crude protein, ADF, lignins, and silica content in grasses. Biomass and moisture content of grasses were measured by harvesting 24 plots (size 0.5m x 0.5m) each month from August 2000 to December 2002. The other forage variables were measured by analyzing samples from three random plots each month. Body conditions of blackbuck females were assessed visually by ranking five indicative body parts. Blackbuck females were located in different blocks of the study area and females in herds were sampled to estimate the proportion of females lactating (studied from February 2000 to September 2002). I used the number of females lactating as a proportional index of number of females calving.
- Some of the forage variables showed considerable seasonal changes, while some did not. Biomass was the highest in the cold and late wet seasons and lowest in the dry season. Crude protein content was the highest in wet season and the lowest in dry season. ADF and silica content did not show considerable seasonal changes. In one year, lignins content in the dry season was higher than the wet season, but in general it does not seem to vary much through the year in VNP. Body condition of females was the best in the wet season and worst in the dry season.
- Blackbuck calving was clustered during two separate periods of a year (bimodal calving pattern), but a basal level calving (5 – 15%) occurred through out a year. Maximum calving occurred in the months of March and April (dry season), and August and September (wet season) during the study. The calving seasons were considerably spread out with season lengths ranging from 7 – 15 weeks, and these calving seasons

appear to be cyclical, occurring with an interval of 23 – 28 weeks between successive calving peak points. There was no evidence for calving synchrony in VNP.

- Lactation status of females was not related to body condition, but was influenced by season. Calving was not strongly correlated to any of the predictor variables assessed. However, graphical analysis suggested that the two calving peaks (wet and dry calving seasons) seem to have different relationships with the predictor variables. The dry season calving peak preceded the crude protein peak, and the wet season calving peak followed the crude protein peak and coincided with high biomass availability and high body condition of females.
- Blackbuck in VNP appear to have a cyclical calving pattern. The dry season calving peak was probably timed to the impending peak in forage quality, which would have benefited the calves when they weaned. The wet season calving peak occurred after a gap that corresponded to inter-calving interval in blackbuck. The females that calved in the wet season perhaps provided greater maternal nutritional investment into the young, which might have compensated for the lower quality forage that was available to the calves when they weaned.

CHAPTER 5. ACTIVITY PATTERNS AND TIME BUDGETS OF BLACKBUCK HERDS IN VELAVADAR NATIONAL PARK

5.1. INTRODUCTION

Bunnell and Harestad (1989) summarised that the daily activity pattern of an animal is influenced by energy requirements, predators and thermal stress. Similarly, the proportion of time an animal invests in various activities is influenced by many environmental, physiological, and ecological factors. Ruminant ungulates divide a day's time for various activities, including foraging, resting, ruminating, travelling, vigilance, breeding and other social interactions. The factors that determine the time-budgets of ungulates range from body size (Bell 1970, 1971, Jarman 1974, Van Soest 1982, Demment and Van Soest 1985, Lucas 1987, Robbins 1993, Schmidt-Nielsen 1997), other anatomical, physiological, and morphological attributes (Jarman 1974, Jarman and Sinclair 1979, Kingdon 1982, Arnold 1985, Bunnell and Gillingham 1985, Kamil *et al.* 1987, Dove 1996), competition for resources (Bertram 1978, Alcock 1984, Krebs and Davies 1993, White 1993), predation (Jarman and Jarman 1973, Kruuk 1970, 1972, Underwood 1982, Sih 1992, Caro 1994, Fitzgibbon and Lazarus 1995, Owen-Smith 2002), to caring for young (Bunnell and Gillingham 1985, Laca and Demment 1996, Owen-Smith 2002). Further, ambient temperature would influence activity patterns of ungulates (Parker and Robbins 1985, Schmidt-Nielsen 1997, Owen-Smith 1998). Foraging increases thermal load through muscular activity and by exposure to direct and indirect solar radiation. High temperature is known to have a depressant effect on feeding activity. The higher the ambient temperature over the body temperature, the more difficult it is to dissipate heat and the animals would suffer heat stress (Parker and Robbins 1985, Schmidt-Nielsen 1997). In addition to the above-mentioned factors, two important factors that influence time allocation to feeding are availability and nutritive quality of forage. These food-related factors determine many aspects of foraging behaviour of ungulates and consequently influence their overall survival and fitness (Herbers 1981, Bunnell and Gillingham 1985, Hudson and

White 1985, Belovsky 1986, Stephen and Krebs 1986, Laca and Demment 1996, Owen-Smith 2002).

For ungulates, especially ruminants, body size, morphology of mouthparts and stomach anatomy determine the kind and quantity of food that they can consume. Body size determines gut capacity, mouthparts define whether an animal is a specialist or generalist feeder, a grazer or a browser and anatomy of stomach determines the efficiency and rate of processing of food (Bell 1970, 1971, Jarman 1974, Jarman and Sinclair 1979, Kingdon 1982, Owen-Smith and Novellie 1982, Van Soest 1982, Arnold 1985, Bunnell and Gillingham 1985, Demment and Van Soest 1985, Van Hoven and Boomker 1985, Robbins 1993, Schmidt-Nielsen 1997, Owen-Smith 2002). In addition, for ruminants, rumen capacity would influence time allocated to feeding, since it physically constrains the amount that an animal could consume at any one time (Van Soest 1982, Arnold 1985, Robbins 1993, Dove 1996, Schmidt-Nielsen 1997, Owen-Smith 2002). Apart from these factors, there are others that constrain the time an animal would allocate to feeding, and a major among those is social behaviour: ungulates form large social groups to reduce the risk of predation and for other socio-biological factors (Jarman 1974, Krebs and Davies 1993, White 1993, Laca and Demment 1996). However, this also increases intra-group competition for food. On the other hand, solitary animals would need to spend more time being vigilant and thus lose out time that they could otherwise allocate for feeding (Jarman 1974, Underwood 1982). The time spent feeding would depend on energetic demands of an animal (e.g. pregnancy or lactation would incur a higher energy demand), forage dispersion (time searching is higher when food is dispersed widely), abundance, and quality (searching time is less when forage is abundant and the rumen would process food efficiently when forage quality is high; Arnold 1985, Bunnell and Gillingham 1985, Owen-Smith 2002).

Blackbuck is a medium sized ruminant. It is primarily a grazer and feeds on browse in the absence of grass and can be considered a mixed feeder (Schaller 1967, Mungall 1978, Prasad and Rao 1984, Chattopadhyay and Bhattacharya 1986, Jhala 1997). It inhabits arid and semi-arid, open

habitats of India and was once abundant throughout the Indian sub-continent. Hunting and loss of habitat has decreased its numbers and is now listed as being vulnerable to extinction (IUCN 2000). It is protected by the Wildlife Protection Act (1972) of India as a Schedule-1 species. Despite this antelope having been abundant and widespread in the past, more is needed to be known about its ecology. Most studies hitherto have been on behavioural aspects of blackbuck (Schaller 1967, Mungall 1978, 1991, Prasad and Rao 1984, Prasad 1985, Isvaran and Jhala 2000, Isvaran 2003), with an exception of Jhala (1997), which focussed on the nutritional ecology of this species. Activity patterns of blackbuck, time allocation to different activities and the influence of forage availability and nutritive quality on these aspects of behaviour have not yet been studied in detail.

I studied the daily activity patterns and time budgets of blackbuck herds in VNP and assessed the changes in activity patterns during dry, wet and cold seasons. I examined if air temperature had an influence on daily activity pattern of blackbuck. I compared the proportional time investment in feeding, moving and resting/ruminating activities and the distances moved by the blackbuck herds in the different seasons. I further examined if forage quantity and quality influenced the time investment in feeding by blackbuck herds in VNP.

The research hypotheses that I tested are:

- Blackbuck would rest more and feed less during periods of high temperature and vice versa.
- Time invested in feeding activity would be higher in dry and cold seasons (due to low quality forage) as compared to wet season.
- Time invested in resting/ruminating activity would be higher in dry season as compared to wet and cold seasons.
- Time investment in feeding (as opposed to foraging) by blackbuck would be positively correlated with forage abundance.
- Time investment in feeding by blackbuck would be negatively correlated to forage quality.

5.2. METHODS

Temperature and day-length

Temperature in VNP was measured using an automatic temperature logger (Hobo-Onset computer Corp., Bourne, Massachusetts, U.S.A). This was set up in the grassland at a height of 2 feet from the ground and was set to log the ambient temperature every 15 minutes. From these, hourly means of temperature were calculated. Temperature was recorded for the dry and wet seasons and could not be measured for the cold season. Day-length was calculated from sunrise and sunset times obtained by a Global Positioning System (GPS) receiver.

Sampling of blackbuck activity

I used scan sampling (Altmann 1974) to study the foraging activity of blackbuck in the grassland area of VNP. For each season, three female dominated mixed herds of blackbuck were sampled in the study area. Sampling was done during April 2002 (dry season), September 2002 (wet season) and January 2003 (cold season). Scans were done from dawn to dusk with a scan interval of 15 minutes. I attempted to age and sex all animals in the herds during scans, but this was not possible many times as the animals were hidden among grass when they were sitting, feeding or with their heads down in the grassland. Therefore, the total animals that were sampled have been used for analysis without any sex or age-class segregation among them. A spotting scope (magnification 10 – 20x, Bushnell) mounted on a tripod was used for scan sampling (Plate No.6a). Scans were done from watchtowers or from an open jeep. A distance of 100-200m was kept from the herd when sampling, so that the animals would not get disturbed.

The activities of blackbuck were classified into moving, feeding, standing, sitting and other activities such as grooming, social interactions were grouped as 'others' (Plate No. 6b). Standing and sitting activities were added to give resting/ruminating activity. In VNP, to make out whether

blackbuck that were standing and sitting were ruminating was difficult, particularly when they were in the grassland farther than 200m. Standing and sitting (= resting) together can be considered to indicate rumination time since rumination generally occurs, in standing, sitting and lying positions (Jarman and Jarman 1973).

Blackbuck movement

Blackbuck herds were followed from dawn to dusk and their locations were recorded using a GPS unit. The herds did not move together as a single unit but as loose sub-groups. GPS fixes were recorded of the position where greater than 70% of the herd was found. The approximate centre of the herd was recorded as the herd location. Locations were recorded every two hours or when the herds had moved for about 500m. The herd movements were monitored along with scan sampling for the same herds. The linear distances moved between successive locations were measured using Arcview (version 3.1 software, ESRI, Redlands, LA, U. S. A) and the total daily distances moved were calculated.

Biomass and moisture

Above-ground biomass (g /m^2) was measured in 8 systematically (see Chapter 4) laid plots of size 0.5m x 0.5m in the foraging range of each blackbuck herd during the months of activity sampling. Moisture (%) was determined from fresh and dry weights of the harvested grass. Moisture was strongly positively correlated to protein content in grass (see Chapter 4) and so was considered to indicate protein content and thereby grass quality. Biomass and moisture values from the foraging range of each herd was compared to the time invested for feeding by each of the respective herds, in each season.

Statistical analysis

To examine the seasonal differences in activities of blackbuck herds, the proportion of animals in various activities (moving, feeding, resting/ruminating and others) in each scan was calculated and the proportions were averaged

to the hour. The hourly activity pattern of blackbuck in different seasons was described and the feeding, moving and resting/ruminating activities were compared among the three seasons. Further, to examine seasonal differences in feeding, moving and resting/ruminating activities in different periods of the day, data from individual scans were averaged within each time period. The time periods were, early morning (daylight to <8:00 hrs), late morning (8:00 – < 10:00 hrs), noon (10:00 – <12:00 hrs), afternoon (12:00 – <14:00 hrs), evening (14:00 – <16:00 hrs) and late evening (16:00 to darkness). The total time spent in feeding, moving and resting/ruminating and other activities was calculated by adding the proportions of animals in each activity at the end of the scan session (Altmann 1974, Martin and Bateson 1993, Lehner 1996). For statistical analysis, the activity proportions were arcsine transformed ($\theta = \arcsine (\sqrt{\text{proportion calving}})$) to improve normality of data (Sokal and Rohlf 1995).

A two-way factorial Analysis of Variance (ANOVA) model, with period of day and season as the fixed factors, was used to test for the effect of season and period of day on feeding, moving and resting/ruminating activity of blackbuck. Relationships between proportion time spent in feeding and the two predictor variables (biomass and moisture) was assessed using Spearman's rank correlation. For all statistical hypothesis testing, type-I error rate of 5% ($\alpha = 0.05$) was used. I have also calculated the effect sizes and their confidence intervals and used them to complement hypothesis testing in interpreting the results.

5.3. RESULTS

Temperature and day-length

Dry season daily temperature in VNP ranged from 21.3 °C at 5:00 hrs to 45 °C at about 14:00 hrs. It gradually rose during the day until afternoon and fell to about 35 °C at 18:00 hrs (Fig. 5.1). In the period from 10:00 to 16:00 hrs, temperature remained consistently high (greater than 40 °C). Wet season daily temperature ranged from 22.4 °C at 5:00 hrs to 39 °C at about 14:00 hrs. Mean temperature was 30.3 °C at 18:00 hrs. From 10:00 to 16:00 hrs, temperature was moderately high and remained between 30 to 40 °C (Fig. 5.2). Mean sunrise time was 6:20 hrs in dry season, 6:30 hrs in wet season and 7:20 hrs in cold season. Mean sunset time was 19:00 hrs in dry season, 18:45 hrs in wet season and 18:20 hrs in cold season.

Activity patterns

In the dry season from 6:00 to 8:00 hrs, 80% of the blackbuck were engaged in feeding activity and the rest were mostly moving (Fig. 5.1). At 9:00 and 10:00 hrs, there was a sharp decline in the proportion of animals feeding to about 40%, while 20% to 30% were resting or were moving. The proportion of animals feeding increased to about 50% to 65% from 11:00 to 14:00 hrs. At 15:00 hrs, proportion of animals feeding dropped to 25% and proportion of animals moving increased to 20%. Resting was the highest at 15:00 and 16:00 hrs with the proportion of animals resting rising to 45% to 50% (Fig. 5.1). In the subsequent hours, proportion of animals resting decreased sharply to 20% and 11%. In the hours before sunset, moving activity also was less, but proportion of animals feeding sharply increased to about 70% to 80%.

In the wet season too, greater than 70% of blackbuck were engaged in feeding activity in the morning hours (until 7:00 hrs) and the rest were mostly moving (Fig. 5.2). At 8:00 and 9:00 hrs, there was a decline in the proportion of animals feeding to about 45% to 55%, while 30% to 45% were resting. The proportion of animals feeding was high (greater than 75%) from 9:00 to 14:00

hrs. At 15:00 hrs, the proportion of animals feeding dropped slightly and then increased to about 80% at 16:00 hrs. At 17:00 hrs, feeding decreased to about 60% and resting increased to about 30%. In the hour before sunset (18:00), feeding activity peaked to about 90%.

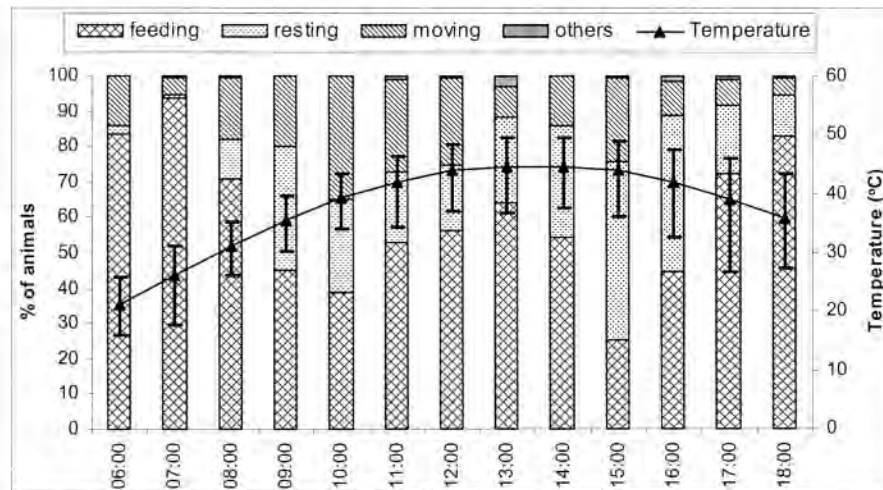


Fig. 5.1. Dry season hourly mean % of blackbuck occupied with various activities (feeding, resting/ruminating, moving and others; as estimated from 4 group scans in an hour) and the mean hourly ambient temperature (line) in Velavadar National Park. The bars on the temperature markers are the maximum and minimum temperatures for that hour.

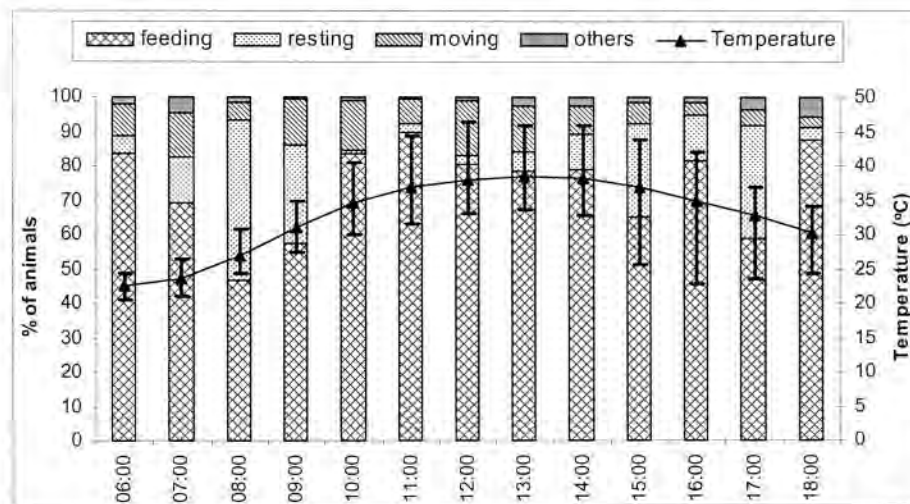


Fig. 5.2. Wet season hourly mean % of blackbuck occupied with various activities (feeding, resting/ruminating, moving and others; as estimated from 4 group scans in an hour) and the mean hourly ambient temperature (line) in Velavadar National Park. The bars on the temperature markers are the maximum and minimum temperatures for that hour.

In the cold season, 85% to 90% of blackbuck were engaged in feeding activity in the morning hours (until 8:00) and the rest were mostly moving (Fig. 5.3). From 9:00 to 10:00 hrs, there was a sharp decline in the proportion of animals feeding to about 30%, correspondingly, the proportion of blackbuck resting rose to about 70%. The proportion of animals feeding increased to about 65% at 11:00 hrs and to about 80% at 12:00 hrs. At 14:00 hrs and 15:00 hrs, feeding activity dropped to about 35% and the proportion of animals resting increased to about 40%. Moving activity was also high at about 25% during 15:00 and 16:00 hrs (Fig. 5.3). The proportion of animals feeding increased to 70% and then to 90% in the hours before sunset.

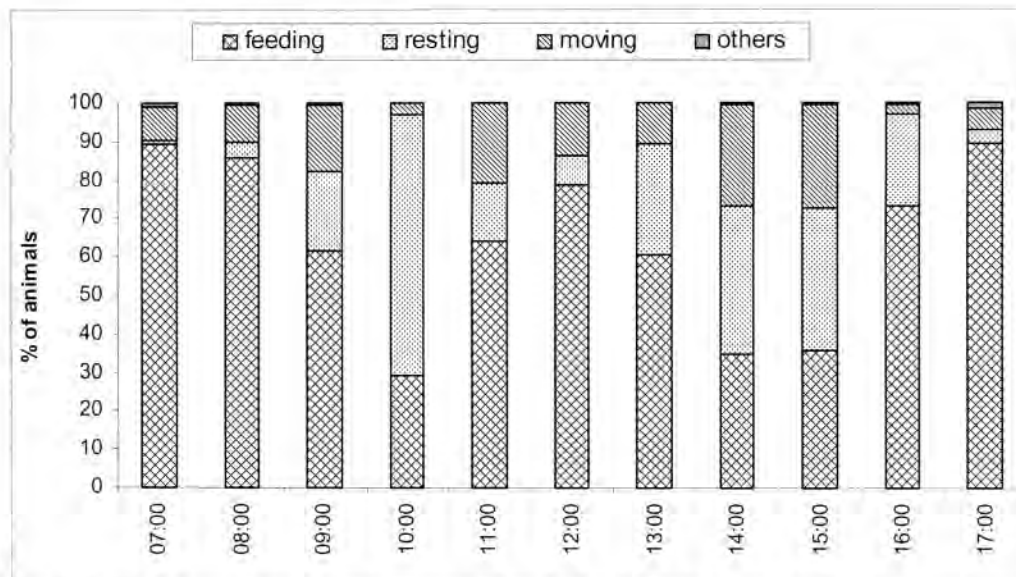


Fig. 5.3. Cold season hourly mean % of blackbuck occupied with various activities (feeding, resting/ruminating, moving and others; as estimated from 4 group scans in an hour) in Velavadar National Park.

Overall, a large proportion of blackbuck spent their time in feeding activity during many hours in all three seasons. For instance, over 60% of blackbuck spent their time feeding during 11 hours (out of 13 hours daylight time) in wet season, 8 hours (out of 11 hours) in cold season, and 6 hours (out of 13 hours) in dry season. Blackbuck showed intensive feeding activity in the early morning hours, followed by sharp decrease in feeding and consequent increase in resting activity (Fig. 5.4). This kind of cycling between feeding and resting/ruminating activity continued through the day. In dry and cold seasons, feeding peaks were

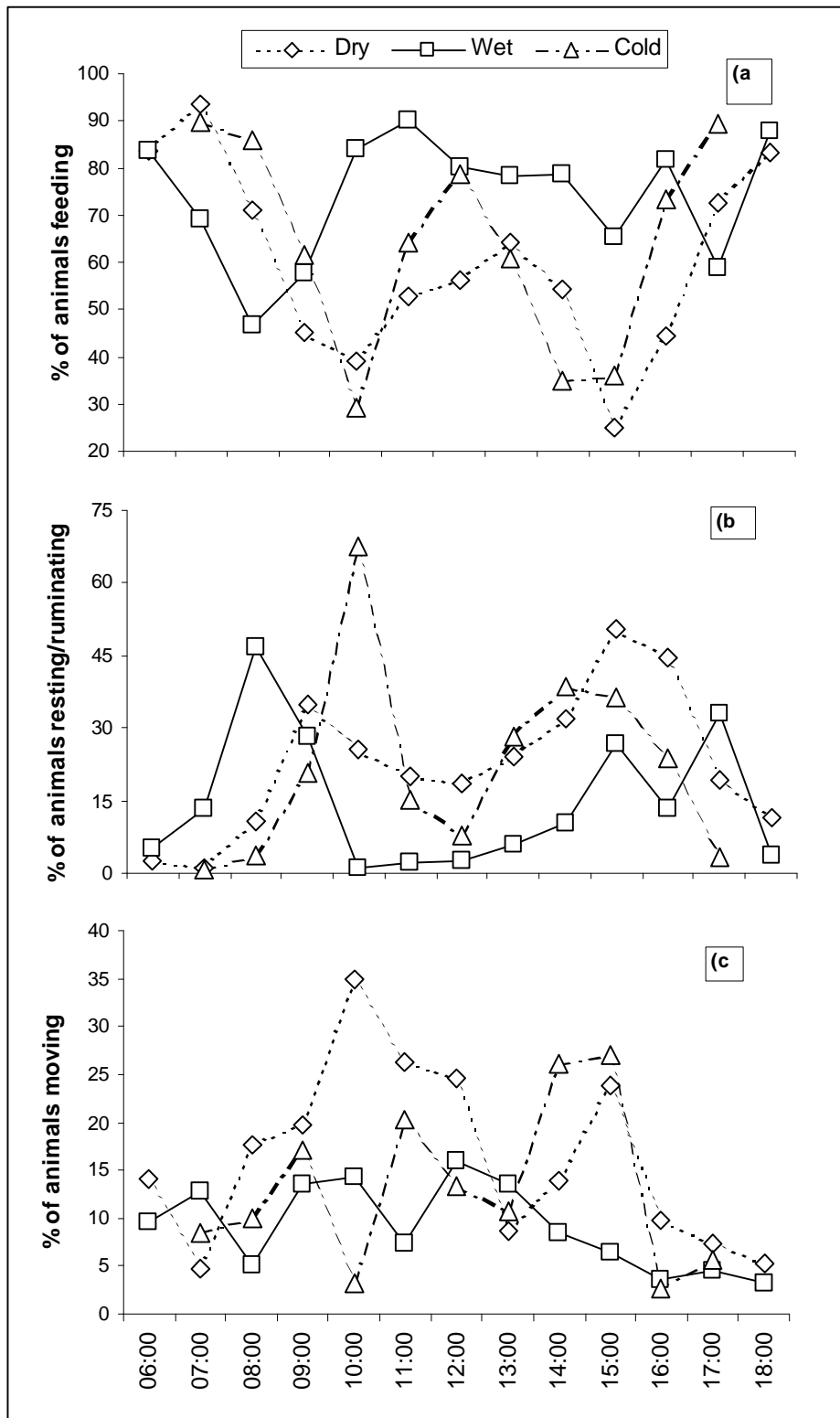


Fig. 5.4. Hourly % (a) feeding, (b) resting/ruminating and (c) moving activity of blackbuck herds in Velavadar National Park (n = 3 groups in each season) in different seasons.

seen in the early morning period (dawn to 8:00 hrs), afternoon (12:00 to 14:00 hrs) and in the late evening. However, the feeding activity was lower during the mid-day peak in the dry season as compared to cold season. In the wet season, feeding activity remained high throughout the mid-day and evening hours. The hourly changes in resting/ruminating activity had a pattern reverse to that of feeding activity in all seasons (Fig. 5.4). The level of moving activity was much higher in the late morning hours of dry season as compared to the other seasons, and moving activity in the late afternoon and evening hours were much lower in the wet season than the other seasons. Also, moving activity was generally low at all times in the wet season. The apparent out-of-synchrony seen in feeding and resting activities of cold season was due to the later sunrise and earlier sunset during that season as compared to other seasons.

Time budget of blackbuck herds

Blackbuck spent major part of a day feeding in all three seasons (Fig. 5.5). 66%, 80% and 69% of their time was spent feeding in dry, wet and cold seasons respectively. Blackbuck herds spent a higher proportion of time feeding in the wet season as compared to other two seasons. Time spent resting/ruminating in wet season was low, and was about half that of the time spent in dry and cold seasons. Moving activity was almost of similar proportion in all the three seasons. Blackbuck engaged in other activities, which included social interactions, grooming, displays etc., to a very small extent.

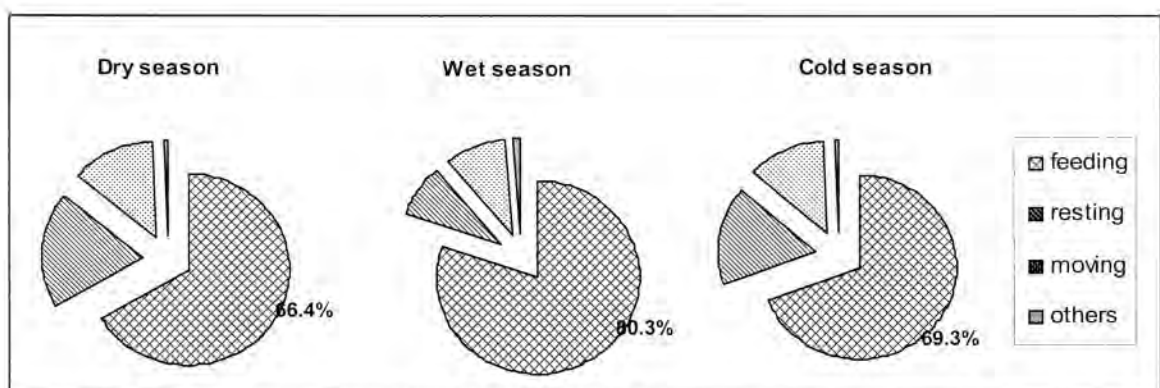


Fig. 5.5. Time budget of blackbuck herds for feeding, resting/ruminating, moving and other activities in different seasons in Velavadar National Park. The values adjacent to the figures are the percent of time spent by animals feeding in the respective seasons.

There was high inter-herd variability in the time invested in feeding in the three seasons and these inter-herd differences did not seem to be related to group size (Fig. 5.6). The differences in the mean proportion of time invested in feeding among the three seasons were not statistically significant (Table 5.1). The differences in the mean proportion of time invested in moving and resting/ruminating among the three seasons also were not significant (Table 5.1). The inter-herd variability in the linear distances moved in a day by blackbuck herds in all the seasons were considerably high (Fig. 5.7). The differences in mean linear distances moved among the three seasons were not significant (ANOVA, $F_{(2,9)} = 1.064$, $P = 0.402$). Overall, no significant seasonal differences were seen in any of the three types of activities or in the linear distances moved by blackbuck herds.

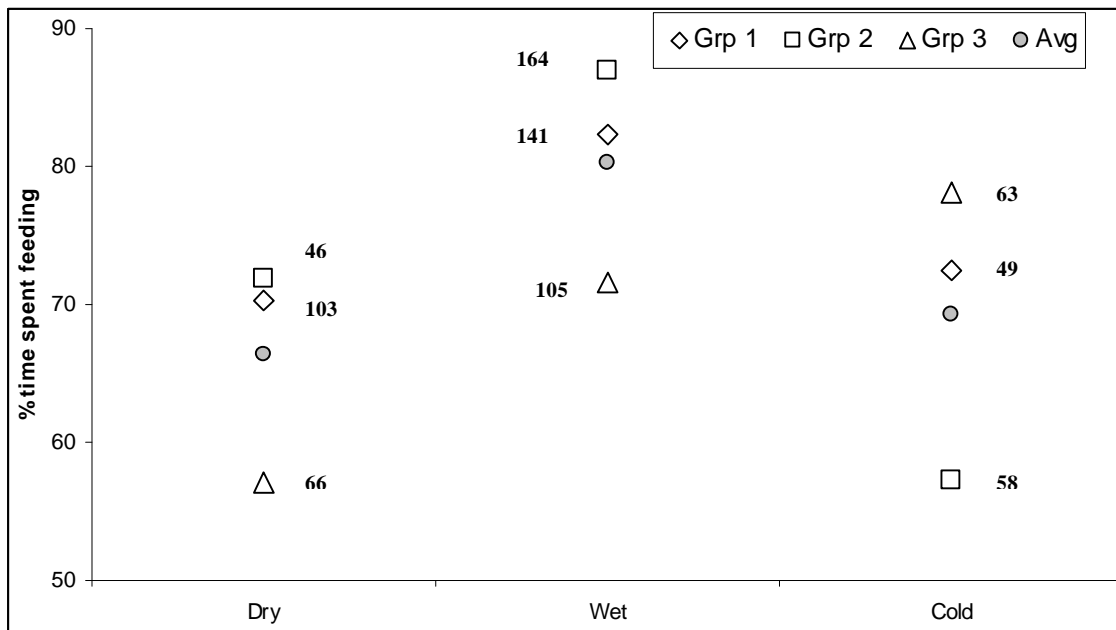


Fig. 5.6. Variability in time spent feeding by 3 blackbuck herds in dry, wet and cold seasons. The shaded circles are the means of the groups sampled in each season. Values adjacent to the markers are mean group sizes of each of the sampled herds.

Table 5.1. The effect of season and period of day on % of time spent in various activities (arcsine transformed) as assessed by a 2-way factorial ANOVA analysis.

Effect	df	Feeding		Resting		Moving	
		F	P	F	P	F	P
Season	2, 35	2.32	0.11	1.56	0.22	2.24	0.12
Period of day	5, 35	3.62	0.01	3.55	0.01	2.54	0.05
Season x Period of day	10, 35	1.57	0.16	1.57	0.16	1.06	0.42

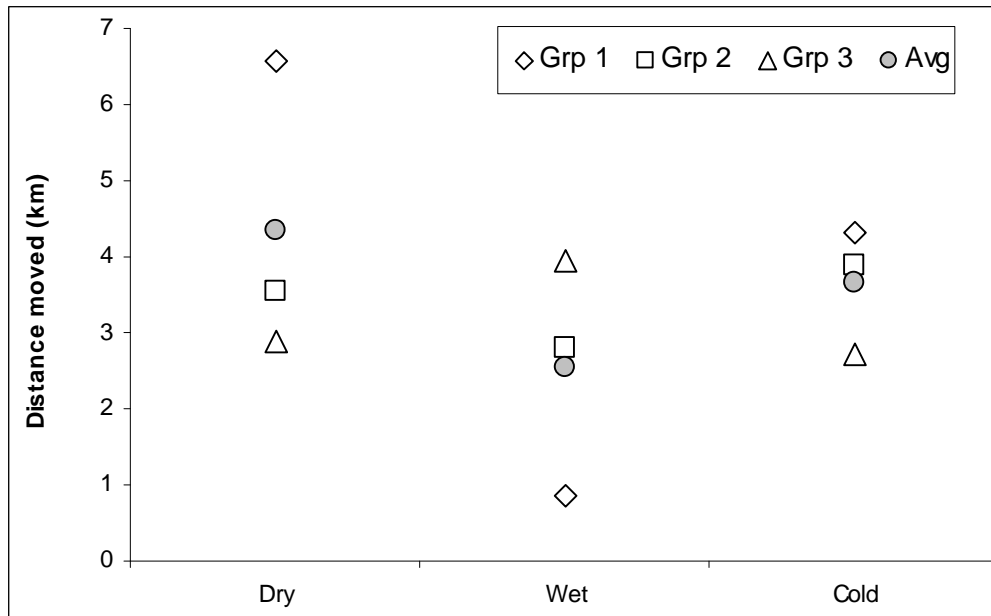


Fig. 5.7. Distance moved during the day (sum of linear distances between feeding patches) by three blackbuck herds in different seasons in Velavadar National Park. The shaded circles are means of groups sampled in each season.

Influence of season and period of day on blackbuck activity

In the dry and cold seasons, percent feeding was higher in early mornings than all other periods of day and particularly higher than noon and evening (Fig. 5.8). Whereas in the wet season, percent animals feeding was more or less similar during all periods of day except late mornings. Percent of animals resting/ruminating was similar in dry and cold seasons. In these seasons animals rested little in the early morning period and more in the evening than

in other periods (Fig. 5.9). In the wet season, resting/ruminating was lowest in noon and afternoon periods. Percent of animals moving was more or less similar during all periods of day in all the seasons except late evening, when moving activity was marginally lower than other periods (Fig. 5.10). Although there seemed to be a higher percent of animals moving during noon in the dry season, and evening in the cold season as compared to other seasons, the high variability makes it difficult to compare these data (Fig. 5.10). Differences among seasons in percent of time spent in feeding, moving and resting activities were not statistically significant, but the differences among periods of day were significant (Table 5.1). There was no evidence to show that the combination of season and period of day (interaction term) had an effect on blackbuck activity. Post-hoc multiple comparisons showed that the differences in feeding and resting/ruminating activity between early morning and evening periods were statistically significant; and difference in moving activity between afternoon and late evening was significant (Table 5.2). Feeding activity was much higher in early morning as compared to evening, resting was much higher in evening as compared to early morning and moving activity was lower in late evening than afternoon.

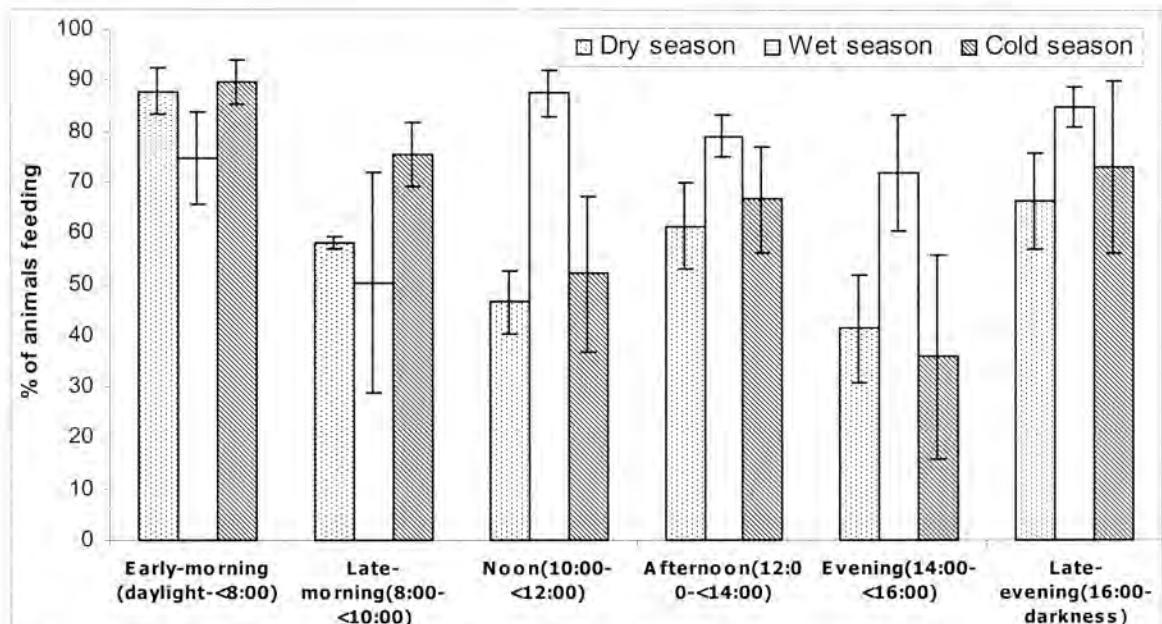


Fig. 5.8. Percent of blackbuck feeding in different periods of day (means of all scans) in different seasons. Error bars represent 1 SE.

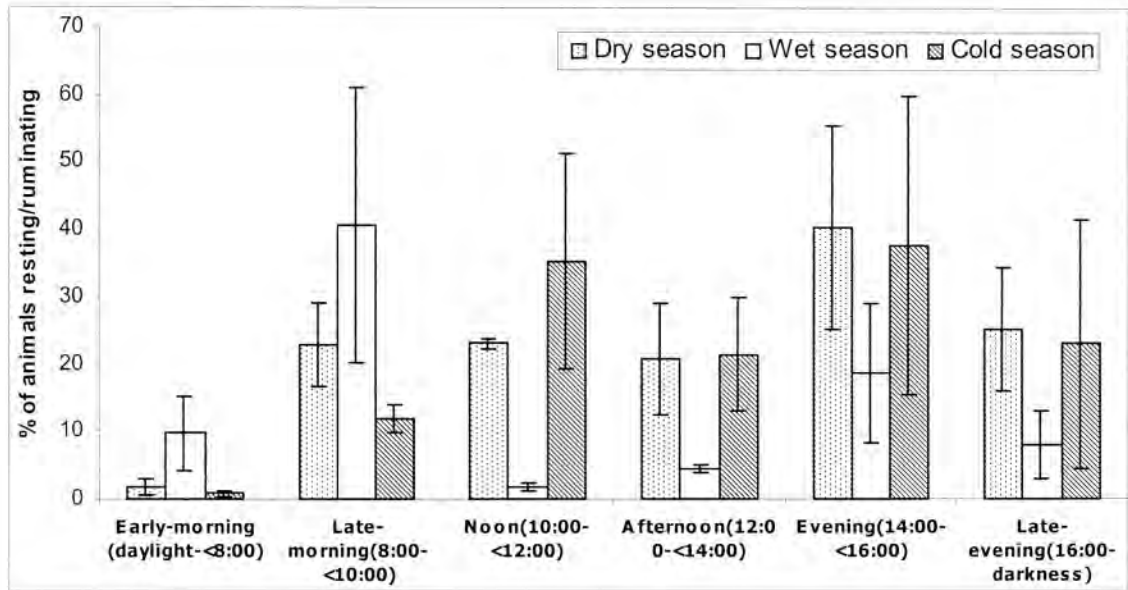


Fig. 5.9. Percent of blackbuck resting/ruminating in different periods of day (means of all scans) in different seasons. Error bars represent 1 SE.

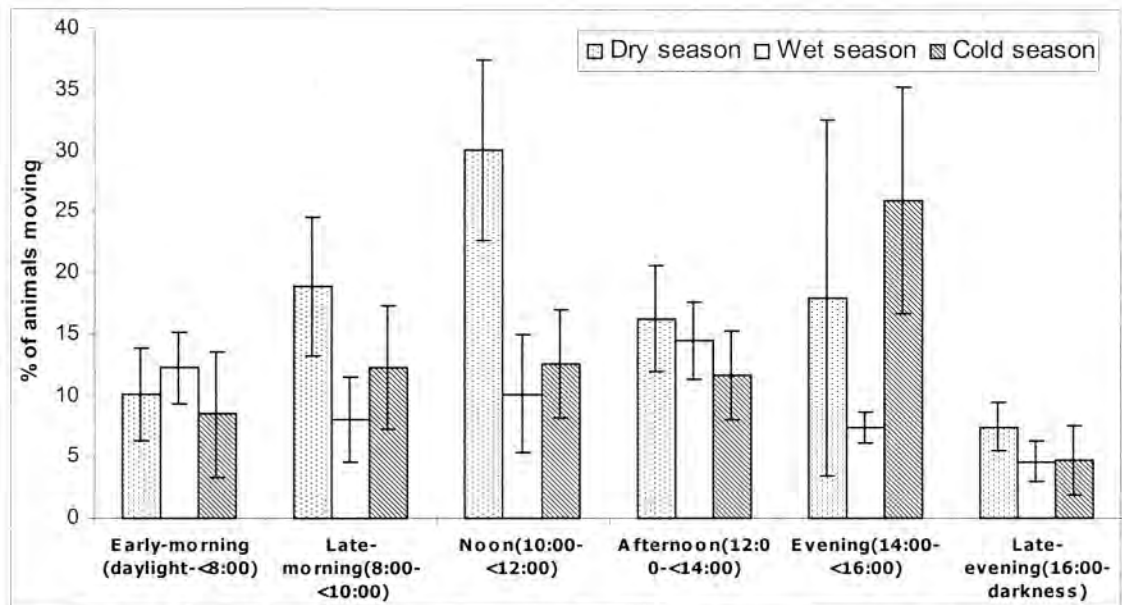


Fig. 5.10. Percent of blackbuck moving in different periods of day (means of all scans) in different seasons. Error bars represent 1 SE.

Table 5.2. Differences between periods of day (the ones that were found to be statistically significant are given here) in % of time spent in various activities by blackbuck (arcsine transformed), as determined by post-hoc pairwise comparisons.

Activity	Post-hoc tests ^a	Period of day and % activity in parenthesis		Effect sizes (difference in means – arcsine transformed) ± 1SE	P value	95% Confidence Interval of effect size	
						Low	High
Feeding	Tukey's HSD	Early morning (84.04)	Evening (49.7)	0.414 (±0.106)	0.005	0.093	0.735
Resting	Tamhane's	Early morning (4.06)	Evening (32.24)	0.4230 (±0.107)	0.042	0.011	0.834
Moving	Tamhane's	Afternoon (14.1)	Late-evening (5.08)	0.1720 (±0.066)	0.029	0.012	0.331

^aTukey's HSD test was done for feeding since the error variances were found to be equal among groups and Tamhane's was done for moving and resting activities as the error variances were found to be unequal.

Relationships of feeding activity with air temperature, biomass, and moisture content of grasses

Hourly percent time spent feeding by blackbuck seemed to have a weak negative relationship with hourly air temperature (Spearman's $\rho = -0.521$, $P = 0.006$, $N = 26$, Fig. 5.11). Seasonal means of (arcsine transformed) % time invested in feeding by blackbuck and seasonal means of grass biomass in the foraging ranges of the herds did not seem to have a relationship (Spearman's $\rho = 0.367$, $P = 0.332$, Fig. 5.12). Similarly, seasonal means of (arcsine transformed) % time invested in feeding by blackbuck and seasonal means of moisture content of grasses did not seem to have a relationship (Spearman's $\rho = -0.010$, $P = 0.798$, Fig. 5.13).

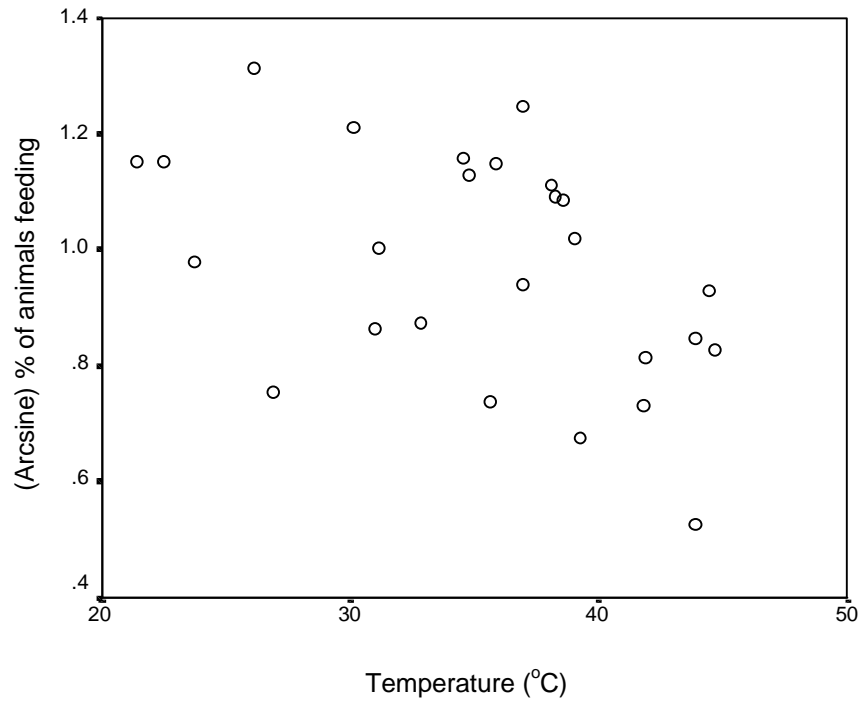


Fig. 5.11. Relationship between (arcsine transformed) hourly % time spent feeding by blackbuck and hourly temperature (in ° C) in Velavadar National Park. (Spearman's $\rho = -0.521$, $P = 0.006$, $n = 26$).

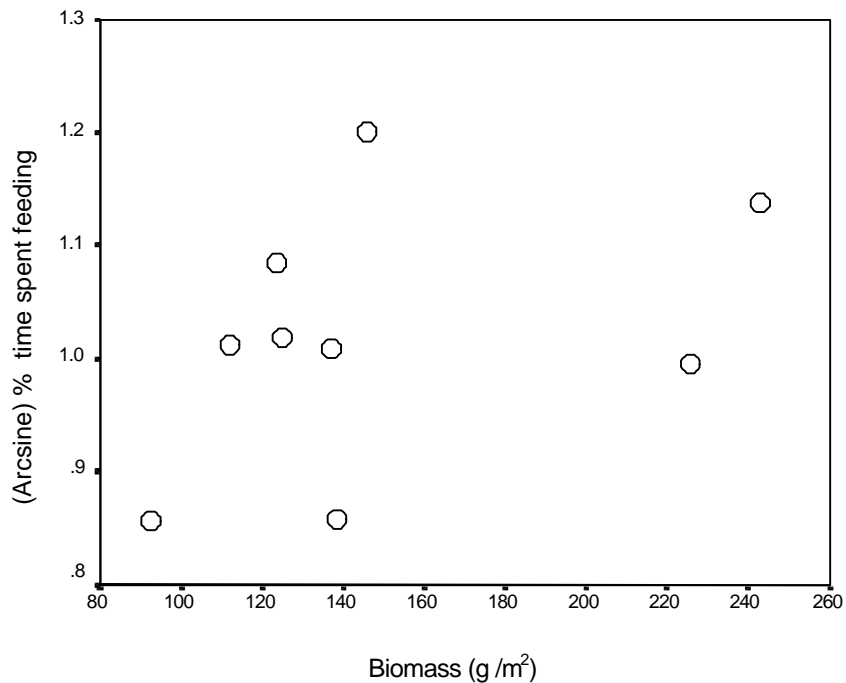


Fig. 5.12. Relationship between (arcsine transformed) % time investment in feeding by blackbuck herds and biomass (g/m^2) of grasses in the foraging ranges of the herds during the periods of activity sampling (Spearman's $\rho = 0.37$, $P = 0.33$, $n = 9$).

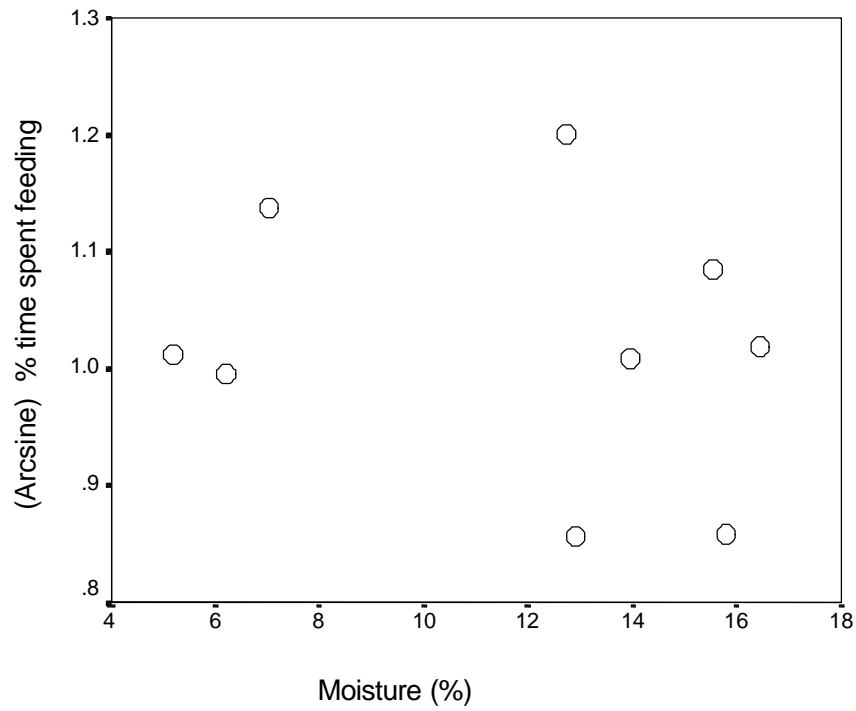


Fig. 5.13. Relationship between (arcsine transformed) % time investment in feeding by blackbuck herds and moisture (%) of grasses in the foraging ranges of the herds during the periods of activity sampling (Spearman's $\rho = -0.10$, $P = 0.8$, $n = 9$).

5.4. DISCUSSION

The daily activity pattern of blackbuck was largely cyclical, alternating mainly between feeding and resting/ruminating activities (Fig. 5.4). There were three feeding peaks and two resting/ruminating peaks during daylight hours. Intensive feeding activity was seen in early morning, around noon and late evening hours. This cyclical activity pattern was more or less similar in all the three seasons. In the wet season, large proportions of each hour were spent feeding throughout the day, or in other words, the resting peaks were not prominent. A large proportion of the day (>65%) was spent in feeding by blackbuck herds in VNP in all the seasons (Fig. 5.5). Hourly feeding activity did not seem to have a relationship with air temperature and seasonal feeding activity did not seem to have relationships with grass biomass and moisture content of grasses (which indicates protein content).

Ruminants are physically constrained by the rumen/gut capacity (Bell 1970, McNab 1980, Van Soest 1982, Demment and Van Soest 1985, Robbins 1993, Dove 1996). Once the rumen is full after an intensive bout of feeding, the ruminants would need to rest and process the consumed food (ruminate) until the rumen can accommodate more food. When the fibre content is high in the forage, higher is the retention time in the rumen as the processing by microbes in the rumen becomes slow (Bunnell and Gillingham 1985, Robbins 1993, Schimdt-Nielsen 1997). Although grass biomass availability shows a seasonal difference, the forage quality does not show substantial seasonal differences (refer to Chapter 4) and is low in the grasses of VNP (low protein and high fibre content). However, even the small seasonal difference in forage quality seems to affect the digestibility of grasses by blackbuck in VNP (Jhala 1997). The increase in forage quality in the wet season results in a higher digestibility. Consequently, in the wet season, blackbuck could spend a larger proportion of the hour feeding and a smaller proportion of time in resting/ruminating (thus, the resting/ruminating peaks are not prominent).

Most studies on other species of ungulates (e.g., Jarman and Jarman 1973, Klein and Fairall 1986, Twine 2002), including some on blackbuck

(Schaller 1967, Mungall 1978; except for Prasad 1985) reported distinct feeding peaks in a daily cycle, with an intensive feeding peak in the early morning period. The description of activity patterns of blackbuck by Prasad (1985) was not clear due to the following reasons: feeding activity was reported to be less than 30% during most hours of the day, in all the seasons, which is exceptionally low as compared to other studies on ungulates (Jarman and Jarman 1973, Mungall 1978, Arnold 1985, Bunnell and Gillingham 1985, Bunnell and Harestad 1989, Owen-Smith 2002). Prasad (1985) observed feeding peaks during noon and evening in the monsoon; in early morning, noon and evening in winter; and feeding activity was more or less constant until noon and evening (afternoon activity was not recorded) in the dry season. Activity was not sampled in the early morning hours in monsoon and consequently, the early morning feeding peak may have been missed out.

Cyclical pattern of activity with alternating feeding and ruminating phases as observed for blackbuck in this study, have been reported in several other species of ungulates such as impala, *Aepyceros melampus* (Jarman and Jarman 1973, Klein and Fairall 1986), greater kudu, *Tragelaphus strepsiceros* (Owen-Smith 1998), black wildebeest, *Connochaetus gnou* (Twine 2002), and blesbok, *Damalicus dorcas* (Klein and Fairall 1986, Twine 2002). Schaller (1967) and Mungall (1978) have also described similar cyclical activity patterns for blackbuck. Schaller (1967) and Mungall (1978) reported that blackbuck spent most of the night-time lying down and resting, with a single feeding peak between 2:00 and 4:00 hrs and that too with only a small proportion of animals feeding. A similar night-time feeding peak has also been reported for impala (Jarman and Jarman 1973) and greater kudu (Owen-Smith 1998) in Africa. Night-time activity was not examined in the present study. However, it was observed that the blackbuck herds would congregate in open areas at dusk and largely stayed there until dawn. Some feeding activity was noticed in the nights, but was limited to the peripheries of the open patches where they rested in the nights.

Activity pattern of blackbuck in VNP seemed to have been synchronised with time of day and this was maintained in all the three

seasons. There was an apparent out-of-synchrony in feeding and resting/ruminating activities in the cold season due to the later sunrise and early sunset during that season. Feeding activity of ungulates is known to be greatly influenced by daylight and this could determine the beginning of feeding activity. Impala began their daytime feeding activity with dawn since these animals depended on vision for detecting predators (Jarman and Jarman 1973). Blackbuck, being an open habitat ungulate and preyed upon by mainly coursing predators, may depend on vision for predator detection (Schaller 1967, Mungall 1978, Ranjithsinh 1989). Therefore, daylight could be the cue for blackbuck in VNP for beginning their feeding activity, which also starts the cycle of alternating between feeding and resting/ruminating activities.

The air temperature did not seem to affect hourly feeding activity of blackbuck herds. They showed a peak in feeding activity in the noon hours, even in dry season, when the ambient air temperature was very high (>40 °C). The apparently weak negative correlation observed between hourly feeding activity and air temperature is a statistical artefact, because of the early morning and late evening feeding peaks when temperatures were low and the trough in feeding during afternoon when temperatures were high. These peaks and troughs are probably due to the cycling pattern of activity rather than related to temperature. Many desert mammals (including ungulates) inhabiting hot tropics and arid areas are adapted to high temperature (Schmidt-Nielsen 1972, Taylor 1972). They have various physiological adaptations by which they are able to withstand higher ambient temperatures than otherwise possible. Studies on influence of ambient temperature on feeding activity of other tropical ungulates (impala – Jarman and Jarman 1973; greater kudu – Owen-Smith 1998, black wildebeest and blesbok – Twine 2002) also suggest that the effect of temperature is small and the animals are not greatly influenced by high daytime temperature. All these species showed substantial feeding activity even when the ambient temperatures were high.

A large proportion of daytime was spent feeding by blackbuck herds in all the three seasons. In addition, the time invested in feeding activity and the daily distance moved did not change much among seasons. The overall time spent foraging typically ranged between 40-70% for grazing ungulates (Jarman and Jarman 1973, Arnold 1985, Bunnell and Gillingham 1985, Hudson and Frank 1987, Bunnell and Harestad 1989, Owen-Smith 2002). The dominant species of grasses found in VNP are perennial. The protein content of grass is low and fibre and silica content of grass is high in VNP (see Chapter 4). Blackbuck in VNP may need to forage for long periods to meet their energy and protein demands from the low quality forage. A higher time spent feeding during low forage quality periods and habitats have been found for many other ungulate species both in tropical and temperate areas (Jarman and Jarman 1973, Jarman 1974, Van Soest 1982, Bunnell and Gillingham 1985, Hudson and White 1985, Bunnell and Harestad 1989, Robbins 1993, Berteaux *et al.* 1998, Owen-Smith 1998). Jarman and Jarman (1973) found that impala (*A. melampus*) spent more time feeding in Serengeti as the forage quality fell. There was a higher utilisation of the fibrous foods in impala by the increase in the rumen volume without a reduction in the gut passage rate (Hofmann 1984, Klein and Fairall 1986). This has also been reported for greater kudu (*T. strepsiceros*) in South Africa, where it includes less palatable forage species in its diet, in addition to an increase in the digestive capacity to accommodate higher forage intake (Owen-Smith 1994). Blackbuck is a medium sized antelope with an average adult female weight of about 23-30 Kg and male weight of about 35-40 kg (Mungall 1978) and is a mixed feeder, but primarily feeds on grass (Prasad and Rao 1984, Bunnell and Harestad 1989, Jhala 1997). They do exhibit seasonal shifts in diet (Schaller 1967, Mungall 1978, Chattopadhyay and Bhattacharya 1986, Jhala 1997), but in VNP this happens only during the short monsoon period when other species of annual grass and forbs become available and in summer they feed on *P. juliflora* pods (Jhala 1997). Therefore, to get the required energy and protein from the low quality forage in VNP, blackbuck may need to spend a large proportion of time feeding.

In both tropical and temperate ruminants, digestible energy and protein are two factors that are major determinants of the time investment in feeding activity (Owen-Smith and Novellie 1982, Arnold 1985, Bunnell and Gillingham 1985, Demment and Van Soest 1985, Hudson and White 1985, Robbins 1993, Berteaux *et al.* 1998, Mysterud 1998). Ruminants are expected to modify their time investment in feeding corresponding to digestible energy and protein content of forage. There is increased digestibility of grasses for blackbuck in VNP in the wet season as compared to dry and cold seasons (Jhala 1997). Consequently, the energy gain for blackbuck per unit time feeding would be lower in dry and cold seasons than wet season. Therefore, blackbuck should feed more in dry and cold seasons. However, time investment in feeding in dry and cold seasons was lower than wet season by 10-15% (Fig. 5.5). It is most probably because the lower quality forage means more time needed for digestion/rumination and thereby a lower percentage of time could be spent feeding. Also, in the wet season, blackbuck would feed much despite higher digestibility and convert extra energy as body reserves to meet future reproduction and lactation costs (Ofstedal 1985, Robbins 1993).

The time investment in feeding by blackbuck did not seem to be influenced by either grass biomass or protein content of grass. This is probably because, firstly, the blackbuck spent a large proportion of time feeding in both periods: low forage abundance and quality (dry and cold seasons) and high forage abundance and quality (wet season). In the low forage quality period, blackbuck needed to spend a large percent of time feeding because of low digestibility of forage, and in the high forage quality period, blackbuck spent a large percent of time feeding that enabled them to put on body reserves. Secondly, the magnitude of change in forage quality among seasons was rather small (a maximum of 2.3% change in crude protein among all pairs of seasons; see chapter 4) and this small change in quality is not expected to change the time investment in feeding greatly. Therefore, a statistically discernible relationship could not be seen between time investment in feeding and the forage-related explanatory variables.

However, a finer-scale assessment of both feeding activity and forage quality than done here may reveal any existing relationships.

Such a lack of influence of forage quantity and quality on time spent feeding was also reported in other ungulates. For greater kudu, the consumption rate (likely to indicate time spent feeding) was not influenced by the changing food abundance (Owen-Smith 1994). Also, it has been observed that as the abundance and quality of forage increased, feeding activity would still be high, although time spent in searching for good quality food would decrease (Bunnell and Gillingham 1985). The processing efficiency of the rumen would also be high when the forage becomes more digestible and there would be increased energy gain by which ungulates could build body reserves for energy demanding processes of reproduction or lactation (Hudson and White 1985, Robbins 1993, Schimdt-Nielsen 1997). Further, Spalinger and Hobbs (1992) suggest that the feeding time (intake or consumption rate) would be limited by physiological and morphological attributes (rumen capacity and bite size) rather than by changing biomass, because the maximum intake rate would be limited by these attributes.

5.5. SUMMARY

- I studied the daily activity patterns and time budgets of blackbuck in VNP. I compared the seasonal changes in daily activity patterns, time investment in feeding and resting/ruminating activities and examined if these were influenced by changes in air temperature, forage quality and quantity.
- Activity of blackbuck was sampled using scan sampling. Each season, three herds were followed from dawn to dusk and their daily activities were studied and distance moved was measured. Temperature was measured using an automatic temperature logger placed in grassland. Forage variables (grass biomass and moisture content as a correlate of crude protein content) were measured in eight plots (0.5m x 0.5m) from the foraging range of each blackbuck herd in each season.
- A large proportion of blackbuck spent their time in feeding activity during many hours in all seasons. Blackbuck showed intensive feeding activity in the early morning, afternoon and late evening periods. Feeding activity was lower in midday in the dry season, but was higher throughout midday and evening in the wet season. Hourly changes in resting/ruminating activity had a pattern reverse to that of feeding activity in all seasons. Moving activity was higher in late morning hours of dry season and was lower during late afternoon and evening hours in wet season.
- Blackbuck spent a major part of the day feeding in all seasons. 66%, 80%, and 69% of daytime was spent feeding in dry, wet and cold seasons, respectively. Feeding, resting/ruminating, and moving activities of blackbuck did not show significant seasonal differences, but showed significant differences among periods of day.
- Daily activity of blackbuck showed a cyclical pattern, mainly alternating between feeding and resting/ruminating activities. There were three feeding peaks and two resting/ruminating peaks during daylight hours. This cyclical pattern was similar in all seasons, except in wet season, when the midday resting/ruminating peak was not prominent. This could have been because of higher digestibility of forage available in that

season, which might have required less rumination time and allowed more feeding time.

- Blackbuck continued to feed during periods of day even when temperatures were high and thus the air temperature did not seem to affect feeding activity. The weak negative correlation observed could be a statistical artefact, because of the early morning and late evening feeding peaks, when temperatures were low and the trough in feeding during afternoons, when temperatures were high.
- Time investment in feeding activity by blackbuck did not seem to have a significant relationship with the forage variables. This was probably because blackbuck spent a large proportion of time feeding in both seasons of low and high forage quality and abundance. Also, the magnitudes of changes in forage quality among seasons were not large (a maximum of 2.3% change in crude protein among all pairs of seasons) and therefore it may not have been a strong factor to influence changes in time investment in feeding. It is also possible that blackbuck in VNP were influenced more by intake rate, rumination time and other limitations posed by morphological and physiological attributes, rather than by seasonal differences in forage quality and quantity.

CHAPTER 6. EFFECTS OF GRASS HARVESTING AND GRAZING (BIOMASS REMOVAL AND FERTILIZATION) ON GRASSLAND PRODUCTIVITY AND GRASS QUALITY

6.1. INTRODUCTION

Studies have shown that the effects of ungulates on plants are profound and cascade through all trophic levels (McNaughton 1977, 1979, 1985, Detling 1988, Hobbs 1996). Hobbs (1996) describes ungulates as not merely outputs of ecosystems but as important regulators of ecosystem processes. Research by various investigators in different continents have shown that the ungulates modify the environment for plants and many other organisms (Caughley 1976, McNaughton 1977, 1979, 1985, 1988, 1990, Cumming 1982, Detling 1988, Milchunas *et al.* 1988, Day and Detling 1990, Frank and McNaughton 1992, Milchunas and Lauenroth 1993, Owen-Smith 1994, 2002, Hobbs 1996, Frank 1998).

Although grassland community structure is largely determined by edaphic and other environmental factors, large mammalian herbivores do exert a strong influence on the processes and functions of the ecosystem (McNaughton *et al.* 1988, Ruess and Seagle 1994, Hobbs 1996, Ritchie *et al.* 1998). Ungulate influence in ecosystems, specifically grassland and savanna ecosystems range from nutrient cycling, litter decomposition, altering productivity and nutritive quality of grasses, species composition and community structure. Ungulate grazing removes the more mature tissues from the top of the grass stands and promotes growth at the basal meristems. Increased penetration of light by the removal of mature tissues from the top increases photosynthetic rate by increasing photosynthate allocation to shoot growth, and increases tillering (lateral bud) growth (Hilbert *et al.* 1981). Ungulates affect the cycling of nutrients directly and indirectly. By grazing, they facilitate movement of Nitrogen from below ground to above ground parts (Detling 1988, Ruess and Seagle 1994, Hobbs 1996). They raise the level of soil nutrients locally by adding urine and faeces. 85-90% of Nitrogen in grasslands is recycled in the form of urine and added to the soil in a readily

absorbable form for plants (Day and Detling 1990, Ruess and Seagle 1994, Hobbs 1996). Patchy use by ungulates also regulates the distribution of nutrients spatially (McNaughton *et al.* 1988, Day and Detling 1990, McNaughton 1990).

Extensive studies on grassland-ungulate interactions have been done in Africa (McNaughton 1977, 1979, 1985, 1988, 1990, Weber *et al.* 1998), North and South America (Day and Detling 1990, Frank and McNaughton 1992, Chaneton *et al.* 1996, Frank 1998, Frank and Groffman 1998). These studies have shown that ungulate diversity, their foraging behaviour and varied intensities of their grazing affect the phenology, productivity, and quality of grasslands. Selective or non-selective grazing affects the competitive interactions between plant species and this may change the ratio of palatable to non-palatable species, and may even result in the transformation of a perennial grassland to an annual one (Detling 1988, Hobbs 1996, Van de Koppel *et al.* 1997). An important aspect to be considered by studies on grassland-grazing interactions is the grazing history of grasslands and their co-evolution with grazing ungulates, both wild and domestic (McNaughton 1985, Milchunas *et al.* 1988, Frank and McNaughton 1992). The grazing history would have a large impact on the physiognomy of the grassland and would determine their ability to support grazing. For example, tillering response to grazing would largely depend on the growth form and grazing history of the grass species (Milchunas *et al.* 1988).

Results from studies on effects of herbivore grazing on plant productivity, regrowth and mineralization processes have been varied. However, it is established that under moderate levels of grazing coupled with appropriate environmental conditions, plants respond positively to herbivore grazing by increasing productivity and improving their quality (McNaughton 1977, 1985, Detling 1988, Hobbs 1996, Weber *et al.* 1998). On the other hand, it has also been shown that high densities of wild herbivores and overstocking of domestic livestock that depend on natural and cultivated rangelands for fodder, have had irreversible detrimental effects on rangelands (Sinclair and Fryxell 1985, Van de Koppel *et al.* 1997, Weber and Jeltsch

2000, Verchot *et al.* 2002). Since many terrestrial grazing lands are known to be extremely vulnerable to effects of grazing pressure (Van de Koppel *et al.* 1997), it is important to understand the impact of grazing on remnant protected grasslands such as the one in VNP. Livestock population in India was 464.5 million in 2003 and the fodder requirement was projected to be 632.6 million tonnes against an availability of dry and green fodder of about 550 million tonnes (URL: <http://www.indiastat.com>, September 2004). Under such a scenario, the last remaining grasslands would face a high pressure from grazing. Much less than needed is known of the ecology of grasslands and the roles of large herbivores in such ecosystems in India. Understanding the dynamics of grasslands and the ecological processes that are involved are necessary to effectively manage both native and cultivated grassland systems (Boyce 1998, Sinclair 1998). Protected grasslands such as VNP could act as baselines for such an understanding. Also, to manage such remnant grassland habitats that support a variety of wild animals, it is necessary to know the kind and magnitude of effects of grass harvesting and grazing would have on the grasslands and thereby to set limits to the permissible levels of harvesting or grazing.

VNP is a semi-arid grassland which has been a grazing land for at least several decades (Ranjithsinh 1989). It was declared a protected area in 1969 and since then the cattle grazing has been minimal inside the Park. The large herbivores that depend on the grasses of VNP are blackbuck (*Antilope cervicapra*), nilgai (*Bosephalus tragocamelus*) and the occasional cattle and buffaloes that belong to neighbouring villages. Other areas of the *Bhal* region outside VNP are a stark contrast to VNP in that they are heavily grazed and trampled and are barren for most part of the year. Stocking densities of livestock are high in this region (livestock population of Gujarat State and Bhavnagar District in 2003 were 14,322,591 and 648,432 respectively), and a large proportion of human population depend on livestock rearing for livelihood (URL: <http://www.indiastat.com>, September 2004). Due to high pressure for fodder from the local communities, the Park management allows harvesting of grass in selected patches in the grassland area of VNP, by people from the neighbouring villages in January and February.

I studied the effects of above-ground biomass removal and simulated grazing (biomass removal along with urine fertilisation) on the above-ground productivity and quality of grasses (in terms of Nitrogen content) in the *Dicanthium annulatum* dominated grassland in VNP. *D. annulatum* is a highly palatable species of grass (remains palatable throughout the year; Dabadghao and Shankarnarayan 1973) and is the dominant grass species eaten by ungulates in VNP (Jhala 1997). I assessed the effects of different intensities of biomass removal and simulated grazing on above-ground biomass productivity and Nitrogen content of these grasses in VNP by way of an experiment.

The research hypotheses that I tested are:

- There would be higher biomass production and Nitrogen content in grasses in moderately harvested or grazed areas than in ungrazed areas.
- The above ground grass productivity and quality (Nitrogen content) would be higher at low and medium levels of removal of biomass and lower at high level of removal of biomass.
- The above-ground grass productivity and quality (Nitrogen content) would be higher at low and medium levels of simulated grazing and lower at high level of grazing.
- Grazing treatment would have higher productivity and quality of above-ground biomass as compared to comparable levels of clipping (harvesting) alone.

6.2. METHODS

Exclosure layout

The study area was divided into 12 equal sized blocks (size approx 0.8 km x 0.8 km). Within each block, grassland patches dominated by *D. annulatum* were identified and exclosures were randomly placed within the patches. One exclosure (size 3m x 2m) in each block was constructed with a wire mesh (size 10cm x 10cm) of electroplated 10-gauge wire, totalling to 12 exclosures in the study area. Within each exclosure, the treatment plots were systematically demarcated with a distance of 20 cm between them. Also a distance of 20 cm was kept from the exclosure fence to the experiment plots. The height of the exclosures were kept at approximately 1.65m (5.5 feet) to prevent large ungulates from grazing the enclosed area (Plate No. 7a). The plots were marked with metal tags to identify specific treatments. All the treatment plots were harvested to the ground level before the arrival of monsoon rains (in May each year). The size of the plots in the first experiment year (2000) was kept at 0.25m x 0.5m and in the second year (2001-02), the plot size was increased to 0.5m x 0.5m, to reduce the variability in the data.

Experimental treatments

The experiment consisted of examining the effect of three different levels of clipping and simulated grazing on above-ground productivity and nutritional quality of grasses. Clipping meant above-ground biomass removal and grazing included clipping along with fertilisation by synthetically prepared bovine urine. I selected six treatments that corresponded to high, medium and low intensities of clipping and grazing. High intensity clipping involved removal of biomass of up to 80% of what was standing in a plot; medium involved removal of 50% biomass; and low involved removal of 10% biomass. In the grazing plots, bovine urine proportional to the clipping intensity (see below) was applied. Two randomly laid plots in each block were harvested each month during the entire experiment period to measure the standing above-ground biomass. Care was taken that these plots were placed only in

ungrazed areas. If a plot fell in an area with signs of grazing, it was discarded and a fresh plot was placed randomly and harvested.

I clipped grass biomass corresponding to the different treatment levels by visual estimation. For this, I first calibrated my visual estimation by the following method. Before beginning the experimental treatments, 30–50 plots were laid each month in all enclosure areas and covering localities with varying grass heights and clump sizes and the above-ground grass biomass in the plots were visually estimated. Then the plots were completely harvested and the total fresh biomass measured. I calibrated my visual estimates with the actual measurements and thus got trained to estimate above-ground grass biomass visually. I continued the calibration until I was able to estimate the total fresh above-ground biomass in a plot to the nearest 5gms. During the experiment, I visually estimated total biomass in the treatment plots and then clipped the grass in increments and measured them so that the biomass clipped equals the treatment level (10% of total biomass for low-intensity clipping, etc.). I thus, clipped grass to the specific level required by the different treatments. The experiment was done for two years (2000 and 2001-02) in the grass-growing season in VNP and treatments were same for both the years. In 2000 experiment, treatments were applied monthly from August 2000 until December 2000 when the final harvest was done. The period of 2001-02 experiment was modified so as to cover the grass-growing period that extended beyond December. Due to heavy rains and inundation of the grassland in August 2001, the experimental treatments were first measured in September 2001 and the next set of treatments were done in October 2001. After October, the grass was allowed to grow for two months and treatment was applied in December 2001. The final harvesting was done in the first week of March 2002. Due to lack of space inside the enclosures, the medium clipping treatment (biomass removal at 50%) was not done in 2001-02 experiment. The grass communities were dominated by *D. annulatum* and were similar in all the treatment plots.

Application of bovine urine (as fertiliser)

Synthetic bovine urine was prepared as described by Day and Detling (1990). The chemicals used to prepare a one-litre stock solution were urea (13.65 g), magnesium chloride (0.76 g), magnesium sulphate (0.73 g), calcium chloride (0.09 g), potassium chloride (7.02 g), potassium bicarbonate (6.83 g), and sodium chloride (1.21g). These chemicals with the respective weights were dissolved in one-liter distilled water in a volumetric flask to make a stock solution. This solution with different dilutions was used for fertilising the different treatment plots. The total volume of the fertiliser solution that was applied was kept constant at 1.2 l/ m², but the urine concentration differed. For high intensity grazed plots (clipped plus fertilised) 800 ml/m² urine concentration was applied; for medium intensity grazed plots 400 ml/m² urine concentration and for low intensity grazed 100 ml/m² urine concentration were applied. The amount of urea (NH₂CONH₂) that would have got added to the treatment plots via urine was 10.92 g/m² (2.54 g of Nitrogen/m²) for high intensity grazed treatment; 5.46 g/m² (1.27 g of Nitrogen/m²) for medium grazed treatment; and 1.4 g/m² (0.33 g of Nitrogen/m²) for low grazed treatment. The stock solution of the fertiliser was prepared fresh just before the time of application. The fertiliser application was done on the plots after sunset, to reduce volatilisation of the components (especially urea) of the fertiliser.

Laboratory analysis

The fresh biomass was measured with a Pesola spring balance or an electronic balance (OHAUS). The samples were dried to constant weight in an oven (at less than 60 °C) and dry weights were measured. The dried samples were ground and stored in airtight bags in the field for later laboratory analysis. Grass samples from three randomly selected plots for each treatment in each month and samples from three standing biomass plots each month were analysed for Nitrogen content. The ground and dried samples were made to pass through 1mm mesh screen (stainless steel) of a Wiley mill in the laboratory. The samples were analysed for Nitrogen content by the micro-Kjeldahl method (AOAC 1990). Samples were digested in a digestive

mix containing 1.5g of 9:1 K₂SO₄ (pottassium sulphate): CuSO₄ (copper sulphate) and digestion was done in a digestion chamber for ≥ 6 hours at 375 °C in 6 ml of sulphuric acid and 2ml of hydrogen peroxide. The digested acidic sample was distilled and the gaseous ammonia was collected in boric acid. It was then titrated against 0.1 Normal sulphuric acid with a double indicator of bromo-cresol-green and methyl red in a 3:1 ratio. The titre value was used to calculate Nitrogen content of the sample.

Statistical analysis

The accumulated above-ground biomass (sum of biomass removed each month and the biomass harvested at the end of the experiment) was used as a response variable for comparisons. Standing biomass was not used for comparison with treatment plots, as they were not considered true controls. Therefore, statistical tests were done only for comparing the effect of different treatments on biomass productivity and Nitrogen content of grasses. For the year 2000 experiment, December 2000 standing biomass (which was the highest monthly standing biomass for that experiment period) was compared (graphically) with the accumulated biomass in the different treatments. Similarly, for the 2001-02 experiment, September 2001 biomass (which was the highest monthly standing biomass during the experiment period) was compared with accumulated biomass in the treatments graphically. March 2002 standing biomass was much lower than the maximum biomass (September 2001) produced in the study area during the experiment period (probably because of withering, litter fall or herbivory). Nitrogen content of grasses, that is % Nitrogen, was translated into Nitrogen g/m². The % Nitrogen was calculated as the average of the three samples analysed in the laboratory for each month and converted to Nitrogen g/m² using the following formula: Nitrogen (g/m²) = % Nitrogen x biomass (g/m²)/100. Then, using these Nitrogen g/m² values, the accumulated Nitrogen was calculated and used in statistical analysis, for testing the effect of treatments on Nitrogen productivity.

To examine the effect of various experimental treatments on accumulated above-ground biomass and Nitrogen content, an Analysis of Covariance model (ANCOVA) was used. Although I had harvested all the treatment plots before monsoon rains (in May) in both the experiment years to reduce the factors that may confound treatment effects, I could not control for the already existing grass clumps with established roots. Since root biomass and associated variables could not be measured, I estimated grass cover (% of the plot area covered by grass) in the treatment plots visually and used the grass cover as a covariate in the ANCOVA model to correct for variability in the density of grass in different treatment plots. Post-hoc pair-wise comparisons were made with Tukey's HSD test (Sokal and Rohlf 1995). In addition to ANCOVA analysis, I also compared treatment effects with a t-test for paired comparisons (Sokal and Rohlf 1995). I controlled for the variation in local conditions of each enclosure area, by standardising the treatment biomass with the maximum monthly standing biomass in that enclosure area (accumulated biomass in treatment plots - maximum monthly standing biomass) and conducted paired t-tests between pairs of treatments. Finally, to test for concordance of treatment effects in both the experiment years, a Kendall's tau-b rank correlation was done (Sokal and Rohlf 1995). For all statistical hypothesis testing, $\alpha = 0.05$ was used.

6.3. RESULTS

There was high variability in accumulated above-ground biomass among plots in all the treatments during the experiment year 2000 (Fig. 6.1a). Medium grazed (clipped plus fertilised) had comparatively low variability, followed by high grazed. Treatment plots had higher accumulated biomass as compared to the standing biomass in the study area during the month of maximum biomass (December 2000; Fig. 6.1b). However, there was no appreciable difference in accumulated biomass among the different treatments. Even after controlling for grass cover (covariate; $r^2 = 0.3$, $P < 0.001$), the differences in means of biomass among treatments during the experiment year 2000 were not statistically significant (ANCOVA, $F_{(5, 65)} = 0.29$, $P = 0.92$).

During the year 2001-02 experiment, there was again high variability in accumulated above-ground biomass among plots in all the treatments (Fig. 6.2a). Standing above-ground biomass in the study area during the month of maximum biomass (September 2001) had relatively low variability and had two outliers. It also was much lower as compared to the accumulated biomass in the treatment plots (Fig. 6.2b). The accumulated above-ground biomass was lower for low clipped and low grazed treatments as compared to the other treatments (Fig. 6.2b). After controlling for the grass cover (covariate; $r^2 = 0.1$, $P = 0.02$), the differences in means of accumulated biomass among treatments were found to be statistically significant (ANCOVA, $F_{(4, 49)} = 2.54$, $P = 0.05$). Post-hoc pair-wise comparisons (Tukey's HSD test) showed that the differences between 3 pairs of treatments were statistically significant (Table 6.1). However, the 95% CI of the differences (effect sizes) were very wide, resulting in an ambiguity about the true magnitude of differences. Paired t-tests showed that the difference in biomass between all pairs of treatments were not statistically significant for both the experiment years (Table 6.2).

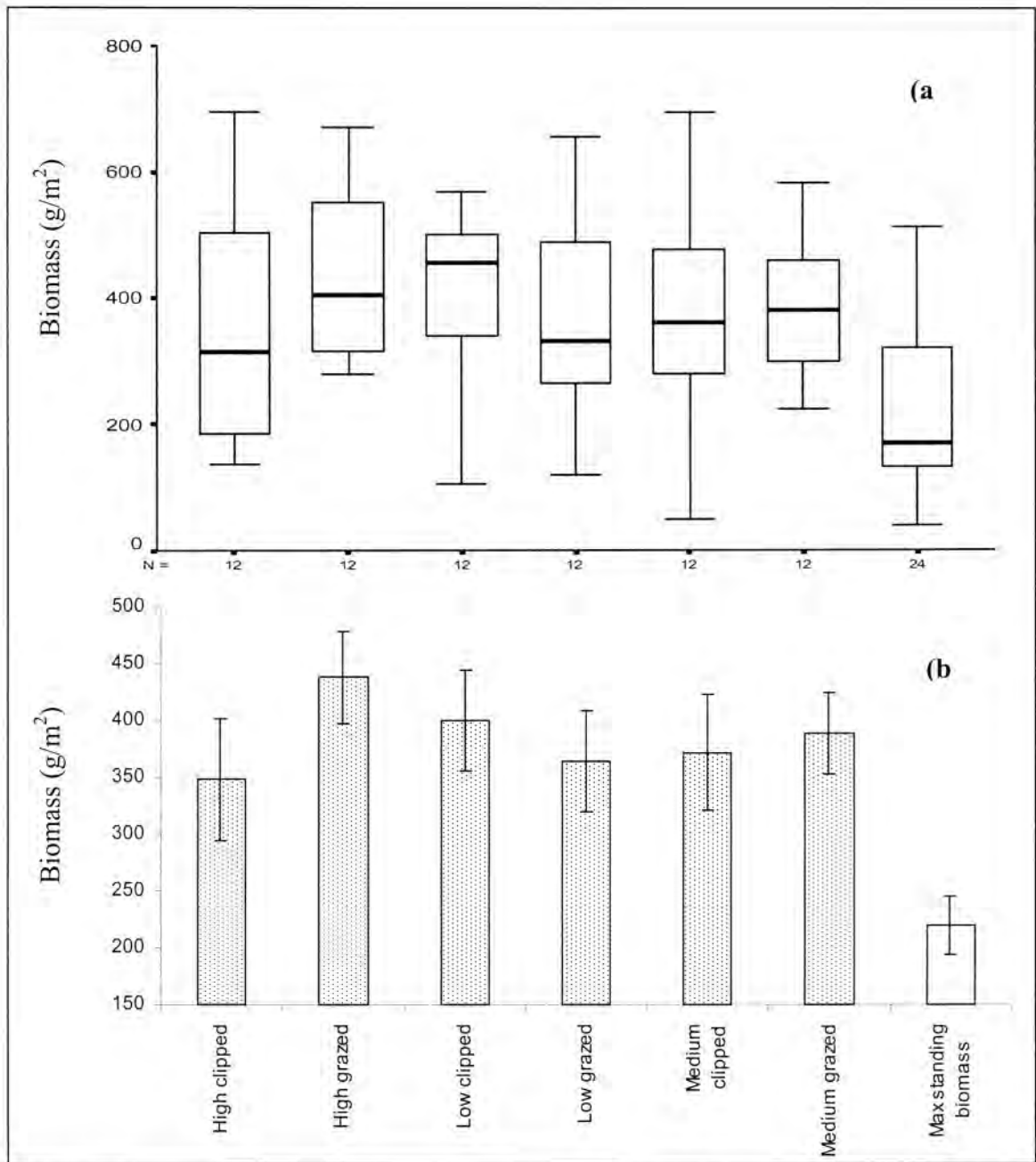


Fig 6.1. Accumulated biomass in treatment plots during year 2000 experiment (May to Dec 2000). Standing biomass in the study area during the month of maximum biomass (Dec 2000) during the experiment period is given for comparison. (a) Box-plots of biomass in the different treatments. The line across the box indicates the median value; hinges of the box give the range containing 50% of the values and the whiskers, the maximum and minimum values; (b) Mean accumulated biomass in the different treatments (shaded bars) at the end of the first experiment year (Dec 2000) and the maximum standing biomass (unshaded bar). Error bars represent ± 1 SE.

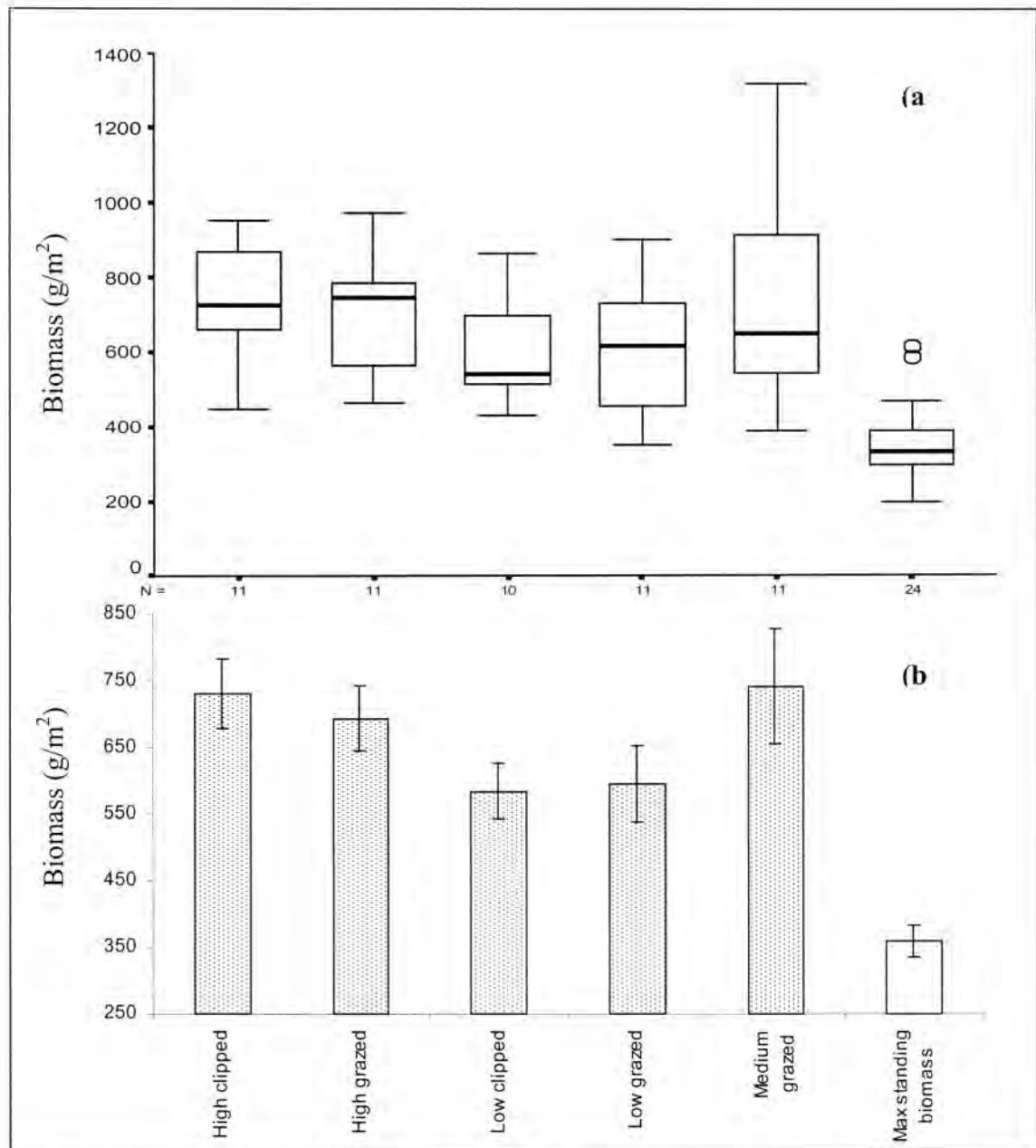


Fig 6.2. Accumulated biomass in treatment plots during year 2001-02 experiment (May 2001 to March 2002). Standing biomass in the study area during the month of maximum biomass (Sep 2001) during the experiment period is given for comparison. (a) Box-plots of biomass in the different treatments. The line across the box indicates the median value; hinges of the box give the range containing 50% of the values and the whiskers, the maximum and minimum values. Circles denote outliers; (b) Mean accumulated biomass in the different treatments (shaded bars) at the end of the second experiment year (March 2002) and the maximum standing biomass (Sep 2001; unshaded bar). Error bars represent ± 1 SE.

Table 6.1. Differences in the means of accumulated biomass (g/m²) and accumulated Nitrogen in grasses (g/m²) among various treatments during the experiment year 2001-02 (May 2001 to March 2002). Results of post-hoc pair-wise comparisons (Tukey's HSD test) and the 95% Confidence Intervals of effect sizes are given (only the results that are significant at $\alpha = 0.05$ are given here).

Variables	Comparisons between treatments ^a	Effect Size (difference in means) \pm 1 SE	P value	95% Confidence Interval of effect size	
				Low	High
Grass biomass (g/m ²)	High clipped - Low clipped (758.67 - 557.71)	200.96 (\pm 81.82)	0.018	36.52	365.39
	High clipped - Low grazed (758.67 - 585.54)	173.13 (\pm 78.82)	0.033	14.73	331.53
	Medium grazed - Low clipped (737.48 - 557.71)	179.76 (\pm 82.61)	0.034	13.74	345.79
Nitrogen in grass (g/m ²)	High clipped - Low clipped (4.47 - 3.60)	1.1 (\pm 0.48)	0.027	0.130	2.070
	High clipped - Low grazed (4.47 - 3.05)	1.56 (\pm 0.46)	0.002	0.626	2.494
	High grazed - Low grazed (4.27 - 3.05)	1.44 (\pm 0.470)	0.004	0.498	2.389
	Medium grazed - Low grazed (3.98 - 3.05)	0.976 (\pm 0.462)	0.04	0.047	1.903

^a Treatment means are given in parentheses

Table 6.2. Differences in accumulated grass biomass (g/m^2) between pairs of treatments in both years of the experiment. Results of paired t-test and 95% Confidence Intervals of effect sizes are given.

Experiment year	Comparison between pairs of treatments ^a	Effect size (difference in means) $\pm 1\text{SE}$	<i>T</i>	<i>P</i>	95% Confidence Interval of effect size	
					Low	High
2000	Low grazed - Medium grazed (144.6 - 168.6)	24 (± 44.8)	0.53	0.6	-74.6	122.68
	Low grazed - High grazed (144.6 - 218)	73.3 (± 36)	2.03	0.06	-5.91	152.57
	Medium grazed - High grazed (168.6 - 218)	49.3 (± 40.8)	1.2	0.25	-40.6	139.24
	Low grazed - Low clipped (144.6 - 179.3)	34.6 (± 50)	0.7	0.5	-75.2	144.61
	Medium grazed - Medium clipped (168.6 - 152)	16.6 (± 52.5)	-0.31	0.75	-132.3	99.02
	High grazed - High clipped (218 - 128)	90 (± 49.4)	-1.81	0.09	-198.9	18.93
2001-02	Low grazed - Medium grazed (231.3 - 376)	144.7 (± 73.7)	1.96	0.07	-19.58	309
	Low grazed - High grazed (231.3 - 329.1)	97.8 (± 74.1)	1.32	0.21	-67.45	263
	Medium grazed - High grazed (376 - 329.1)	47 (± 100)	-0.47	0.65	-269.8	176
	Low grazed - Low clipped (238.2 - 231.8)	6.4 (± 78.3)	-0.08	0.93	-183.7	170.9
	High grazed - High clipped (329.1 - 365.8)	36.7 (± 60.1)	0.61	0.55	-97.3	170.7

^a Treatment means are given in parentheses

Differences in the means of accumulated Nitrogen in grass (% Nitrogen x biomass) among treatments during the experiment year 2000 were not statistically significant (ANCOVA, $F_{(4, 54)} = 0.41$, $P = 0.8$). However, the differences in the means of accumulated Nitrogen in grass among treatments during the experiment year 2001-02 were found to be statistically significant (ANCOVA, $F_{(4, 48)} = 3.8$, $P = 0.01$). The differences were statistically

significant for 4 pairs of treatments (Table 6.1): between high clipped and low clipped; high clipped and low grazed; high grazed and low grazed; and medium grazed and low grazed. As expected, the treatment effects were similar for both accumulated Nitrogen and accumulated biomass during both the experiment years. Since % Nitrogen was converted to Nitrogen g/m² by multiplying with biomass, the effects of treatments, if any on % Nitrogen, independent of biomass, could not be ascertained from this analysis. Therefore, to assess this, mean nitrogen content (% Nitrogen) in the different treatments were compared (Figs. 6.3, and 6.4). In the experiment year 2000, the Nitrogen content of grasses from standing biomass plots was lower than all the treatments in all the months, since the first month of treatment (August 2000) until the final month (December 2000; Fig. 6.3). However, there was no such consistent difference in % Nitrogen among the different treatments. When compared within months, there was no statistically significant difference among the treatment means (%Nitrogen). In the experiment year 2001-02 too, the treatment effects on %Nitrogen were similar to the experiment year 2000 (Fig. 6.4). Nitrogen content of standing biomass plots was lower than all the treatments in all the months; and the differences among treatments were not consistent. In December 2001, Nitrogen content of high clipped and high grazed plots could not be measured, as there was limited growth in those plots. In the experiment year 2001-02, when compared within months, there was no statistically significant difference among treatment means (%Nitrogen).

The rank order correlation coefficient as a measure of concordance among the treatment effects of the experiments in both the years were, Kendall's $\tau_b = -0.2$, $P = 0.6$, and $N = 5$ for biomass, and Kendall's $\tau_b = 0$, $P = 1$, and $N = 5$ for Nitrogen. This shows an absence of agreement in the results of the experiments in the two years, for both the variables (biomass and Nitrogen).

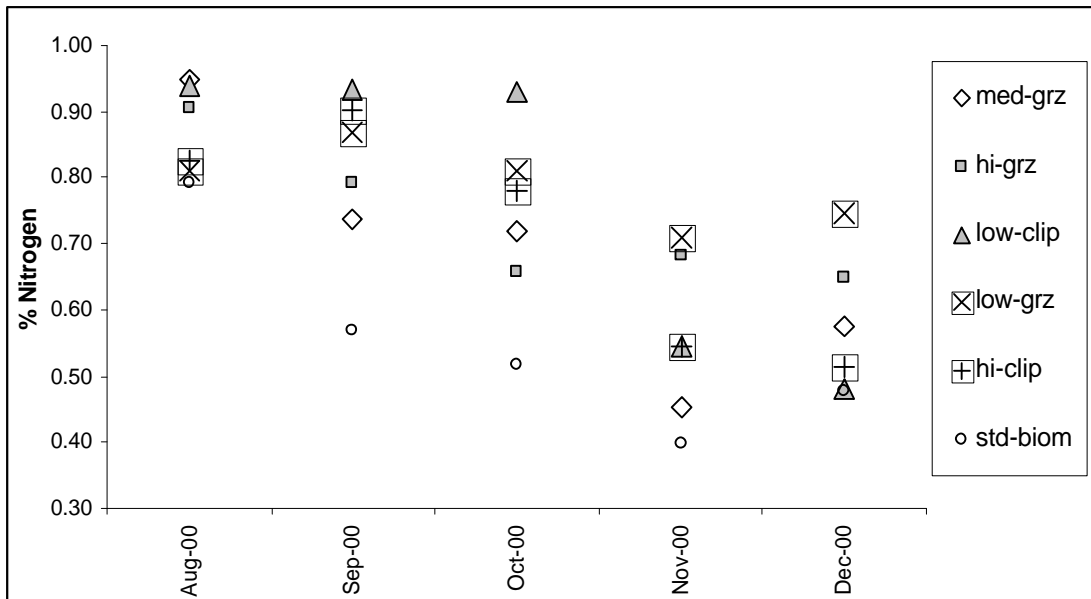


Fig. 6.3. Nitrogen content of grasses (% Nitrogen) in the different treatment plots during year 2000 experiment. Nitrogen content of grasses in the standing biomass plots for each month is given for comparison (circles).

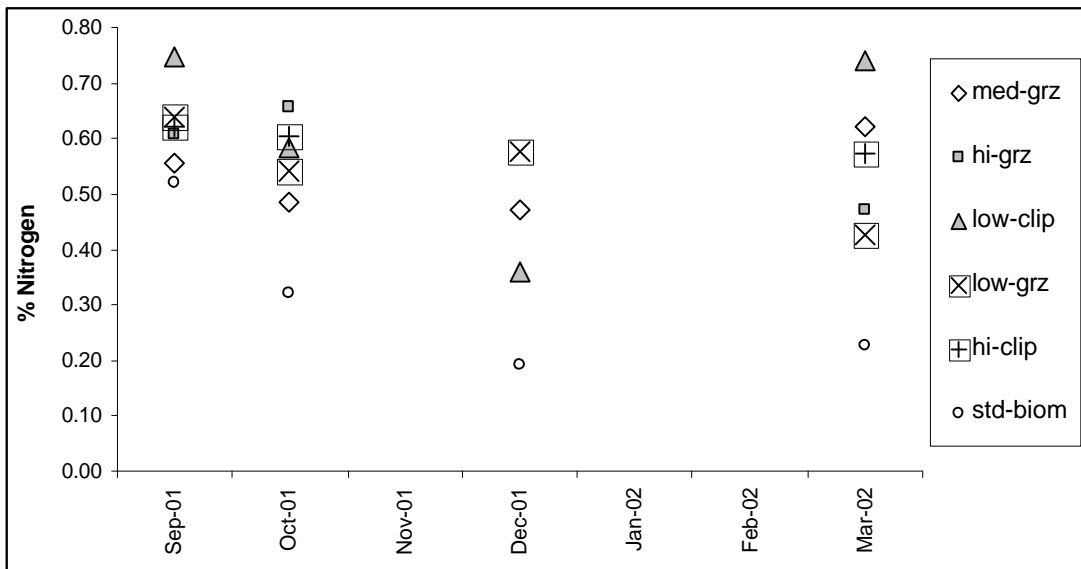


Fig. 6.4. Nitrogen content of grasses (%Nitrogen) in the different treatment plots during year 2001-02 experiment. Nitrogen content of grasses in the standing biomass plots for each month is given for comparison (circles). Nitrogen content of high clipped and high grazed treatments were not measured in December 2001 (see Results).

6.4. DISCUSSION

Clipping and grazing treatments (of all levels) increased above-ground grass biomass productivity and Nitrogen content of grasses. However, there were no appreciable differences in the effects of treatments on both the variables (biomass and Nitrogen content of grasses) among the different treatments. Additionally, the effects of treatments were not consistent in the two years of the experiment. Overall, there was a high variability in the data and the differences among treatments were small, leading to equivocal results.

Above-ground grass biomass productivity in all the treatments were higher as compared to standing biomass (controls), in both the experiment years. Similarly, Nitrogen content of grasses (%Nitrogen) were higher in all the treatments than that of grass from standing biomass plots. Grazing by ungulates is known to increase grass productivity and Nitrogen content in grass (McNaughton 1977, 1985, Day and Detling 1990, Hobbs 1996, Augustine and McNaughton 1998, Frank and Groffman 1998). Defoliation (harvesting) also increases grass biomass productivity to some extent (Detling 1988, McNaughton 1985, Hobbs 1996). When grass is grazed or harvested, there is facilitation of release of energy and nutrients from below ground parts of grass to above ground parts. When ungulates graze, they add urine, which contains Nitrogen in a readily usable form (aqueous urea) to the ground, and thereby effect mineralisation (Day and Detling 1990, Hobbs 1996, Augustine and McNaughton 1998, Frank and Groffman 1998). 85% of Nitrogen in ecosystems is known to be recycled as ungulate urine (Day and Detling 1990, Hobbs 1996). Additionally, removal of mature tissues from the top level of grass increases light penetration to the basal meristems, which in turn increases their photosynthetic rate, and this coupled with the presence of moisture leads to an increase in productivity (Detling 1988, McNaughton 1985, Hobbs 1996).

Grasses in VNP were mostly perennial, clumps were mature, and there has been no heavy grazing or application of fire as a management tool. However, some harvesting of grass has been allowed as a part of Park

management's eco-development programme (Plate No. 7b). Therefore, grass productivity and Nitrogen content of grasses in VNP were expected to increase with grazing and harvesting, due to the above mentioned factors. However, there could be other unstudied physiological responses to grazing happening alongside (e.g., effect on root biomass productivity, loss of tissue Nitrogen etc., McNaughton *et al.* 1998, Ritchie *et al.* 1998). Also, grazing and harvesting did not always promote growth. Studies in rangelands and on grass species in the laboratory indicated that the response of grasses to grazing and biomass removal (harvesting) were highly varied and depended on several interacting factors, such as geographical location, species composition, productivity, consumption level, grazing history, type of grasses and grassland (C_3 , C_4 grasses; tall or short grassland), etc. (Detling 1988, Milchunas *et al.* 1988, Milchunas and Lauenroth 1998, Heitschmidt *et al.* 1999). Milchunas and Lauenroth (1998), comparing data from many studies in various regions, found that grazing effects on biomass productivity were varied. In their analysis of grassland studies, they found that productivity of the habitat and consumption levels affected the response of productivity to grazing. When productivity of the grassland was high, the difference in biomass production between grazed and ungrazed sites was small. Also, at higher levels of consumption, the difference in productivity between grazed and ungrazed sites was small. Detling (1988) found that grass productivity in short and tall grass prairies (of both C_3 and C_4 grasses) was not affected by grazing, whereas, grasses in Northern mixed grass prairie and desert grassland showed varied responses. In Northern mixed grass prairie, C_3 grasses showed a higher productivity in ungrazed patches, while C_4 grasses showed a higher productivity in grazed patches. In desert grasslands, C_4 grasses showed a higher productivity in ungrazed patches (Detling 1988). Similar to the result from northern mixed grass prairie, the C_4 grass community of VNP showed increased productivity after grazing treatment.

I found no significant differences among the different experimental treatments in both the years. Low to medium levels of grazing or harvesting were expected to have higher productivity and quality of grasses, as compared to high levels of grazing or harvesting, as have been found in other

studies (McNaughton 1979, 1983, Detling 1988, Frank and McNaughton 1992, Milchunas and Lauenroth 1993, Frank and Groffman 1998). The grasses in Serengeti of eastern Africa had an increased biomass productivity and quality (Nitrogen content) with low to medium levels of grazing (McNaughton 1977, 1983, 1985, McNaughton *et al.* 1988). However, high level of grazing affected grass productivity detrimentally and there was additional impact of trampling by the migratory wildebeest (*Connochaetus taurinus*). Similar results were found in grasslands of Yellowstone National Park in North America (Frank 1998, Frank and McNaughton 1998). In the present study, differences among treatments could not be seen clearly, and this seems to be largely due to the small effect sizes and high variability in the data. Although I controlled for some of the sampling variability by harvesting all the treatment plots at the beginning of the experiment, so as to have similar starting points for all the plots in all the treatments, and further used grass-cover as a co-variate in an Analysis of Co-variance (ANCOVA) model, the variability was still high. Further, I accounted for the variability in local environmental conditions of exclosure sites by standardising the treatment biomass value of each exclosure with the maximum standing biomass of that area, and conducted additional statistical analysis (paired t-tests). However, the variability still remained high and the differences were not found to be statistically significant.

I laid out the treatment replicate plots in 12 different exclosures spread out in the study area, to capture the variability in response to treatments, but this seemed to have contributed to the high variability in the data. Many factors that influence productivity, such as local soil conditions, root biomass of grass clumps etc., may also have contributed to the high variability. Some of these factors could potentially be controlled in future studies, by including them as co-variates and analysing the data in an ANCOVA type of model. In an ANCOVA model, the effect of co-variates on response variables could be controlled retrospectively, and thus inclusion of co-variates would reduce the unexplained variation in the response variable (Underwood 1997). However, some factors may still remain unknown because of the complexity of the system. It would be best to do such experiments in completely controlled

conditions, such as the ones done by McNaughton and his colleagues for their Serengeti studies, where they reproduced natural conditions in the laboratory and supplemented lab studies to field studies (McNaughton 1979, McNaughton 1984, McNaughton *et al.* 1988, Frank and McNaughton 1992, Ruess and Seagle 1994, McNaughton *et al.* 1997, Williams *et al.* 1998).

In the present study, results of both years of the experiment were inconsistent. The first year of the experiment was a drought year and second was a good rainfall year. Although the difference in the inter-year rainfall would not have affected within-year comparisons of grass productivity and quality, the rainfall probably had influenced different grass response to the treatments in the two years and that perhaps has led to inconsistent results. Rangelands are known to respond differently to external treatments in periods of drought and good rainfall (Heitschmidt *et al.* 1999). I repeated the experiment in the second year so that results from the first year's experiment could be confirmed and stronger inferences could be made. But the discordant results indicate a need for further replication of the experiment or a redesigning of the experiment, improving on the drawbacks of the present design. This study is a good example as to why whole experiments need to be replicated temporally and spatially, or complemented with laboratory work, before conclusions could be drawn on effect of treatments.

Although it was shown that grazing and biomass removal (harvesting) did enhance productivity and quality of grasses in VNP, the upper limits to grazing and harvesting, so as to maintain the increased productivity and to control it from being over grazed/harvested, and consequently from becoming highly degraded, could not be determined. Even in other parts of the world, despite long-term research and theoretical studies, there seems to be no unanimity on the thresholds to grazing and harvesting. This is because the long-term effects of management practices and the complex interactions are still not completely understood (Friedel 1991, Laycock 1991, Glasscock *et al.* 2005). The long-term effects of different intensities of grazing and harvesting need to be known in VNP, but are beyond the scope of this study. It would be imperative to assess the effects of grazing and harvesting in a comprehensive

way for better management and conservation of grasslands. Grassland habitats like VNP are declining in size and are becoming endangered in India and elsewhere in the world (Van de Koppel *et al.* 1997). With increasing pressure of humans and livestock on grasslands, it becomes important to scientifically manage the remaining grasslands. This is needed to prevent them from being degraded completely as it happened in the grasslands of Sahel region of northern Africa, where sustained restoration work has also been largely unsuccessful (Sinclair and Fryxell 1985, Van de Koppel *et al.* 1997).

The unprotected areas outside VNP are completely overgrazed and barren, and are in stark contrast to the dense grassland inside the protected Park. Because of low productivity, low Nitrogen levels, high soil salinity, frequent droughts, unimodal rainfall pattern, and a high stocking density of livestock in this region, there is a high pressure on the Park for fodder needs of local human communities. However, before grazing or harvesting of grass is allowed in VNP, additional studies that address the effects of such practices on below ground productivity, long term effects on the habitat, and impacts on other components of the ecosystem become necessary. In the studies carried out in similar semi-arid grasslands of western India (Singh *et al.* 1991), it was suggested that winter burning or moderate grazing could enhance productivity, but the authors have not considered the negative feedback effects, or other ecological processes that might get impacted by such practices. Therefore, until the upper limits to grazing and harvesting, so as to maintain the enhanced productivity and quality are known, and other grassland dynamics are understood, it would be difficult to suggest ways to optimally manage these grasslands. A conservative approach to management may be necessary until then.

6.5. SUMMARY

- I studied the effects of harvesting (biomass removal) and simulated grazing (biomass removal along with urine fertilisation) on the above-ground productivity and quality of grasses (in terms of Nitrogen content) in the *Dicanthium annulatum* dominated grassland in VNP, by way of an experiment.
- Three levels of treatment – low, medium, and high intensities of harvesting (clipping) and grazing (clipping and fertilisation with chemically prepared bovid urine), were applied to plots in 12 exclosures distributed systematically in the study area. The treatments were applied monthly and the experiment was done in the grass-growing season for two years (2000 and 2001-02). The forage variables were measured and the effects compared among treatments and with the maximum standing biomass of the study area.
- All harvesting and grazing treatments increased above-ground biomass and Nitrogen content of grasses (as compared to standing biomass), but there were no substantial differences among the different treatments. The small effect sizes and high variability in the treatment plots seems to have rendered the effect of treatments on grass productivity and quality statistically not significant. This is despite controlling for some of the variability by using grass cover as a co-variate. Even when I accounted for variability in local environmental conditions of exclosure sites by standardising the treatment biomass of each exclosure with maximum standing biomass of the surrounding area, and conducted analyses using a paired t-test design, the magnitude of treatment effects remained uncertain.
- It seems that there might have been unknown factors such as root biomass, and soil quality that confounded the effect of treatments and added to the variability, leading to equivocal results.
- Although it was observed that harvesting and grazing did increase above-ground productivity and quality of grasses, the upper limits to harvesting and grazing, so as to maintain the increased productivity, and at the same time to control it from being over-grazed or harvested and consequently

from becoming degraded could not be determined. Therefore, before grazing or harvesting of grass is allowed in VNP, further studies on this aspect and studies that address the effects of such practices on below ground productivity, long term effects on the habitat, and impacts on other components of the ecosystem become necessary.

LITERATURE CITED

- Alcock, J. 1984. Animal behaviour: An evolutionary approach. 3rd edition. Sinauer Associates Incorporation, Sunderland, Massachusetts.
- Altmann, J. 1974. Observational study of behaviour: Sampling methods. Behaviour 49: 228 - 267.
- Amundsen, T. and T. Slagsvold. 1998. Hatching asynchrony in great tits: A bet-hedging strategy? Ecology 79: 295 - 304.
- Anderson, J. L. 1979. Reproductive seasonality of the nyala *Tragelaphus angasi*: the interaction of light, vegetation phenology, feeding style and reproductive physiology. Mammal Review 9: 33 - 46.
- Anderson, J. L. 1984. Reproduction in nyala (*Tragelaphus angasi*) (Mammalia: Ungulata). Journal of Zoology 204: 129 - 142.
- AOAC. 1990. Pages 1-684 in K. Helrich, editor. Official methods of analysis of the Association of official analytical chemists, Volume I, 15th edition. Virginia, USA.
- Arnold, G. W. 1985. Regulation of forage intake. Pages 81 - 101 in R. J. Hudson and R. G. White, editors. Bioenergetics of Wild herbivores. CRC Press, Boca Raton, Florida.
- Augustine, D. J. and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. Journal of Wildlife Management 62: 1165 - 1183.
- Bell, R. H. V. 1970. The use of herb layer by grazing ungulates in the Serengeti. Pages 11 - 124 in A. Watson, editors. Animal populations in relation to their food resources. Symposium of British Ecological Society, Blackwell, Oxford, United Kingdom.
- Bell, R. H. V. 1971. A grazing ecosystem in the Serengeti. Scientific American 226: 86 - 93.

- Belovsky, G. E. 1986. Optimal foraging and community structure: Implications for a guild of generalist grassland herbivores. *Oecologia* 70: 35 - 52.
- Berger, J. 1992. Facilitation of reproductive synchrony by gestation adjustment in gregarious mammals: A new hypothesis. *Ecology* 73: 323 - 329.
- Berger, J. and S. L. Cain. 1999. Reproductive synchrony in brucellosis exposed bison in the Southern Greater Yellowstone Ecosystem and in non-infected populations. *Conservation Biology* 13: 357 - 366.
- Berteaux, D., M. Crête, J. Huot, J. Maltais and J.P. Ouellet. 1998. Food choice by white-tailed deer in relation to protein and energy content of the diet: A field experiment. *Oecologia* 115: 84 - 92.
- Bertram, B. C. R. 1978. Living in groups: Predators and prey. Pages 64-96 in J. R. Krebs and N. C. Davies, editors. *Behavioural ecology: An evolutionary approach*. Sinauer Associates Incorporation, Sunderland, Massachusetts.
- Berwick, S. H. 1974. The community of wild ruminants in the Gir forest ecosystem, India. Ph. D. dissertation, Yale university, New Haven, Connecticut.
- Bowyer, R. T. 1991. Timing of parturition and lactation in southern mule deer. *Journal of Mammalogy* 72: 138 - 145.
- Boyce, M. S. 1998. Ecological process management and ungulates: Yellowstone's conservation paradigm. *Wildlife Society Bulletin* 26: 391 - 398.
- Bronson, F. H. 1989. *Mammalian Reproduction Biology*. University of Chicago Press, Chicago.
- Bunnell, F. L. 1982. The lambing period of mountain sheep: synthesis, hypotheses and tests. *Canadian Journal of Zoology* 60: 1 - 4.
- Bunnell, F. L. and A. S. Harestad. 1989. Activity budgets and body weights in mammals: How sloppy can mammals be? *Current Mammalogy* 2: 245 - 305.

- Bunnell, F. L. and M. P. Gillingham. 1985. Foraging behaviour: Dynamics of dining out. Pages 53 - 79 in R. J. Hudson and R. G. White, editors. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Florida.
- Caro, T. M. 1994. Ungulate anti-predator behaviour: Preliminary and comparative data from African bovids. Behaviour 128: 189 - 228.
- Cassels, D. M., R. L. Gillen, F. T. McCollum, K. W. Tate and M. E. Hodges. 1995. Effects of grazing management on standing crop dynamics in tallgrass prairie. Journal of Range Management 48: 81 - 84.
- Caughley, G. 1976. Plant-herbivore systems. Pages 94 -113 in R. M. May, editor. Theoretical ecology: Principles and applications. 2nd edition, Blackwell Science Publications.
- Chaneton, E. J., J. H. Lemcoff and R. S. Lavado. 1996. Nitrogen and phosphorus cycling in grazed and ungrazed plots in subhumid grassland in Argentina. Journal of Applied Ecology 33: 291 - 302.
- Chattopadhyay, B. and T. Bhattacharya. 1986. Food habits of blackbuck *Antelope cervicapra* Linn. of Ballavpur Wildlife Sanctuary, West Bengal, India. Tropical Ecology 27: 93 - 100.
- Clutton-Brock, T. H., F. E. Guinness and S. D. Albon. 1983. The costs of reproduction to red deer hinds. Journal of Animal Ecology 52: 367 - 383.
- Cook, R. C., D. L. Murray, J. G. Cook. P. Zager and S. L. Monfort. 2001. Nutritional influences on breeding dynamics in elk. Canadian Journal of Zoology 79: 845 - 853.
- Cumming, D. H. M. 1982. The influence of large herbivores on savanna structure in Africa. Pages 217 - 245 in B. J. Huntley and B. H. Walker, editors. Ecology of tropical savannas. Springer-Verlag Publications.
- Dabadghao, P. M. and K. A. Shanakarnarayan. 1973. The grass cover of India. Indian Council of Agricultural Research, New Delhi.
- Dasmann, R. F. and A. S. Mossman. 1962. Reproduction in some ungulates in Southern Rhodesia. Journal of Mammalogy 43: 533 - 537.

- Dauphine, C. T. and R. L. McClure. 1974. Synchronous mating in barren-ground caribou. *Journal of Wildlife Management* 38: 54 - 66.
- Day, T.A and J.K. Detling. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology* 71: 180 - 188.
- Demment, M. W. and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *The American Naturalist* 125: 641 - 672.
- Detling, J. K. 1988. Grasslands and Savannas: Regulation of energy flow and nutrient cycling by herbivores. Pages 131 - 148 in L. R. Pomeroy and J. J. Alberts, editors. *Concepts of ecosystem ecology: A comparative view*. Springer-Verlag, New York.
- Detling, J. K. 1998. Mammalian herbivores: Ecosystem level effects in two grassland national parks. *Wildlife Society Bulletin* 26: 438 - 448.
- Dharmakumarsinh, K. S. 1978. Velavadar National Park, Gujarat, India. *Tigerpaper* 5: 6 - 8.
- Dove, H. 1996. The ruminant, the rumen and the pasture resource. Pages 219-245 in J. Hodgson and A. W. Illius, editors. *The ecology and management of grazing systems*. CAB international Publications, United Kingdom.
- Emlen, S. T and L. W. Oring. 1977. Ecology, Sexual selection and the evolution of mating systems. *Science* 197: 215 - 223.
- Emlen, S. T. and N. J. Demong. 1975. Adaptive significance of synchronised breeding in a colonial nesting bird: A new hypothesis. *Science* 188: 1029 - 1031.
- Estes, R. D. 1976. The significance of breeding synchrony in the wildebeest. *East African Wildlife Journal* 14: 135 - 152.
- Feer, F. 1982. Sexual maturity and annual cycle of reproduction in *Neotragus batesi*, an African bovid. *Mammalia* 46: 65 - 74.

- Festa-Bianchet, M. 1988. Birthdate and survival in bighorn lambs (*Ovis canadensis*). *Journal of Zoology* 214: 653 - 661.
- Field, C. R. and L. H. Blankenship. 1973. Nutrition and reproduction of Grant's and Thomson's gazelles, Coke's hartebeest and giraffe in Kenya. *Journal of Reproduction and Fertility* 19: 287 - 301.
- Fitzgibbon, C. D. 1990. Anti-predator strategies of immature Thomson's gazelles: Hiding and prone response. *Animal Behaviour* 40: 846 - 855.
- FitzGibbon, C. D and J. Lazarus. 1995. Antipredatory behaviour of the Serengeti ungulates: Individual differences and population consequences. Pages 274 - 296 in A.R. E. Sinclair and P. Arcese, editors. *Serengeti II, Dynamics, Management and conservation of an ecosystem*. University of Chicago Press, Chicago and London.
- Fournier, F., D. W. Thomas and T. Garland, Jr. 1999. A test of two hypotheses explaining the seasonality of reproduction in temperate mammals. *Functional Ecology* 13: 523 - 529.
- Frank, D. A. 1998. Ungulate regulation of ecosystem processes in Yellowstone National Park: Direct and feedback effects. *Wildlife Society Bulletin* 26: 410 - 418.
- Frank, D. A. and P. M. Groffman. 1998. Ungulate vs landscape control of soil C and N processes in grasslands of Yellowstone National Park. *Ecology* 79: 2229 - 2241.
- Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. *Ecology* 73: 2043 - 2058.
- Friedel, M. H. 1991. Range condition assessment and concept of thresholds: A viewpoint. *Journal of Range Management* 44: 422 - 426.
- Fryxell, J. M. 1987. Food limitation and demography of a migratory antelope, the white-eared kob. *Oecologia* 72: 83 - 91.
- Geist, V. 1981. On the reproductive strategies in ungulates and some problems of adaptation. Pages 111 - 132, in G. G. E. Scudder and J.

- L. Reveal, editors. Evolution today. Proceedings of the Second International Conference of Systematic and Evolutionary Biology.
- Glasscock, S. N., W. E. Grant and D. L. Drawe. 2005. Simulation of vegetation dynamics and management strategies on South Texas, semi-arid rangeland. *Journal of Environmental Management* 75: 375 - 397.
- Goering, H. K. and P. J. Van Soest. 1970. Forage fibre analysis. Agricultural handbook No. 379. Agricultural research service, U. S. Department of Agriculture.
- Gregg, M. A., M. Bray, K. M. Kilbride and M. R. Dunbar. 2001. Birth synchrony and survival of pronghorn fawns. *Journal of Wildlife Management* 65: 19 - 24.
- Hatchwell, B. J. 1991. An experimental study of the effects of timing of breeding on the reproductive success of common guillemots (*Uria aalge*). *Journal of Animal Ecology* 60: 721 - 736.
- Heideman, P. D. and R. C. B. Utzurrum. 2003. Seasonality and synchrony of reproduction in three species of nectarivorous Philippines bats. *BMC Ecology* 3: 11.
- Heitschmidt, R.K., M. R. Haferkamp, M. G. Karl and A.L. Hild. 1999. Drought and grazing: 1. Effects on quantity of forage produced. *Journal of Range Management* 52: 440 - 446.
- Herbers, J. M. 1981. Time resources and laziness in animals. *Oecologia* 49: 252 - 262.
- Hilbert, D. W., D. M. Swift, J. K. Detling and M. I. Dyer. 1981. Relative growth rates and the grazing optimisation hypothesis. *Oecologia* 51: 14 - 18.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60: 695 - 713.
- Hofmann, R. R. 1984. Comparative anatomical studies imply adaptive variation of ruminant digestive physiology. *Canadian Journal of Animal Science* 64 (suppl.): 203 - 205.

- Howery, L. D., J. A. Pfister and S. Demarais. 1989. Seasonal reproductive activity of 4 exotic ungulates in Texas. *Journal of Wildlife Management* 53: 613 - 617.
- Hudson, R. J. and S. Frank. 1987. Foraging ecology of Bison in aspen boreal habitats. *Journal of Range Management* 40: 71 - 75.
- Hudson, R. J. and R. G. White. 1985. *Bioenergetics of Wild Herbivores*. CRC Press, Boca Raton, Florida.
- Huntley, B. J and B. H. Walker. 1982. *Ecology of tropical savannas*. Springer-Verlag Publications.
- Iason, G. R. and F. E. Guinness. 1985. Synchrony of oestrus and conception in red deer (*Cervus elaphus L.*). *Animal Behaviour* 33: 1169 - 1174.
- Ims, R. A. 1990a. The ecology and evolution of reproductive synchrony. *Trends in Ecology and Evolution* 5: 135 - 140.
- Ims, R. A. 1990b. On the adaptive value of reproductive synchrony as a predator swamping strategy. *The American Naturalist* 136: 485 - 498.
- Irby, L. R., J. E. Norland, J. A. Westfall Jr. and M. A. Sullivan. 2002. Evaluation of forage allocation model for Theodore Roosevelt National Park. *Journal of Environmental Management* 64: 153 - 169.
- Isvaran, K. 2003. The evolution of lekking: Insights from a species with a flexible mating system. Ph. D. dissertation. University of Florida, Gainesville.
- Isvaran, K. and Y. V. Jhala. 2000. Variation in lekking costs in blackbuck (*Antelope cervicapra*): Relationship to lek territory location and female mating patterns. *Behaviour* 137: 547 - 563.
- IUCN. 2000. IUCN Red list of threatened species. IUCN - The World Conservation Union. Gland, Switzerland.
- Janzen, D. H. 1976. Why Bamboos wait so long to flower? *Annual Review of Ecology and Systematics* 7: 347 - 391.

- Jarman, P. J and M. V. Jarman. 1973. Social behaviour, population structure and reproductive potential in Impala. *East African Wildlife Journal* 11: 329 - 338.
- Jarman, P. J. 1974. The social organisation of antelope in relation to their ecology. *Behaviour* 48: 215 - 267.
- Jarman, P. J. and A. R. E. Sinclair. 1979. Feeding strategy and the pattern of resource partitioning in ungulates. Pages 130 - 163 in A. R. E. Sinclair and M. Norton-Griffiths, editors. *Serengeti: Dynamics of an ecosystem*. University of Chicago Press, Chicago and London.
- Jhala, Y. V. 1991. Habitat and population dynamics of wolves and blackbuck in Velavadar National Park, Gujarat, India. Ph. D. dissertation. Virginia Polytechnic Institute and State University, Blacksburg, Virginia.
- Jhala, Y. V. 1997. Seasonal effects on the nutritional ecology of blackbuck *Antelope cervicapra*. *Journal of Applied Ecology* 34: 1348 - 1358.
- Jhala, Y. V. 1999. Conservation of Indian wolf. Technical report, Wildlife Institute of India, Dehradun.
- Johnson, D. A. and K. H. Asay. 1993. Viewpoint: Selection for improved drought response in cool season grasses. *Journal of Range Management* 46: 194 - 202.
- Johnson, D. H. 1999. The insignificance of statistical significance testing. *Journal of Wildlife Management* 63: 763 - 772.
- Kamil, A. C, J. R. Krebs and R. H. Pulliam. 1987. Foraging behaviour. New York Plenum Press, New York.
- Karban, R. 1982. Increased reproductive success at high densities and predator satiation for periodical cicadas. *Ecology* 63: 321 - 328.
- Karunaichamy, K. S. T. K. and K. Paliwal. 1989. Primary productivity and transfer dynamics of grazing lands at Madurai, southern India. *Tropical Ecology* 30: 111 - 117.

- Kelly, D. and V. L. Sork. 2002. Mast seeding in perennial plants: Why, How and Where? *Annual Review of Ecology and Systematics* 33: 427 - 447.
- Keyser, P. D., D. C. Guynn Jr., and H. S. Hill Jr. 2005. Population density – physical condition relationships in white-tailed deer. *Journal of Wildlife Management* 69: 356 - 365.
- Kingdon, J. 1982. *East African mammals: An atlas of evolution in Africa. Vol III D: Bovids.* University of Chicago Press, Chicago.
- Kistner, T.P., C. E. Trainer and N. A. Hartmann. 1980. A field technique for evaluating physical condition of deer. *Wildlife Society Bulletin* 8: 11 - 17.
- Klein, D. R. and N. Fairall. 1986. Comparative foraging behaviour and associated energetics of impala and blesbok. *Journal of Applied Ecology* 23: 489 - 502.
- Knowlton, N. 1979. Reproductive synchrony, parental investment and the evolutionary dynamics of sexual selection. *Animal Behaviour* 27: 1022 - 1033.
- Krebs, J. R. and N. B. Davies. 1993. *An Introduction to Behavioural Ecology.* 3rd Edn, Blackwell Science Publications.
- Kruuk, H. 1970. Interactions between populations of spotted hyaenas (*Crocuta crocuta erxleben*) and their prey species. Pages 359 - 373 in A. Watson, editor. *Animal populations in relation to their food resources.* Symposium of the British Ecological Society.
- Kruuk, H. 1972. *The Spotted Hyaena.* University of Chicago Press, Chicago.
- Laca, E. A. and M. W. Demment. 1996. Foraging strategies of grazing animals. Pages 137 - 158, in J. Hodgson and A. W. Illius, editors. *The ecology and management of grazing systems.* CAB International, United Kingdom.
- Langvatn, R., A. Mysterud, N. C. Stenseth and N. G. Yoccoz. 2004. Timing and synchrony of ovulation in Red deer constrained by short northern summers. *The American Naturalist* 163: 763 - 772.

- Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: A viewpoint. *Journal of Range Management* 44: 427 - 433.
- Legendre, P. and L. Legendre. 1998. Numerical ecology. 2nd edition, Elsevier science, Amsterdam.
- Lehner, P. N. 1996. Handbook of ethological methods. 2nd edition, Cambridge University Press, Cambridge.
- Linnell, D. C. and R. Andersen. 1998. Timing and synchrony of birth in a hider species, the roe deer *Capreolus capreolus*. *Journal of Zoology* 244: 497 - 504.
- Lucas, J. R. 1987. Foraging time constraints and diet choice. Pages 239 - 269 in A.C. Kamil, J. R. Krebs and H. R. Pulliam, editors. Foraging behaviour. New York Plenum Press, New York.
- Martin, P. R. and P. P. G. Bateson. 1993. Measuring behaviour: An introductory guide. 2nd edition, Cambridge University Press, Cambridge.
- McClintock, M. 1978. Estrous synchrony and its mediation by airborne communication. *Hormones and Behaviour* 10: 264 - 278.
- McGarigal, K., S. Cushman and S. Stafford. 2000. Multivariate statistics for wildlife and ecology research. Springer, New York.
- McNab. B. K. 1980. Food habits, energetics and the population biology of mammals. *The American Naturalist* 116: 106 - 124.
- McNaughton, S. J. 1977. Grassland – Herbivore dynamics. Pages 46 - 79 in A. R. E. Sinclair and M. Norton-Griffiths, editors. Serengeti: Dynamics of an ecosystem. University of Chicago Press, Chicago and London.
- McNaughton, S. J. 1979. Grazing as an optimisation process: Grass-Ungulate relationships in the Serengeti. *The American Naturalist* 113: 691 - 703.
- McNaughton, S. J. 1983. Serengeti grassland ecology: The role of composite environmental factors and contingency in community organisation. *Ecological Monographs* 53: 291 - 320.

- McNaughton, S. J. 1984. Grazing lawns: Animals in herds, Plant form and Co-evolution. *The American Naturalist* 124: 863 - 886.
- McNaughton, S. J. 1985. Ecology of a grazing ecosystem: The Serengeti. *Ecology* 55: 259 - 294.
- McNaughton, S. J. 1988. Mineral nutrition and spatial concentrations of African ungulates. *Nature* 334: 343 - 344.
- McNaughton, S. J. 1990. Mineral nutrition and seasonal movements of African migratory ungulates. *Nature* 345: 613 - 615.
- McNaughton, S. J., D. G. Milchunas and D. A. Frank. 1996. How can net primary production be measured in grazing ecosystems? *Ecology* 77: 974-977.
- McNaughton, S. J., F. F. Banyikwa and M. M. McNaughton. 1998. Root biomass and productivity in a grazing ecosystem: The Serengeti. *Ecology* 79: 587 - 592.
- McNaughton, S. J., G. Zuniga, M. M. McNaughton and F. F. Banyikwa. 1997. Ecosystem catalysis: soil urease activity and grazing in the Serengeti ecosystem. *Oikos* 80: 467- 480.
- McNaughton, S. J., R. W. Ruess and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. *Bioscience* 38: 794 - 800.
- Medina, E. 1982. Physiological ecology of neotropical savanna grasses. Pages 308 - 335, in B. J. Huntley and B. H. Walker, editors. *Ecology of tropical savannas*. Springer-Verlag Publications.
- Milchunas, D. G. and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63: 327 - 366.
- Milchunas, D. G., O. E. Sala and W. K. Lauenroth. 1988. A generalised model of the effects of grazing by large herbivores on grassland and community structure. *The American Naturalist* 132: 87 - 106.

- Mishra, C., P. Ketner and T. A. Groen. 2001. Rangeland vegetation in the high altitudes of the Spiti valley, Indian trans-himalaya. Pages 45 - 59 in C. Mishra, Doctoral thesis, "High altitude survival: Conflicts between pastoralism and wildlife in the trans-himalayas". Wageningen University, Netherlands.
- Misra, K. C. 1979. Tropical Grasslands: Introduction. Pages 189 - 195, in R. T. Coupland, editor. Grassland Ecosystems of the world. International Biological Program, Series 18, Cambridge University Press, Cambridge.
- Misra, M. K. and B. N. Misra. 1984. Biomass and primary production in an Indian grassland. *Tropical Ecology* 25: 239 - 247.
- Morgan, S. G. and J. H. Christy. 1994. Plasticity, constraint and optimality in reproductive timing. *Ecology* 75: 2185 - 2203.
- Mungall, E. C. 1978. The Indian Blackbuck Antelope: A Texas view. Kleberg studies in Natural Resources, College Station, Texas.
- Mungall, E. C. 1991. Establishment of lying out: An example for blackbuck (*Antelope cervicapra*). *Applied Animal behaviour Science* 29: 15 - 37.
- Murray, M. G. 1982. The rut of impala: Aspects of seasonal mating under tropical conditions. *Zeitschrift Tierpsychologie* 59: 319 - 337.
- Mysterud, A. 1998. The relative role of body size and feeding type on activity time of temperate ruminants. *Oecologia* 113: 442 - 446.
- Neter, J, M. H. Kutner, C. J. Nachtsheim and W. Wasserman. 1996. Applied linear statistical models. 4th edition, McGraw-Hill, Boston, MA, U. S. A.
- Oftedal, O. T. 1985. Pregnancy and lactation. Pages 215 - 238 in R. J. Hudson and R. G. White, editors. Bioenergetics of Wild herbivores. CRC Press, Boca Raton, Florida.
- Owen-Smith, N. 1994. Foraging responses of kudu to seasonal changes in food resources: Elasticity in constraints. *Ecology* 75: 1050 - 1062.

- Owen-Smith, N. 1998. How high ambient temperature affects the daily activity and foraging time of a subtropical ungulate, the greater kudu (*Tragelaphus strepsiceros*)? *Journal of Zoology* 246: 183 - 192.
- Owen-Smith, N. 2002. Adaptive herbivore ecology: From resources to populations in variable environments. Cambridge University Press, Cambridge.
- Owen-Smith, N. and P. Novellie. 1982. What should a clever ungulate eat? *The American Naturalist* 119: 151- 178.
- Parker, K. L. and C. T. Robbins. 1985. Thermoregulation in ungulates. Pages 161 - 182 in R. J. Hudson and R. G. White, editors. *Bioenergetics of wild herbivores*. CRC Press, Boca Raton, Florida.
- Parker, K. L., M. P. Gillingham, T. A. Hanley and C. T. Robbins. 1999. Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. *Wildlife Monographs* 143: 1 - 48.
- Peek, J. M. 1980. Natural regulation of ungulates (What constitutes a real wilderness?). *Wildlife Society Bulletin* 8: 217 - 227.
- Prakash, I. 1960. Breeding of mammals in Rajasthan, India. *Journal of Mammalogy* 41: 386 - 389.
- Prasad, N. L. N. S. 1985. Activity time budget in blackbuck. *Proceedings of the Indian Academy of Sciences* 94: 57 - 65.
- Prasad, N. L. N. S. and J. V. Ramana Rao. 1984. Evaluation of habitat structure of blackbuck *Antelope cervicapra* in Andhra Pradesh with special reference to Mudmal and it's relevance to behaviour. *Geobios* 11: 17 - 21.
- Pekins, P. J., K. S. Smith and W. W. Mautz. 1998. The energy cost of gestation in white-tailed deer. *Canadian Journal of Zoology* 76: 1091 - 1097.
- Price, M. A. and R. G. White. 1985. Growth and development. Pages 183 - 213 in R. J. Hudson and R. G. White, editors. *Bioenergetics of wild herbivores*. CRC Press, Boca Raton, Florida, U. S. A.

- Rachlow, J. L. and R. T. Bowyer. 1991. Interannual variation in timing and synchrony of parturition in Dall's sheep. *Journal of Mammalogy* 72: 487 - 492.
- Rahmani, A. R. 1991. Present distribution of the blackbuck *Antelope cervicapra* Linn in India, with special emphasis on lesser known populations. *Journal of Bombay Natural History Society* 88: 35 - 46.
- Ranjithsinh, M. K. 1989. The Indian Blackbuck. Natraj Publishers, Dehradun.
- Raychaudhari, S. P., R. R. Agarwal, N. R. Datta Biswas, S. P. Gupta and P. K. Thomas. 1963. Soils of India. Indian Council of Agricultural Research, New Delhi.
- Reardon, P. P. and L. B. Merrill. 1976. Vegetative response under various grazing management systems in the Edwards plateau of Texas. *Journal of Range Management* 29: 195 - 198.
- Rhine, R. J. 1995. Quantifying synchrony among reproductive or other states. *American Journal of Primatology* 36: 201- 212.
- Rice, C. G. 1988. Reproductive biology of Nilgiri tahr, *Hemitragus hylocrius* (Mammalia: Bovidae). *Journal of Zoology* 214: 269 - 284.
- Richter, A. R. and R. F. Labisky. 1985. Reproductive dynamics among disjunct white-tailed deer herds in Florida. *Journal of Wildlife Management* 49: 964 - 971.
- Ritchie, M., M. Tilman and J. M. H. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79: 165 - 177.
- Robbins, C. T. 1993. Wildlife feeding and nutrition, New York Academic Press, New York.
- Robertson, J. B. and P. J. Van Soest. 1980. The detergent system of analysis and it's application to human foods. Pages 123 - 158 in W. P. T. James and O. Theander, editors. The analysis of dietary fibre in foods. Marcel Dekker, New York, U. S. A.

- Rubenstein, D. R. and M. Wikelski. 2003. Seasonal changes in food quality: A proximate cue for reproductive timing in marine iguanas. *Ecology* 84: 3013 - 3023.
- Ruess, R. W. and S. W. Seagle. 1994. Landscape patterns in soil microbial processes in the Serengeti National Park, Tanzania. *Ecology* 75: 892 - 904.
- Rutberg, A. T. 1984. Birth synchrony in American bison (*Bison bison*): Response to predation or season? *Journal of Mammalogy* 65: 418 - 423.
- Rutberg, A. T. 1987. Adaptive hypothesis of birth synchrony in ruminants: An interspecific test. *The American Naturalist* 130: 692 - 719.
- Sadleir, R.M.F.S. 1969. The ecology of reproduction in wild and domestic ungulates. Methus and Company, London.
- Satyanarayana, V. V. 1985. Evaluation of carrying capacity of Velavadar blackbuck National Park: An ecological perspective, Part 2. M. Sc. Thesis, Saurashtra University, Gujarat, India.
- Schaller, G. B. 1967. *The Deer and the Tiger*. University of Chicago Press, Chicago.
- Schmidt-Nielsen, K. 1972. Recent advances in the comparative physiology of desert animals. *Symposium of Zoological Society of London* 31: 371 - 382.
- Schmidt-Nielsen, K. 1997. *Animal physiology: Adaptation and environment*. 5th edition, Cambridge University Press.
- Shankar Raman, T. R. 1998. Antler cycles and breeding seasonality of the Chital (*Axis axis erxleben*) in southern India. *Journal of Bombay Natural History Society* 95: 377 - 391.
- Shankarnarayan, K. A., G. G. S. N. Rao and B. V. Ramana Rao. 1985. Grassland productivity and its associative climatic characteristics in western Rajasthan. *Tropical Ecology* 26: 157 - 163.

- Sih, A. 1992. Prey uncertainty and the balancing of antipredatory and feeding needs. *The American Naturalist* 139: 1052 - 1069.
- Sinclair, A. R. E. 1977a. Lunar cycle and the timing of mating season in Serengeti wildebeest. *Nature* 267: 832 - 833.
- Sinclair, A. R. E. 1977b. *The African Buffalo: A study of resource limitations of populations.* University of Chicago Press, Chicago and London.
- Sinclair, A. R. E. 1979. Dynamics of the Serengeti environment. Pages 1 - 30 in A. R. E. Sinclair and M. Norton-Griffiths, editors. *Serengeti: Dynamics of an Ecosystem.* University of Chicago Press, Chicago and London.
- Sinclair, A. R. E. 1998. Natural regulation of ecosystems in protected areas as ecological baselines. *Wildlife Society Bulletin* 26: 399 - 409.
- Sinclair, A. R. E., S. A. R. Mduma and P. Arcese. 2000. What determines phenology and synchrony of ungulate breeding in the Serengeti? *Ecology* 81: 2100 - 2111.
- Sinclair, A. R. E. and J. M. Fryxell. 1985. The Sahel of Africa: Ecology of a disaster. *Canadian Journal of Zoology* 63: 987 - 994.
- Singh, J. S. and M. C. Joshi. 1979a. Ecology of the semi-arid regions of India with emphasis on land use. Pages 243 - 275 in B. H. Walker, editor. *Developments in agricultural and managed-forest ecology 7: Management of semi-arid ecosystems.* Elsevier Scientific Publications.
- Singh, J. S. and M. C. Joshi. 1979b. Primary production. Pages 197 - 218, in R. T. Coupland, editor. *Grassland Ecosystems of the world.* International Biological Program, Series 18, Cambridge University Press, Cambridge.
- Singh, R. S., S. C. Srivastava, A. S. Raghubanshi, J. S. Singh and S. P. Singh. 1991. Microbial C, N, and P in dry tropical savanna: Effects of burning and grazing. *Journal of Applied Ecology* 28: 869 - 878.
- Sokal, R. R and F. J. Rohlf. 1995. *Biometry.* W.H. Freeman and company. New York.

- Spalinger, D. E. and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: New models of functional response. *The American Naturalist* 140: 325 - 348.
- Stephens, D. W and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey.
- Taylor, C. R. 1972. The desert gazelle: A paradox resolved. *Symposium of Zoological Society of London* 31: 215 - 227.
- Thornthwaite, C. W. and J. R. Mather. 1955. *The water balance*. Publications in Climatology 8: 1 - 104.
- Twine, W. 2002. Feeding time budgets of selected African ruminant and non-ruminant grazers. *African Journal of Ecology* 40: 410 - 412.
- Underwood, A. J. 1997. *Experiments in ecology: Their logical design and interpretation using Analysis of variance*. Cambridge University Press, Cambridge.
- Underwood, R. 1982. Vigilance behaviour in grazing African antelopes. *Behaviour* 79: 82 - 107.
- Van de Koppel, J., M. Rietkerk and F. J. Weissing. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends in Ecology and Evolution* 12: 352 - 356.
- Van Hoven, W. and E. A. Boomker. 1985. Digestion. Pages 103 - 119 in R. J. Hudson and R. G. White, editors. *Bioenergetics of Wild herbivores*. CRC Press, Boca Raton, Florida.
- Van Soest, P. J. 1963. Use of detergent in the analysis of fibrous feeds: II. A rapid method for the determination of fibre and lignin. *Journal of Association of Official Agricultural Chemists* 46: 829 - 835.
- Van Soest, P. J. 1982. *Nutritional ecology of the Ruminant*. O & E books, Corvallis, Oregon.
- Verchot, L. V., P. M. Groffman and D. A. Frank. 2002. Landscape versus ungulate control of gross mineralization and gross nitrification in semi-

arid grasslands of Yellowstone National Park. *Soil Biology and Biochemistry* 34: 1691 - 1699.

Weber, G. E. and F. Jeltsch. 2000. Long term impacts of livestock herbivory on herbaceous and woody vegetation in semi arid savannas. *Basic Applied Ecology* 1: 13 - 23.

Weber, G. E., F. Jeltsch, N. Van Rooyen and S.J. Milton. 1998. Simulated long term vegetation response to grazing heterogeneity in semi arid rangelands. *Journal of Applied Ecology* 35: 687 - 699.

Westneat, D. F. 1992. Nesting synchrony by female red-winged blackbirds: Effects on predation and breeding success. *Ecology* 73: 2284 - 2294.

White, T. C. R. 1993. *The inadequate environment: Nitrogen and the abundance of animals.* Springer-Verlag Berlin, Heidelberg.

Williams, K. J., B. J. Wilsey, S. J. McNaughton and F. F. Banyikwa. 1998. Temporally variable rainfall does not limit yields of Serengeti grasses. *Oikos* 81: 463 - 470.

Wright, J. P. and C. G. Jones. 2004. Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology* 85: 2071-2081.

Yoccoz, N. G. 1991. Use, overuse and misuse of significance tests in evolutionary biology and ecology. *Bulletin of the ecological society of America* 72: 106 - 111.

APPENDIX 1. List of plant species recorded in VNP during the study period (2000-2002).

Name of plant species	Type of plant
Perennials	
<i>Acacia nilotica</i>	tree
<i>Aelulopus leugopoides</i>	herb
<i>Aristida funiculata</i>	grass
<i>Chloris barbata</i>	grass
<i>Dactyloctenium aegyptium</i>	grass
<i>Dicanthium annulatum</i>	grass
<i>Heteropogon contortus</i>	grass
<i>Prosopis juliflora</i>	tree
<i>Salvadora persica</i>	tree
<i>Sehima nervosum</i>	grass
<i>Sporobolus coromandialis</i>	grass
<i>Sporobolus virginicus</i>	grass
<i>Sueda nudiflora</i>	herb
<i>Themeda triandra</i>	grass
Annuals	
<i>Abutilon fruticosum</i>	herb
<i>Aristida adscensionis</i>	grass
<i>Cyperus alulatus</i>	sedge
<i>Echinochloa colonum</i>	grass
<i>Enicostema littorale</i>	herb
<i>Fimbristylis dichotoma</i>	sedge
<i>Fimbristylis miliaceaea</i>	sedge
<i>Hibiscus tetraphyllus</i>	herb
<i>Rungia parviflora</i>	herb
<i>Setaria glauca</i>	grass
<i>Sporobolus pallides</i>	grass



Plate 1: Grassland habitat in Velavadar National Park. Blackbuck are seen grazing in the middle ground and a *Prosopis juliflora* patch lines the background. There are over 1000 blackbuck estimated to inhabit Velavadar NP. (Photo by: K. Yoganand)



Plate 2 (a): *P. juliflora* patch and barren ground habitat in Velavadar NP. A female-dominated blackbuck herd is seen moving between grassland patches through barren ground. (Photo by: K. Yoganand)



Plate 2 (b): Saline habitat in Velavadar NP. This habitat remains waterlogged during monsoon rains. Blackbuck forage occasionally on the herb *Sueda nudiflora* that grows in this habitat. (Photo by: K. Yoganand)

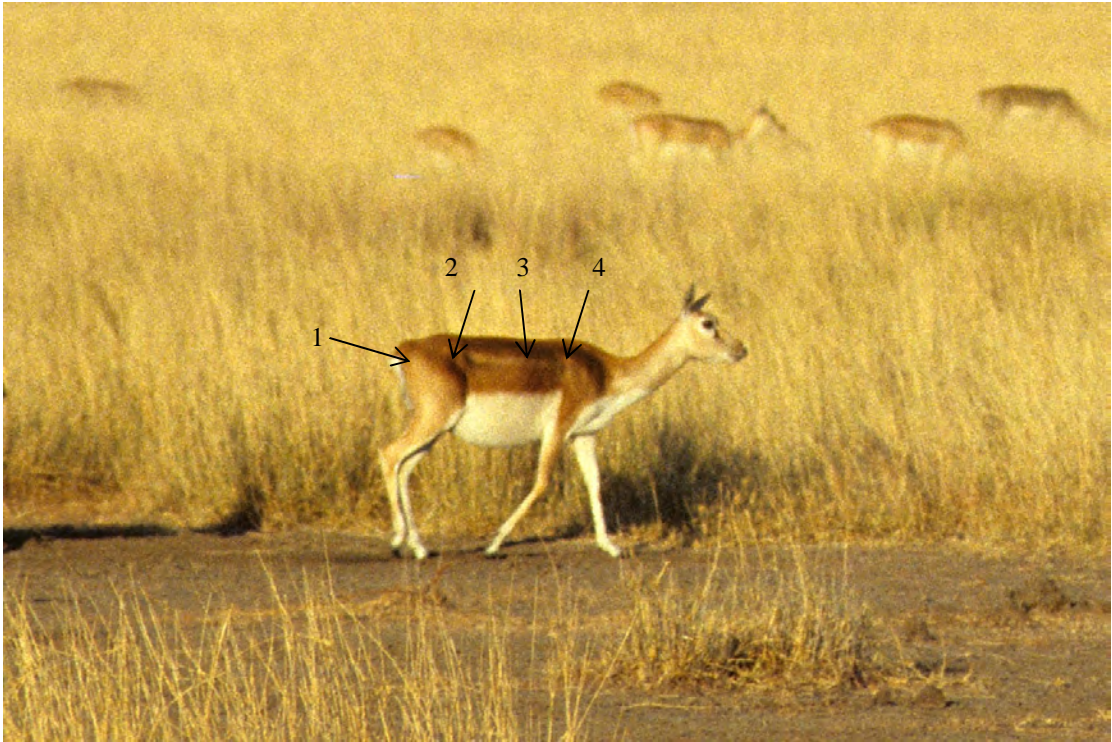


Plate 3 (a): Arrows indicate the body parts used for ranking body condition of female blackbuck in the field – 1) Rump; 2) Pelvic girdle; 3) Ribs; and 4) Pectoral girdle. (Photo by: K. Yoganand)



Plate 3 (b): Arrow indicates the 5th body part used for ranking body condition of blackbuck females – 5) Tail bone depression. (Photo by: Y. V. Jhala)



Plate 4 (a): Blackbuck fawn hiding in the grassland. The fawns do not follow their mother during the first few weeks after being born. (Photo by: Y. V. Jhala)



Plate 4 (b): Blackbuck fawn lying out in a saline patch of land. The fawn hiding behaviour is considered to have evolved as an anti-predator strategy. (Photo by: Y. V. Jhala)

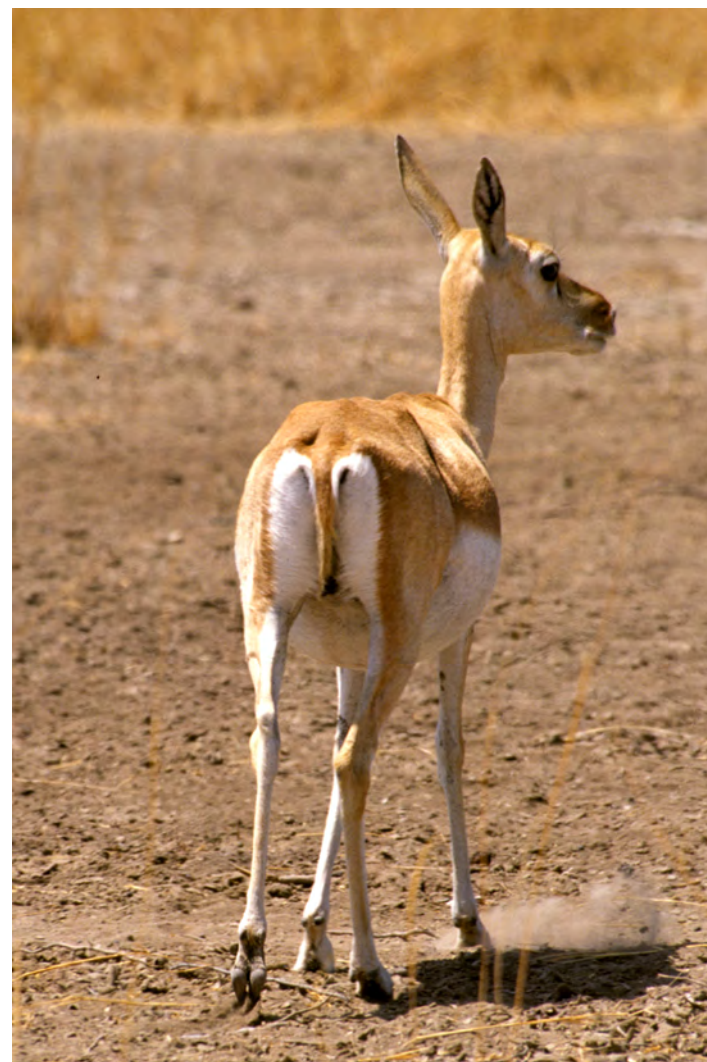


Plate 5: Lactating blackbuck female (left picture) when viewed from behind has its black teats distinctly visible against its white underbelly. In contrast, teats are retracted and not distinctly visible in a non-lactating female (right picture). This character was used to identify lactating females in the field. (Photos by: V. Joseph and Y. V. Jhala, respectively)



Plate 6 (a): Sampling blackbuck activity by scan sampling method, using a spotting scope. Blackbuck herds were followed from dawn to dusk and their activities sampled at 15 minute intervals. (Photo by: K. Yoganand)

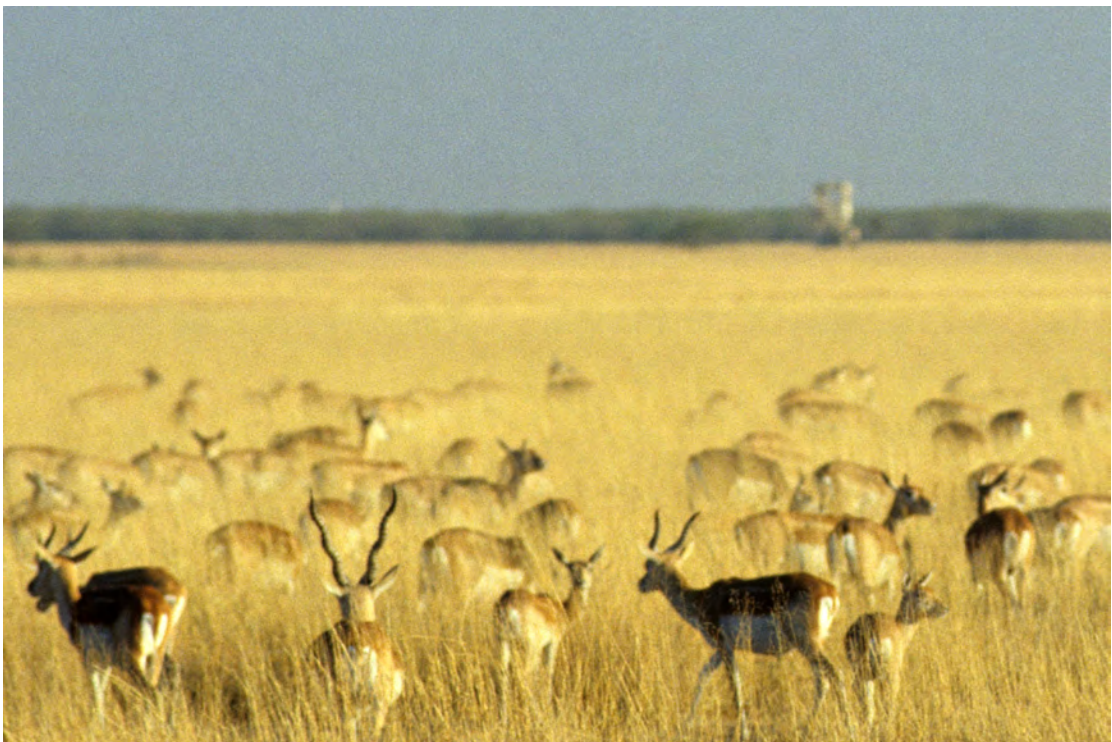


Plate 6 (b): Female dominated herds of blackbuck grazing and moving through grassland habitat in Velavadar NP. Blackbuck spent a major part of the day feeding on grass during the study period. (Photo by: K. Yoganand)



Plate 7 (a): An enclosure put up in the grassland of Velavadar NP to study the effects of grazing and grass harvesting on above-ground productivity and quality of grasses. (Photo by: Y. V. Jhala)



Plate 7 (b): Harvesting of grass by local people in Velavadar NP. The Park management allows regulated harvesting of grass in the cold season of each year by local people to use as fodder for livestock. (Photo by: K. Yoganand)