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Habitat and Population Dynamics of Wolves and Blackbuck in Velavadar National Park, Gujarat, India.

by

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(ABSTRACT)

The management problem of allocating limited resources for conflicting habitat needs of 2 endangered species, (the wolf (*Canis lupus pallipes*) and the blackbuck (*Antelope cervicapra*)) at Velavadar National Park, Gujarat, India, was addressed with the aid of mathematical optimization models. Critical biological data essential for model formulation and management decisions were collected by field research from February 1988 to December 1990.

The semi-arid grassland habitat was dominated by perennial grasses like *Dichanthium annulatum* and *Sporobolus virginicus*. The grassland system seems quite resilient to droughts and grazing. Above-ground production is primarily dependent on precipitation. Two-year rainfall sequence explained 96% of the variability in the peak above-ground plant biomass.

Food habits of blackbuck were determined by lead animal studies and observations on wild blackbuck. Blackbuck relied primarily on grasslands to obtain food. The pods of the exotic shrub, *Prosopis juliflora*, comprised 10% of the diet and were considered to be important during the summers and drought years. Dry matter intake, as estimated from captive blackbuck feeding on natural forage, was cyclical, dropping in the summers and increasing during the monsoons and winters. Apparent digestibility and forage quality were extremely low in summers. Average annual dry matter intake was estimated at 86 gms/$kg^{0.75}$ of blackbuck per day. Relationships were developed for predicting forage quality from fecal ether extract and fecal nitrogen.

The blackbuck population seemed to be in a dynamic equilibrium at about 1850 animals. Periodic droughts and floods cause major population declines. The population takes 4-5 years to recover from such catastrophic mortality. Life-table analysis done by aging jaws of dead blackbuck revealed a bimodal mortality pattern for males. Males between the ages of 7 to 9 years were at high

risk of wolf predation during the rutting season. A population simulation model using a modified Leslie matrix approach estimated the probability of extinction during the next 50 years to be close to zero. The population was predicted to fluctuate between 1100 and 2800 individuals.

Habitat use by wolves was determined by direct observations and by indirect methods using wolf signs. Wolves used the shrubland for lying-up, denning, and for rendezvous sites. Important wolf habitat was marked on a habitat map of the park and management strategies were suggested. The average pack size in the park was 6 wolves. Litters were born in December-January. Mean litter size was 5.5 pups. Pup mortality was estimated at 28%. Food habits of wolves was determined from scat analysis. Consumption was estimated from fresh blackbuck kills. Blackbuck were the major prey (88%); hare and rodents (2.3% and 3.3% respectively) were other important prey items. Consumption by wolves was estimated at 0.07 kg/kg of wolf per day. A ratio of 158 blackbuck to 1 wolf was considered essential to maintain a stable blackbuck population.

The real objective of increasing the forage-based carrying capacity of the park for blackbuck was abstracted into a mathematical objective function for linear programming optimization. Limitations of the annual budget of the park, park area, wolf habitat needs, and the blackbuck population to maintain a desired wolf:blackbuck ratio were built into the model as constraints. The model was run with various scenarios of different budgets and different management options. The stochastic nature of rainfall and associated above-ground forage production was incorporated into the constraints in the form of risk analysis.

The recommendations from the model results were to maintain grasslands free of *Prosopis*, to cut shrublands, away from wolf habitat, for increasing grassland areas, and lastly to develop saline regions into shrublands. Managing well-dispersed *Prosopis* groves, and maintaining them by thinning and pruning were considered ideal methods to provide mast for blackbuck, wolf habitat, and to allow grass growth available to blackbuck. A longterm (25-30 years) shrub rotation schedule was considered appropriate for improving the saline alkali soils.

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INTRODUCTION

Establishing preserves and maintaining them for wildlife conservation in a country faced with over population and increasing demand on the land for agriculture and industry is a very difficult task. India has taken a major step towards conserving its rich natural heritage by creating several Sanctuaries and National Parks. However, with increasing human influence many ecosystem processes are severely impacted and disrupted. A laissez faire parkland policy is not appropriate in most areas. Active management is essential if the integrity of these natural ecosystems is to be preserved.

With limited resources and competing uses, management based on research that takes a holistic approach is essential and appropriate. Such research identifies and seeks to understand key processes in ecosystems so that resources may be optimally allocated for conservation by effective management strategies. Biological data on a species are absolutely essential for its management. In the case of endangered species, the time and resources needed for a thorough understanding of the biology of the species may not be available. A selective study of the critical parameters needed to manage any endangered species is a very relevant task to be performed since it can guide further research and achieve timely results economically.

This study is one of the type suggested above. It addresses a unique situation in Velavadar National Park, Gujarat, India, where there is an endangered predator, the wolf (*Canis lupus*

pallipes), preying on an endangered prey, the blackbuck (*Antelope cervicapra rajputanae*). In the same area there is the additional conflict in which an exotic shrub, *Prosopis juliflora*, is invading the grassland and threatening to reduce the habitat for the blackbuck while improving it, within limits, for the wolf. There is possibly a need for active habitat and population management but the resources available and the understanding of the dynamics of the system are too limited to permit scientific management. The semiarid grassland community is influenced by major annual changes caused by the monsoon, making the system extremely dynamic and interesting for scientific investigation.

The study is of importance and interest not only in itself but also in that it seeks to understand population and habitat interactions and prey-predator relationships in semiarid grassland ecosystems. It focuses on computer applications and optimization techniques for wildlife management which could be adapted for use in other wildlife conservation areas.

In order to conserve and maintain the area along with its fauna and native flora, the park managers have many questions including :

1) If and how a small population of endangered wolves could be conserved ?

2) How do the variations in the monsoon affect forage production and thus the blackbuck population and ultimately the wolves?

3) What factors other than food supply affect blackbuck numbers and the role of (wolf) predation in this ecosystem?

4) What amount of *Prosopis* removal will achieve a desired level of forage over a long planning period, given the variations produced by the monsoon?

The specific objectives of this study, designed to answer the above questions were as follows:

1) To determine the seasonal food habits and nutritional needs of the blackbuck and the wolf.

2) To estimate the energy and protein available to these animals in the Velavadar National Park.

3) To estimate the importance of cover and other needs of the wolf.

4) To describe the likely changes in the habitat and associated blackbuck and wolf populations for a long planning period.

5) To create a computer model that incorporates the dynamics of the environment and major endangered species and allocates limited resources optimally to achieve long-term stability of the system.

The information obtained in the process of achieving the above objectives would provide better understanding of the dynamics of the Velavadar ecosystem. This understanding would aid in the management of the Park.

STUDY SITE

Description and Climate

Velavadar National Park is located at latitude N 21° 56′ and longitude E 72° 10′ in the Bhal region of Saurashtra in the state of Gujarat. It is just above sea level and is only 18 km from the Gulf of Cambay (Ranjitsinh 1982:17). Velavadar is 35 km north from the city of Bhavnagar and 22 km northwest of the town of Vallabhipur.

The Bhal (literally meaning the forehead) is a flat alluvial plain made up of a mosaic of croplands, saline waste lands, grazing grasslands, and marshes (Dharmakumarsinhji 1978b). The Bhal covers an area of about 2,590 sq km. It is bordered on the South by the Kalubhar river, extends North to Dholka and Dhandhuka, and extends Northwest up to Limbdi (Dharmakumarsinhji 1978). The Bhal soils are silt deposits from the rivers Narmada, Mahi, Sabarmati, Sukhbhadar, the Bhogavas, and rivulets like Kalubhar and Alang draining the basalt Kathiawar highlands into the Gulf of Cambay (Dharmakumarsinhji 1978). The Bhal region is believed to have emerged from the sea during the late Tertiary and early Quaternary, much later than the rest of Saurashtra which appeared during the Cretaceous (Dharmakumarsihji 1978, Raychaudhuri et al. 1963).

Velavadar National Park covers an area of 34.08 sq km and is the only grassland preserve in the Bhal area and arguably in the whole of Gujarat. It harbors one of the largest populations of the endangered blackbuck, *Antelope cervicapra rajputanae*. Three seasons can be distinguished in Velavadar. Almost all the precipitation occurs in the monsoon which begins during the later half of June and continues to mid-September. Sporadic showers may occur in October but normally October is a transient period into winter. The temperature ranges from -1°C to 38°C in winter which extends from November to February (Raychaudhri et al. 1963). Rare showers locally called "mavthu" occur during winter. In winter, especially in the month of January, due to the high moisture content of the sea breeze, low fog occurs during early morning hours (Ranjitsinh 1982:24). Dew is a common feature during early morning throughout winter and sporadically in summer. Day temperatures normally range between 37°C to 44°C, but can be as high as 48°C in summer, which extends form March to mid June. Hot winds called "loo" sweep the hard-baked earth; dust storms, whirlwinds and dust devils are common. Mirages form as early as 2-3 hours after sunrise and continue throughout the day into late afternoon.

The Bhal region is prone to droughts and floods. Cyclones occasionally strike the coast of Saurastra. During such times the Bhal becomes a large swamp. Velavadar National Park is at a lower elevation than its surroundings and thus remains submerged for a longer duration. Such floods are a major mortality factor for blackbuck (Dharmakumarsinhji 1978, Rashid 1977). Two such floods have occurred in the recent past. In 1976 more than 924 blackbuck perished in one; in 1982 more than 300 blackbuck were reported to have been killed (Dharmakumarsinhji 1978, Majethia pers. comm., Rashid 1977). The average annual precipitation at Velavadar is about 468 mm (Ranjitsinh 1982:21). Ecoclimate computed by the method of Thornthwaite and Mather (1955) for Velavadar by Ranjitsinh (1982:24) is semi-arid, fourth megathermal,and with no water surplus.

Plant growth is restricted to the monsoon and early winter. Crops are solely dependent on rains as the ground water is saline. Wheat (*Triticum* sp.) is grown in winter in fields left fallow during the monsoon due to a good water retention capacity of Bhal soils. Cotton, (*Gossipyum* sp.) sorghum (*Sorghum* sp.), and kasumbi (*Carthamus tinctorius*) are the other major crops of the Bhal region. Besides agriculture, the most important occupation is livestock rearing, primarily cattle and

water buffaloes for dairy products. The villages of Velavadar, Kanatalav, Gangawada, Bharbhil, and Mithapur surrounding Velavadar National Park have a livestock population grossly estimated at more than 10 thousand. The majority of the livestock population is migratory. During monsoon and early winter, the livestock remain in the Bhal, grazing in the village grounds and illegally within the park. Later in the year, as the grass quality and quantity deteriorates in the Bhal, the herdsmen take their productive stock to regions of South Gujarat for better grazing and for marketing their dairy products.

History

Prior to India's independence (1947), the major part of the Bhal, including the area currently under the preserve, was under the princely state of Bhavnagar. Grasslands of Velavadar and Mithapur were private grazing grounds (vedis) for the Maharaja's cattle. This area was known for its large concentrations of blackbuck. Dharmakumarsinhji (1978), the late Maharaja's brother, estimated the number to be greater than 8000 during the pre-independence era.

During the time of Maharaja Bhavsinhji, blackbuck were hunted in this area by captive trained cheetahs (*Acinonex jubatus*). The late Maharaja Krishnakumarsinhji was an ardent conservationist and enforced strict hunting seasons and regulations.

After India's independence, game became a "common property". The Government of Saurashtra issued firearm licenses freely and encouraged hunting wild ungulates as a means of crop protection (Mungall et al. 1981). Accessibility to remote areas in the Bhal by vehicles increased due to building of new roads. Large parts of the "vedi" (grazing grounds) towards Mithapur village were converted to agricultural fields in early 1960 (Shivbhadrasinhji, pers. comm.). Due to hunting and habitat loss, the Bhal blackbuck population was decimated. By 1966 a population of only 200 blackbuck survived in the Velavadar area (Shivbhadrasinhji, pers. comm.).

Efforts by Dharmakumarsinhji, Shivbhadrasinhji, and Ranjitsinhji succeeded in convincing the Government of the endangered status of the Bhal blackbuck. As a result a sanctuary of 890 ha. was established at Velavadar in 1969 (Ranjitsinh 1982:17, Mungal et al. 1981:20). In 1976, the area was increased to 1,783.88 ha. and the status upgraded to a National Park (Rashid 1977). In 1980, another 1,624.23 ha. were added to the park (Prasad 1985:14). Currently the National Park covers an area of 3,408.11 ha.

Current Management and Problems

The Bhal area was an open treeless habitat as recently as 40 years ago (Dharmakumarsinhji 1978, Mungall et al. 1981). An exotic shrub, *Prosopis juliflora* (mesquite), a native of Southwestern America, was introduced into India in 1876-77 (Muthana and Arora 1983, Verma 1987). *Prosopis juliflora* was planted in the Bhal area about 50 years ago near Mithapur to provide fuel-wood. Though the plant has provided for the much needed fuel-wood, it has since spread rampantly and converted much of the grasslands into savanna and thorn-forest habitat. The practice of cutting *Prosopis* for fuelwood encourages lateral growth that results in a thick, impenetrable thorn scrub (Ranjitsinh 1982:27). Though the *Prosopis* plant itself is not palatable, its nutritious pods are eaten avidly by ungulates (Muthana and Arora 1983). *Prosopis* seeds are not digested by ungulates and are dispersed through dung, resulting in a rapid spread of the plant (Muthana 1988). Currently about 50% of the grassland habitat in Velavadar National Park is under *Prosopis* shrub.

Blackbuck prefer "open" habitat and are known to avoid thick cover (Ranjitsinh 1989:37). Besides preventing access to blackbuck, the thick growth of *Prosopis* is likely to shade out grasses and forbs growing in the herb strata.

Wolves were considered to be "migrant" visitors into Velavadar National Park and wolf predation on blackbuck was considered a rare event (Mungall et al. 1981,1983, Ranjitsinh 1982).

"Recently"the endangered wolves have made Velavadar their home and Ranjitsinh (1989:64) attributes this to the increase in cover made available by *Prosopis* shrublands.

The major management activity within the park is to clear all the grassland areas of established *Prosopis* saplings every year to prevent further encroachment by the shrub. Small areas of *Prosopis* shrubland are cleared by hacking out the roots of the shrub manually. The wood obtained from these cleared shrublands is made into charcoal and auctioned (Majethia and Chudasama pers. comm.).

Besides *Prosopis* management, the other management activities undertaken in the park include the following:

1) Providing water for wildlife by filling up artificial waterholes in summers of all years and throughout the year in drought years;

2) Providing fodder for blackbuck in years of extreme drought and during the lean periods of other years;

3) Protecting wildlife from poaching, preventing grazing of livestock within the park, preventing fuelwood cutting, and exterminating pariah dogs;

4) Managing tourist facilities e.g., by maintaining the park roads, guest house, and providing some interpretation.

LITERATURE REVIEW

My attempt in this chapter is to familiarize the reader with the research done to date at Velavadar National Park in particular and on the endangered fauna inhabiting the park in general. This section is not intended to be an exhaustive literature search on grassland ecosystems, prey-predator relationships, or computer applications to wildlife management. Relevant literature from which concepts were developed to formulate this study is reviewed here or cited in appropriate chapters.

Understanding of the Bhal ecosystem and the historical conditions that prevailed in and around the current Velavadar National Park was obtained from papers published by Dharmakumarsinhji (1967, 1978a, 1978b) and by personal communications with other members of the royal family of Bhavnagar including Shivbhadrasinhji and Nirmalkumarsinhji.

In 1980 a joint United States-Indian blackbuck project (from January 16 to April 15) was undertaken. The blackbuck population at Velavadar National Park was one of the study populations and was visited by the research team in February 1980. This short-term study provided insight into activity patterns, group composition, physical characteristics, predation, and territoriality (Mungall et al. 1981, 1983).

The main source of information on blackbuck at Velavadar National Park was obtained from M. K. Ranjitsinh's (1982) Ph.D. dissertation, "Ecology and Behavior of the Indian Blackbuck", that

was later published (1989), with updated information, in the form of a book "The Indian Blackbuck."

The most useful single source of biological information on the blackbuck is the study done at Texas by Dr. Elizabeth C. Mungall (1978). I have relied greatly on Ranjitsinh (1982, 1989) and Mungall (1978) for information on ecology and behavior of blackbuck. Relevant information on blackbuck was also obtained from Cary (1976), Chattopadhaya and Bhattacharya (1985, 1986), Goyal et al. (1986), Ghosh et al. (1988), Howery et al. (1989), Mungall (1978, 1979, 1991), Oza and Gaekwad (1973), Prasad (1981), Ramana Rao and Prasad (1982), and Rashid (1977).

Satyanarayan (1985) and Prasad (1985) have jointly attempted to quantify the vegetation and carrying capacity of the Velavadar grasslands in a year-long study for their M.S. research project at Saurashtra University. Longterm studies are extremely important to obtain reliable understanding of processes operating in an ecosystem. Unfortunately such studies are rarely attempted due to limited time and funding. A year-long study is, at times, reduced to a single data point for statistical analysis. I have incorporated data on soils and vegetation characteristics at Velavadar National Park from Prasad (1985) and Satyanarayan (1985) for relevant statistical analysis.

Studies by Mungall et al. (1981, 1983) and Ranjitsinh (1982, 1989) in Velavadar National Park identified critical areas where research is needed to guide management decisions. Some of these which are addressed in this study include: (a) demographic characteristics of the blackbuck population, (b) estimation of carrying capacity, (c) estimation of the food habits of blackbuck, (d) study of natural predators, and (e) management options to improve food production.

In comparison to the blackbuck, almost nothing is known about the grey wolf in India. The only published study on the Indian wolf is by Shahi (1982). Shahi (1982) estimated the wolf population in India to be about 800 individuals and recommended research on the ecology and distribution of wolves in India. As a consequence of the current research project, and additional study in other areas, the status of the wolf is better known for the states of Gujarat and Rajasthan (Jhala and Giles 1991). A conservation strategy was proposed which included (1) public support and education, (2) enforcement of legal protection, (3) paying compensation for wolf killed

livestock, (4) survey of wolf population and research on dynamics of select population, (5) protection of breeding habitat, and (6) eradication of feral dogs, (Jhala and Giles 1991). Though some studies have been done on this subspecies of the wolf in Israel and Iran (Joslin 1982, Mendelssohn 1982) the ecology of the Indian wolf is likely to be somewhat different due to the diversity of habitats in which the wolf is known to live (Shahi 1982). Conditions like those in Velavadar, where wolves live in packs and subsist on natural prey, are likely to be quite different from wolves living off livestock in areas with more human pressure. Any data collected on this shy endangered species is likely to aid in its understanding and conservation (Daniel, pers. comm., Ginsburg and McDonald 1990).

The wolf is probably the most studied large carnivore in North America. Information on wolves began to accumulate in the 1940's (Young and Goldman 1944). Modern longterm scientific studies on wolves were initiated by Durward Allen in Isle Royale and Douglas Pimlott in Algonquin Park. Current understanding of the wolf's ecology, behavior and biology was obtained from Mech's (1970) synthesized work "The Wolf", and from Mech's and his co-workers research at Minnesota (Van Ballenberghe et al. 1975, Berg and Kuehn 1982, Fritts and Mech 1981, Fuller 1989, Nelson and Mech 1981), Alaska (Ballard et al. 1987, Gasaway et al. 1983, Peterson et al. 1984) and continued study at Isle Royale (Peterson 1977, Peterson and Page 1988). An important technique for wolf research in North America includes radiotelemetry and aerial tracking. As neither of these was feasible due to the endangered status of the wolf, difficulty in obtaining legal permissions, and financial constraints, field research at Velavadar National Park was similar to summer research conditions on Isle Royale (Peterson, pers. comm.) years prior to the phase of using radiotelemetry. Simulated howling (Pimlot 1960, Joslin 1967) and observation of wolf signs such as scats and tracks were some of the only techniques used in the present study.

"Grasslands Systems Analysis and Man" edited by Breymeyer and Van Dyne (1980) provided the basic understanding of processes operating in grassland ecosystems. Reviews by Van Dyne et al. (1980), Cumming (1982), and Delting (1988) on grassland-large herbivore system and their interaction were used to develop concepts for the Velavadar grassland-blackbuck interactions. The Velavadar grassland-herbivore system was considered in terms of models developed by Caughley

and Lawton (1981), Noy-Meir (1975), Owen and Wiegert (1982), Hilbert et al. (1981) and McNaughton (1979). There is a likelihood that the Velavadar grassland-herbivore system fits Caughley and Lawton's (1981) prey-predator model in years of drought and heavy grazing pressure from livestock and cattle. In years of good above-ground plant production, the system is likely to respond similarly to that predicted by the "grazing optimization hypothesis" (Hilbert et al. 1981).

Most grasslands in India are of secondary origin. They were created and maintained by degradation of original forests by human activities (Misra 1983). The historic aspects of distribution and description of grass cover are available from Dabadghao (1961) and Whyte (1957). Concepts of the ecology and dynamics of grasslands in India were reviewed from Gupta (1985), Karunaichamy and Paliwal (1989), Misra and Misra (1984), Pandeya and Jain (1979), Singh (1973), Singh and Yadava (1973), Singh and Krishnamurthy (1981), Shankarnarayan and Shankar (1984), and Shankarnarayan et al. (1985).

In semi-arid grassland systems, the single major driving force is rainfall. The response of primary production to precipitation and climatalogical parameters has been documented by Arkley and Ulrich (1962), Coe et al. (1976), McGinnies (1979), Phillipson (1975), Ramana Roa et al. (1984), Rosenwig (1968), Shankarnarayan et al. (1985), Webb et al. (1978), and Whittaker (1970). Models and relationships developed by these authors were studied for applicability to the Velavadar system.

According to Mitchell (1983), the relationship between fluctuating net primary production and response in secondary production by herbivores has received little attention. The concept and modeling of optimal numbers of herbivores (Hart 1978), rotational grazing of depleted habitats (Currie 1978), and concepts of carrying capacity (Caughley 1979, 1981, Macnab 1985, Mentis and Duke 1976, Potvin and Hout 1983) incorporating energy and protein (Hobbs and Swift 1985, Hobbs et al. 1982) on a seasonal basis seem appropriate for application at Velavadar National Park.

Results from ecosystem studies from East Africa were thought to provide the most comparable information to the Velavadar ecosystem (Sinclair 1977 and Sinclair and Norton-Griffiths 1979). Though the Velavadar system was simple in comparison to the Serengeti ecosystem, processes involving herbivore-grass interaction, herbivore-herbivore interactions and

herbivore-carnivore interactions were considered to be essentially similar (Afolayan and Fafunsho 1989, Bell 1971, Coughenour et al. 1985, Gwynne and Bell 1968, Kruuk 1972, McNaughton 1976, 1983, 1985, Schaller 1972, Sinclair 1975, 1983,1985).

Models play a role in forcing a clear statement of objectives and consideration of alternatives. They provide a scheme for integrating available information (Harris and Kochel 1981). According to Mitchell (1983) "...logical extension of the use of optimization models in natural resources decision making would be to couple production-oriented simulation models of natural systems to mathematical programming models that allocate land and resources." Though the use of optimization models in explaining and understanding biological systems has generated controversies (Mitchell and Valone 1990, Pierce and Ollason 1987, Pyke 1984), the use of operations research techniques for management of natural resources is not controvertial (Clark 1976, Dykstra 1984). The discipline of management science and operations research are built around standardizing rational approaches to making decisions (Harris and Kochel 1981). Dykstra (1984) summarized mathematical programming as being involved with the optimal allocation of scarce resources among competing ends. An operations research study begins with an effort to understand the real world problem. This is obviously a necessary step before the problem can be abstracted in mathematical terms (Romesburg 1972). Models are an abstraction, a simplification of a process rather than a replication. They never describe the real world exactly and often do not attempt to do so (Starfield and Bleloch 1986). The quality of a model does not depend on how realistic it is, but on how well it performs in relation to the purpose for which it was built (Starfield and Bleloch 1986).

Various forms of linear programming (Hiellier and Lieberman 1986) were considered for application to the management of Velavadar National Park. A major drawback of linear programming to biological systems is that the model inputs and solution are deterministic (Hiller and Lieberman 1986). To incorporate the stochastic nature of the environment, and to consider multiple objectives, parametric programming, chance-constrained programming, minimization of total absolute deviations and goal programming (Bell 1976, Bottoms and Bartlet 1975, Charnes and Cooper 1959, Dykstra 1984, Hazel and Norton 1986, Segarra et al. 1985 and Taylor and Zuhair 1986) were means that were explored.

According to Romesburg (1972), an essential difference in applying operations research to natural resource management problems as it differs from industrial management problems, is that the operations research practitioner is usually somewhat more ignorant of the detailed workings of the real system. Usually modeling studies are attempted on existing large data bases of biological systems (Eberhardt 1981, Rykielja and Kuenzel 1971, Walters et al. 1981). This study is unusual in that it attempts to collect critical biological information and attempts to synthesize this information into an optimization model for making management decisions.

Due to the multitude of components, processes, and interactions operating even in a simple ecosystem and the likelihood of temporal variations, a 2 to 3 year study is unlikely to comprehend the dynamics of an ecosystem, let alone abstract it into a mathematical model. However, from the management point of view, planning decisions have to be made despite the lack of data and understanding (Dykstra 1984;). How do we then make good, scientific decisions under these circumstances? Opportunities to obtain more data in the future on wildlife in general and on endangered species, in particular, may be seriously curtailed as habitats are continuously being degraded and populations are steadily declining. It is in this context that the following chapters are intended to be interpreted.

METHODS

An effort was made to develop and use methodology that was appropriate for the level of resolution sought by the research project and for the constraints imposed by available time and funding.

Vegetation

Habitat Types

The park was divided into the following 4 distinct habitat types :

1) Grasslands : Areas where the predominant vegetation was grasses, forbs, and sedges were classified as grasslands. These areas were devoid of shrubs and halophytic species typical of shrublands and saline regions (Fig. 1a)

2) Shrublands : Areas colonised by *Prosopis* were classified as shrublands. The height of *Prosopis* shrubs in the shrublands ranged from 1 m to 6 m (Fig. 1b).

3) Saline regions : Characterized by sparse vegetation. The plant cover was dominated by halophytes. These areas were devoid of perennial grasses and shrubs (Fig. 1a).

4) Tidal and flood plains : These areas were devoid of any vegetation. They were often flooded by extreme high tides and flash floods occurring in the monsoon.

Habitat types were believed to differ as a result of interactions among the abiotic (predominantly edaphic) factors and biotic factors.

A vegetation map showing the distribution of the 4 habitat types in the park was prepared using a compass and chain measure (Mosby 1980). A patch of habitat type was distinguished if it encompassed an area approximately greater than half a hectare. The map was digitized on a personal computer using the Arc/Info software.

Multivariate analysis of variance and univariate analysis of variance procedures were used to study differences between habitat types using edaphic characteristics and dry biomass of the major plant species growing in these habitats.

Species Composition and Biomass

A collection was made of plant species found growing within the park during the course of the study. An herbarium was prepared of preserved flowering specimens. All the specimens were identified with the aid of the floras of the region (Cooke 1958, Shah 1978, Toby and Hodd 1982) and with the help of taxonomists at the University of Bhavnagar. Identification was later confirmed by taxonomists at the Botanical Survey of India, Pune Branch.

Grasslands, shrublands, and saline regions were divided into approximately equal-sized sectors. Equal number of random samples of the vegetation were taken by the quadrat method

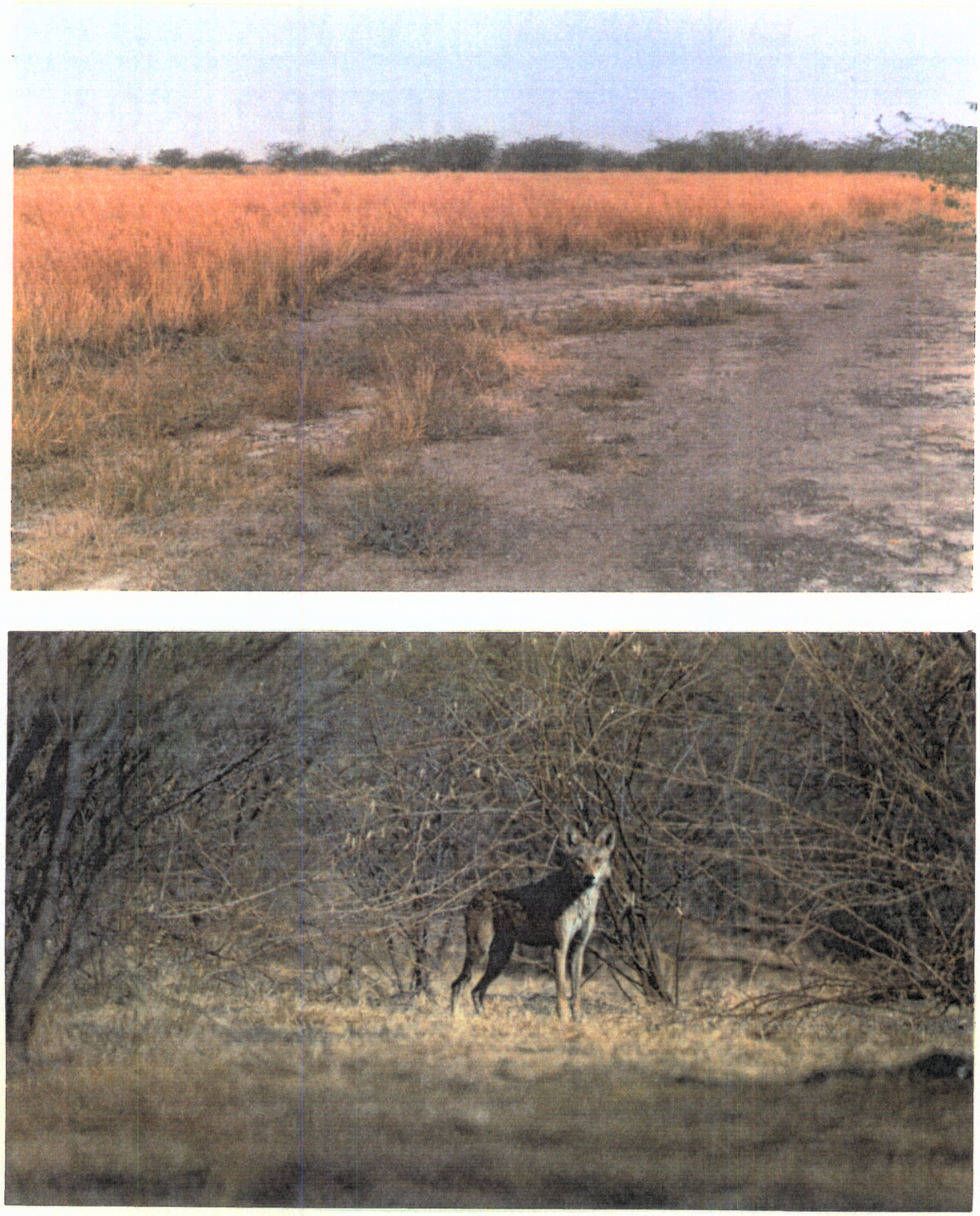


Fig. 1. a)Habitat types at Velavadar National Park. Saline regions in the foreground, *Dicanthium* grasslands, and *Prosopis* shrublands in the background. b) Moderately dense shrublands being used as a rendezvous site by the wolf pack in 1990.

within each sector in a habitat type (Daubenmire 1968, Reppert et al. 1962) in every season. A quadrat size of 50 cm x 50 cm was considered appropriate for sampling the herbage vegetation of the Velavadar region (Daubenmire 1968, Muller-Dambois and Ellenberg 1974, Kershaw 1977). This size would allow sufficient number of samples for statistical analysis, yet not be too small to misrepresent the species composition. Largest number of samples were taken from the grassland habitat, since this habitat was considered to be the most important for blackbuck. In addition, grasslands were the most heterogeneous in terms of species composition and biomass when compared to shrublands and saline regions. Sample size ranged from 60 to 130 quadrats in each habitat type in each season.

Each sampled quadrat was clipped at ground level and sorted into component species. Individual plants of each species were counted and the fresh weight of each species was recorded to the nearest 0.5 gms. Dead biomass in the form of litter and standing dead matter was combined and weighed. Three representative samples of 200-300 gms of each plant species were collected in paper bags in each season and oven dried at 55°C to constant dry weight. Moisture content of each species was calculated as the difference between fresh weight and dry weight. The coefficient so obtained was used for converting fresh weight of each species in each quadrat to dry biomass. The dried sample of each species was ground in a mixer, sieved through a 1 mm screen, and stored in airtight containers for laboratory analysis.

Cover

Cover relevant to wildlife is an estimate of (1) relative visibility of animals and (2) the shelter provided by objects from extremes of climate (Gysel and Lyon 1980). In the case of wolves and blackbuck, relevant cover (or the lack thereof) of the first type would be an estimate of relative visibility from the ground level to about 1 m. Two methods were used to estimate cover.

1. A metal frame of 1 m x 1 m subdivided into 16 equal squares was randomly (as explained for soil sampling) placed vertically in different habitats (density board) (Muller-Dambois and Ellenberg 1974, Nudds 1977). The number of squares not visible from a perpendicular distance of 10 m was recorded. A total of 4 such observations were made for the same location from 4 different directions by rotating the frame 90° for each observation. Cover for a location was estimated as the average percentage of these 4 observations.

2. Random belt transacts of 25 m x 2 m were employed (Anderson and Ohmart 1986) to estimate stem and twig density in the shrubland habitat. All rooted *Prosopis* stems, and all stems or twigs intersected at 1 m height within 1 m on either side of the 25 m transect, were recorded. Diameter at breast height (DBH) of all *Prosopis* stems in the belt transect greater than 2.5 cm were recorded. Height to the nearest 10 cm of all *Prosopis* "trees" was also recorded.

Separate random estimations of cover by both methods were made in areas known to be used intensively by wolves.

Prosopis Management

Three 10 m x 10 m plots of *Prosopis* which were to be harvested for charcoal production were cut and sun-dried for 2 weeks (average maximum temperature 44°C). The wood obtained from each plot was then weighed to give an estimate of fuel wood production.

During the summers of 1988, 1989, and 1990, the park management cleared *Prosopis* and produced charcoal from the harvested wood. Data were obtained from the park manager on the costs, the amount of charcoal produced, and the area cleared.

During the late winter of 1988 and 1989, the grasslands were cleared of all *Prosopis* saplings. Data were collected on the costs associated with this management activity. Invasion rates of *Prosopis* into the grassland were estimated by counting the number of established *Prosopis* saplings in 30 random, 10 m x 10 m plots prior to an eradication management attempt. To quantify the

effect of grazing on *Prosopis* invasion rates, 15 random plots of 10 m x 10 m were sampled in over-grazed grassland areas. The number of established *Prosopis* saplings were counted for comparison of *Prosopis* success rates in moderately-grazed and heavily-grazed grassland areas.

Chemical Analysis of Plant Samples

Duplicates of each dried and ground sample of all plant species in every season were analyzed for acid detergent fiber (ADF), lignin (L), and acid insoluble ash (AIA) by procedures described by Harris (1970). Crude protein (CP) was estimated by Kjeldehl's method (Total N x 6.25) and gross energy content was estimated by bomb calorimeter (Goering 1970, Harris 1970, Assoc. Off. Anal. Chem. 1970, Indian Standards 1976, Pond and Pearson 1970).

Exclosures

Six wire mesh exclosures (3 in the grassland, 2 in the shrubland, and 1 in the saline region) of 6 m x 6 m with a mesh size of 15 cm x 15 cm were constructed to study the impact of grazing on the vegetation (Baker 1960, Holechek et al. 1982). Six to 10 quadrats of 50 cm x 50 cm were randomly clipped within the exclosures in each season. Each quadrat clipped within the exclosure was paired with a quadrat sample clipped outside the exclosure within 6 m of the fence. A 50 cm strip of vegetation along the fence of the exclosure was excluded from sampling to avoid any edge effects (Mullen and Rongstad 1979). The vegetation in each quadrat sample was sorted by species. Individuals of each species were counted and the fresh and dry weight of each species estimated as explained above. Paired statistical comparisons were performed to study differences inside and outside the exclosures.

Soils

Soil samples were collected and analyzed for electrical conductivity (EC), sodium adsorption ratio (SAR), pH, and organic matter (OM) from grasslands, shrublands and saline habitats. Each habitat type was divided into sectors of approximately equal size and equal number of samples were analyzed from each sector in a habitat type. Since grass roots are restricted to the upper soil strata (< 25 cm) in semi-arid grasslands (Singh and Krishnamurthy 1981) the soil samples were taken as a core from the surface to a depth of 20 cm. Each sample was mixed and stored in labeled plastic bags prior to analysis. Analyses for pH, OM, EC, and SAR were performed as described by Jackson (1973) with a soil-to-water ratio of 1:2.5, for a total of 65 soil samples.

Electrical conductivity (EC) depends on the concentration of free ionic radicals and is highly correlated with salinity (Brady 1990:213-251, Hesse 1971:61-87). Indeed, EC is often used as an estimate of salinity (Aggarwal et al. 1983, Brady 1990:213-251, Hesse 1971:61-87, Paliwal and Khodier 1986). Sodium adsorption ratio (SAR) is expressed as:

$$[SAR] = [Na^{+}] / \sqrt{\frac{1}{2}([Ca^{2+}] + [Mg^{2+}])}$$

SAR gives information on the comparative concentrations of Na^{+}, Ca^{2+} and Mg^{2+} in soil solutions. SAR has greater biological significance than exchangable sodium percentage (ESP) because it takes into account the moderating effect of calcium and magnesium ions on the adverse effects of sodium ions on plant growth (Brady 1990:213 - 251, Bower and Hatcher 1962).

A one-way analysis of variance procedure and multiple range tests were used to test for significant differences in EC, SAR, pH, and OM between the grassland, shrubland, and saline habitats.

Blackbuck

Habitat Selection

Scan animal sampling (Altmann 1974) was used on a herd of 30 to 200 blackbuck to determine the proportion grazing in different habitats. The herd was kept under continuous observation for a minimum period of 36 hrs in each season. The herd was distinguished from other herd units by 2 or more identifiable individuals (albinos, horn shapes, etc.). The herd was followed by vehicle or on foot at distances ranging from 10 m to 300 m, depending on the habitat and the circumstances to minimize any disturbance from the observer. Scan observations were made at 10-minute intervals with the aid of 8x50 binoculars. The habitat type being used and the activity of each animal was recorded at the instant of observation.

Blackbuck usually completed a grazing circuit and returned to a central aggregation site in the grassland at sundown. Several herds integrated into one, and it was not possible to distinguish the observation herd as a unique unit. Observations were then recorded for the whole aggregation in which the identifiable individuals had joined, thus increasing the sample size to about 200-400 animals for night observations. Sampling periods were selected to include moonlit nights, making night observation easier. This may have introduced a bias towards greater activity at night as animals are probably likely to be more active on moonlit nights than dark nights. A spotlight was occasionally used when the identity of the observation unit was in doubt. Blackbuck habituated easily to spotlighting and did not show any response after an initial slight disturbance during the first 1 or 2 occasions.

Food Habits

Food habits were studied by observing 3 tame blackbuck feeding in the same habitat as their wild counterparts (Berwick 1974 :114, Bjugstad et al. 1970, Butts et al. 1982, Field 1970, Hobbs et al. 1979 and Wallmo and Neff 1970) and by observing wild blackbuck feeding within a distance of 30 m with the aid of a 30 to 60x spotting scope. A minimum of 3 grazing trials by each captive blackbuck was conducted in each habitat in each season. During each trial more than 400 bites were recorded on audio tape. Bites were recorded opportunistically from wild blackbuck. These ranged from 500 to 2000 bites in each season in each habitat. Bite data from tame and wild blackbuck were pooled for analysis of food habits in each season. These methods were considered most appropriate and feasible, under the circumstances, due to the ease and accuracy of quantification and the nondestructive nature of the techniques. The use of lead animals in studying food habits has the advantage of being able to select sampling areas, and experimental control. It permits obtaining forage samples selected by the animals for identification and analysis (Bartmann 1982, Bartmann and Carpenter 1982, Munro 1982, Wallmo and Neff 1970, and Wallmo et al. 1973).

Four captive blackbuck, 2 males and 2 females, were obtained for the purpose of this study. One male and one female were hand-reared as fawns and were ideal for lead-animal studies (Wallmo and Neff 1970). One subadult male, though not procured as a fawn, was also made tractable and appropriately trained. The remaining female remained extremely shy despite patient efforts to train her. Due to the endangered status of the blackbuck (Saharia 1981:223, Tikarder 1983:113) it is difficult to procure appropriate blackbuck. The time investment required to tame and train blackbuck for the purpose of such a study is enormous. This requirement restricted the captive component of food habits sampling to 3 blackbuck (2 males and 1 female) and it was not possible to use more blackbuck as recommended by Bartmann and Carpenter (1982) from similar studies on mule deer (*Odocoileus hemionus*).

Comparison of Food Choice of Tame and Wild Blackbuck

To compare the food item selection by tame and wild blackbuck, a grassland area of about 1 ha which was intensively used by wild blackbuck was selected. The grass height in this plot ranged from 5 cm to 20 cm. A camouflaged open vehicle was used as a mobile hide. Observations of wild blackbuck feeding within a radius of 25 m from the vehicle were obtained with the aid of a 15 to 60x spotting scope. The number of bites taken of a particular food item was recorded on audio tape.

Tame blackbuck were later taken out to graze in the same area at the same time of the day and the number of bites of different food items were recorded. Statistical comparisons between the food item selected by wild and tame blackbuck were performed. Distinctions of food choice based on age and sex of the blackbuck were not attempted due to small sample of tame animals (Thomas and Taylor 1990).

An "underlying assumption" of most food habit studies made by observing captive tame animals feeding is that the captive animals select food items in the same proportion as their wild counterparts (Berwick 1974:114, Buechner 1950, Butts et al. 1982, Currie et al. 1977, Duncan 1975, Dunkenson 1955, Field 1970, Healey 1968, Hobbs et al. 1979, McMahan 1964 and Wallmo 1951). However, learning does seem to play an important role in forage selection (Arnold and Maller 1977, Bartmann 1982, Bartmann and Carpenter 1982, Leuthold 1971 and Sinclair 1977:126). Studies by Bartmann (1982) and Bartmann and Carpenter (1982) confirm the difference in diet choice between "experienced" mule deer that were exposed to range grazing and unexposed deer. If the tame animals are allowed to graze on the range prior to data collection, the bias is greatly reduced (Bartmann 1982, Bartmann and Carpenter 1982). Captive blackbuck were allowed to graze in the same habitat as the wild blackbuck for a minimum period of 2 weeks prior to data collection. The blackbuck were maintained solely on natural forage grazed by them and or natural forage clipped and provided to them in the holding pen constructed in the park.

Bite Counts

In each season, after habituation to grazing on the range for 2 weeks, captive tame blackbuck were taken out on grazing trails. Sampling was done in all the different habitats specifically in areas known to be intensively used by wild blackbuck. Bites taken of each food item were recorded on audio tape. The data were collected by habitat types.

Three batches of 20 bites each of the major food items were collected from the blackbuck's mouth in each season. Blackbuck, after collecting a sizeable quantity of food material in their mouth, pluck it off the plant with a slight upward jerk of their muzzle (Van Dyne et al. 1980). This amount of food material in their mouth was considered a bite. The bite size varied from plant species to species in accord with the concentration of edible plant parts in a given grass sward. Thus, the average bite size for each species varied from season to season. Blackbuck, when feeding on litter (fallen dead vegetation) in summer do not need to bite off plant parts. In this situation they gather a mouthful of appropriate litter, push it with their tongue to the molars for some mastication before swallowing. This amount gathered in the mouth, prior to mastication, was considered to be a bite. Bites by blackbuck were also simulated by hand plucking plant parts eaten by blackbuck (Hobbs et al. 1979, Munro 1982 and Wallmo et al. 1973). These, along with the actual bites collected from the blackbuck's mouth, were oven dried in paper bags at 55°C and their dry weight determined. Dry weight per bite was estimated from bites collected from the blackbuck's mouth while the hand-simulated bites were used for chemical analysis to avoid biases of salivary contamination.

Computation of Diet Components

Habitats were rated according to the proportion of grazing activity of wild blackbuck in each of them as estimated from scan sampling. I assumed that the proportion of grazing activity in one habitat represented the proportion of bites obtained from that habitat. The amount of forage intake

would depend on the intensity and the duration of grazing (Cary 1976: 40-41). Blackbuck were scored as grazing only when they were actively feeding with their heads down (Prasad 1981:171). The frequency of scan observations was high (once every 10 min). Thus scan animal sampling should be adequate for estimating proportion of grazing activity by recording the number of blackbuck actually grazing at the instant of observation.

The seasonal aggregate of the total number of bites recorded for each food item in each habitat was multiplied by the proportional grazing activity of wild blackbuck in that habitat. The correction was applied to the bites rather than to the biomass of each food item consumed since the scan animal sampling technique directly quantified grazing activity. The biomass per bite of each species would more likely be similar in the same habitat. Duration and intensity of grazing would depend on the dispersion of food items, the ease of obtaining them, and their palatability. These aspects of the foraging phenomenon were assumed to be well represented by the number of bites.

After data on bites were aggregated and corrected, the proportion of bites of each food item in the diet was estimated. The proportion was multiplied by the average dry weight per bite to estimate the contribution of the food item to the blackbucks diet in terms of dry biomass (Hobbs et al. 1979). The proportion of a food item in the blackbuck's diet, when compared to the proportional biomass of the food item available (from vegetation quadrat studies), gave an index of food preference (Jacobs 1974, Loehle and Rittenhouse 1982).

Fifty grams of forage was constituted by adding food items composing the natural diet of the blackbuck in proportion to their occurrence in the food habits studies. This reconstituted diet was used for analysis of crude protein (CP), acid detergent fiber (ADF), acid insoluble ash (AIA), lignin (L), ether extract (EE), and gross energy (GE).

Total Fecal Output (TFO), Dry Matter Intake (DMI), and Digestibility

For any study of energetics, it is important to determine the amount of food consumed and its digestibility. Total fecal output (TFO) was estimated using the external indicator technique (Chruch 1976:115-132, Ruggiero and Whelan 1977, and Theurer 1970). This component of the study was done on 4 captive blackbuck in each season when they were maintained solely on natural forage. It was not possible to have a larger sample size as recommended by Theurer (1970) and Holechek and Vavra (1982) due to the limitations stated earlier. Three gms of chromium sesquioxide (Cr_2O_3) (weighed to the nearest milligram) was mixed with approximately 2 gms of shredded paper (Corbett 1960) and 1.5 gms of wheat flour. These were made into dough and fed to the blackbuck. The blackbuck were accustomed to hand feeding prior to the experiment. Care was taken to ascertain that all of the quantity was ingested. The blackbuck were fed chromic oxide every morning between 7 am and 8 am for 12-15 days every season. After allowing 5 days for equilibrium of chromic oxide (McCann and Theurer 1967) in the gastro-intestinal tract, fecal grab samples were collected twice daily from each blackbuck (Ruggiero and Whelan 1977). The first fecal grab sample was collected between 6 to 8 am and second between 5 to 7 pm. The fecal samples were labeled and oven dried at 60°C in paper bags. Chromium oxide concentration in the dried fecal samples was estimated calorimetrically as described by Hill and Anderson (1958).

Chromic oxide is considered to be indigestible and is not absorbed by the gut mucosa (Church 1976: 115-132). Thus, assuming a thorough mixing of food in the rumen and allowing time for equilibrium in ruminants, chromic oxide achieves a constant rate of expulsion via feces (Theurer 1970, Van Soest 1982: 53). In white-tailed deer (*Odocoileus virginianus*) (Ruggiero and Whelan 1977) and domestic steers (Nelson and Green 1969 and Yadava et al. 1973) a diurnal variation in the excretion rate of chromic oxide has been observed. Grab samples widely spaced in time on the same day are considered to minimize the bias due to this uneven rate of "excretion" of chromic oxide (Theurer 1970). On equilibrium , intake of chromic oxide should equal "excretion" of chromic

oxide via the feces. Thus the blackbuck should excrete 3 gms of chromium oxide in 24 hours. The relationship is (Church 1976):

Intake of chromic oxide = Fecal excretion of chromic oxide

Gms of chromic oxide ingested = Concentration of chromic oxide in feces x TFO

Therefore :

TFO = Chromic oxide ingested/concentration in feces.

To verify the method of estimating TFO by the external indicator (Cr_2O_3) method, total fecal collection of 2 male blackbuck was done for 4 days at the same time at which the experiment using chromic oxide as an external indicator was being conducted. The TFO estimated by the external indicator technique was compared with actual total feces collected by means of a paired t-test.

Lignin and acid insoluble ash (AIA) were considered as potential candidates for an internal indicator to estimate dry matter intake (Theurer 1970, Van Soest 1982:39-57). However, comparison of DMI estimated by lignin to DMI estimated by AIA showed that lignin was digested to some extent by blackbuck (see Results) - an undesirable characteristic for an indicator (Church 1976:115-132). Later estimations of intakes were done from AIA as the internal indicator. Arguing on the same principle as used with the external indicator (Cr_2O_3), we have:

AIA intake (estimated from analysis of composite diet) = Fecal excretion of AIA

AIA concentration in forage x forage intake (DMI) = Concentration of AIA in feces x TFO.

Therefore:

DMI = Concentration of AIA in feces x TFO/AIA concentration in forage.

The accuracy of estimating dry matter intake depends on the accuracy of estimating TFO, and AIA concentrations in feces and forage. However, there is a way to countercheck the validity of the internal indicator technique and the bite count correction method in estimating the blackbuck's diet. The total dry matter intake of the 2 captive male blackbuck (along with TFO) was determined by feeding the blackbuck for 3 days weighed amounts of forage and deducting the amount not consumed. The DMI thus determined was statistically compared with the estimate of intake arrived at with the internal indicator technique. Further, 20 random samples of wild blackbuck fecal pellets of approximately 5 gms each were collected in each season. These were mixed together and 5 grab samples of 1 gm each were randomly drawn for chemical analysis (Jenks et al. 1989). CP, ADF, lignin, AIA, EE, and GE were estimated in these composite fecal samples. The estimates of fecal parameters from wild blackbuck were compared with the fecal parameters of the captive blackbuck by means of a t-test.

Dry matter digestibility (DMD) and nutrient digestibility can be estimated if DMI and TFO are known with reasonable certainty (Church 1976:115-132, Robbins 1983:274-312 and Van Soest 1982: 39-57). Thus:

$$DMD = (DMI - TFO)/DMI$$

Protein digestibility is estimated as:

$$CPD = \{(CP \text{ in forage} \times DMI) - (CP \text{ in feces} \times TFO)\}/CP \text{ in forage} \times DMI$$

Similarly, digestibility of fat (EE) is estimated by:

$$DEE = \{(EE \text{ in forage} \times DMI) - (EE \text{ in feces} \times TFO)\}/EE \text{ in forage} \times DMI$$

Fecal Indices

Determining forage quality for wild ungulates is a tedious task, requiring a great investment of time and money. In the case of endangered species, the problem is further compounded due to limited access to experimental animals. Fecal indices can be used to circumvent these problems by providing a relatively inexpensive and quick estimate of diet quality (Armstrong et al. 1989. Arnold and Dudzinski 1963, Erasmus et al. 1978, Greenhalgh et al. 1960, Holechek et al. 1982, Holloway et al.1981, Lancaster 1949, Leslie and Starkey 1985, Servello et al. 1983.)

Correlation analyses were used to examine the potential of various fecal characteristics like fecal nitrogen (FN), fecal ether extract (FEE), fecal ADF, and fecal lignin as indices of forage quality (Holloway et al. 1981, Leslie and Starkey 1985).

Census Method

Total population estimation was done by total counts by trained volunteers during the early morning hours (Davis and Winstead 1980). A census was conducted twice every season. In summer, 1989, censuses were conducted 5 times on consecutive days to collect data for statistical analysis and estimation of confidence intervals (Madin 1989). Blackbuck are easy to spot in open grassland habitats as long as they are on their feet and moving about. Blackbuck lying down in grass even 20 cm tall are very well camouflaged and are likely to be overlooked. Visibility is severely impaired in the shrubland habitat. Blackbuck were rarely observed to venture into the shrubland habitat after dark. They tend to aggregate into 2 or 3 large herds in the grassland to spend the night. These large aggregates, sometimes over 450 animals, disperse in the morning into smaller units to graze. There is a high intensity and long duration grazing peak in the activity of blackbuck in early morning (Mungall 1978:51). During this period, almost all of the blackbuck are actively feeding and

slowly moving apart from the large aggregations. These 2 behavioral traits were used to advantage to conduct censuses. Trained volunteers were stationed at different locations in the park, and at a set time (early morning 6.30 am to 9 am), counting was done simultaneously. The shrub habitat was crisscrossed to count stray blackbuck. Populations outside the park were monitored prior to the census. Their favorite "lying up" spots for the night were recorded as were their grazing circuits. These populations were counted by vehicle simultaneously when the census was conducted within the park.

Blackbuck were placed in age and sex classes during censuses. Age classes were limited to 4 groups discernible in the field by mere observation. The following description from Mungall (1978:69-74), Walther (1972) and Walther et al. (1983) was used to distinguish between groups.

Fawn (Less than 6 months) : This category was further divided into (1) brown fawn or neonate (< 2 weeks) and (2) older fawn (> 2 weeks). The neonate blackbuck is brown over the pigmented areas. It does not have an orange-tan color like the adult female and most immature males above the fawn stage. The fawn in the second week of life is still shorter at the withers than the bottom line of its mother's belly. By 2 weeks, the fawn (older fawn) has lost its neonate proportions (long legs, a thin short body and short neck) and is well coordinated. At about 1 month age, the fawn's coat changes to approximate the color of its mother. The 1-month-old fawn's withers overlap its mother's side. The coat takes on a light creamy yellow color at 1.5 to 2 months before it finally assumes the typical orange-tan. In males, buds, which will later develop to become horns, can be discerned at about 4 months age.

Adolescent (6 to 12 months) : The adolescent no longer has the long legs, short body and short neck of a fawn but has a longer, deeper body which makes the legs appear relatively shorter and the neck longer than in the fawn stage. The coat is now typical orange-tan. The withers come well up to an adult female's side, but the adolescent is still shorter than the adult in both height and length. Males continue to grow more robust horns. These horns curve forward, grow rings, and begin to spiral.

Subadults (1 to 2 years) : Subadults are as tall as the adults and as long but not as deep through the body. Thus, they are lighter in build than the adults. The face is still shorter than that

of an adult. The white along the ventrolateral side of females is less wide than the pigmented area. At great distances and with poor visibility, distinguishing subadults from adult females becomes difficult. Characteristically the subadult male has horns with two twists with the tips pointing in. When adulthood is reached, the males have 3 twists in their horns with the tip pointing in. Males may start turning black during this stage.

Adults (Greater than 2 years) : Adults are deep through the body and the face is longer than that of subadults. The width of the white on the sides approximates that of the pigmented area. Females often have some darkening on the lower shoulder where the pigmented area borders on the white, on the upper forelegs, and on the stifle. Males may be orange-tan, black, or any color in between, regardless of their age. Their horns have anywhere from 3 to 5 twists. Old adults have a sagging underline to the body, which remains deep but looks more oblong than square between the elbow and stifle. Old males who are dark may show conspicuous gray mixed into the coat on the pigmented areas of the head.

The blackbuck population within Velavadar National Park, along with peripheral populations at Gokulpara, Mevasa, Mithapur, Bharbhil, Kanatalav, and Gangawada village areas, are one biological unit. These populations often intermingled and exchanged individuals. Thus all of these "subpopulations" were included in each census to avoid biases of emigration and immigration.

Fecundity and Natality

Natality was estimated from the fawn-to-doe ratio. Neonate fawns are extremely cryptic and have the habit of lying motionless until almost trodden upon (Mungall 1991) . They would then bolt off for 100-200 m, and lie up again in a suitable patch of cover. Fawns are extremely active in the early morning hours after their morning feed. During this time, the fawns typically exercise by racing and prancing about their mothers with similar-aged playmates (Mungall 1991) in the security offered by the large herds. Fawns were counted during this time of the day after every

fawning peak. Some fawns were definitely overlooked, some mortality must have occurred between the time of birth of individual fawns and the census counts, and it is likely that there would be some late births that were not included in the census. It was not possible to capture and sample a significant fraction of female blackbuck to estimate gestating and/or lactating females. Thus the fawn-to-doe ratio was considered the best estimate possible under the circumstances.

Blackbuck can produce 2 fawns in a year, however, 1.5 fawns per reproductive female in 12 months seems to be the average in a population (Mungall 1978:81-84, Ranjitsinh 1982:107). Yearling females were assumed to have a fawning rate of 0.25 fawns per year (Mungall 1978:84). Though blackbuck do produce fawns throughout the year (Howery et al. 1989, Mungall 1978:82), there are 2 fawning peaks in Velavadar National Park, a major one in September and a minor one in March (Ranjitsinh 1982:107-108, 1989:63-64). The September peak coincides with a period of abundant food resources as it occurs just at the end of the monsoon season. However, the March fawning is at a period when food resources are at the ebb. A resource-lean summer period awaits the lactating mother and fawn. Under such circumstances it would seem that only females in very good condition would successfully fawn in March (Mungall 1978:82). Empirical evidence to verify the above claim is lacking. However, observations in the field and prior research (Schaller 1967:154-155) suggest this to be true. Thus, I further assumed that only half of the mature females present in the population fawned in March and nearly all the females fawned in September. Field data support this assumption. Rainfall, the single major factor governing food production, was above average during all 3 monsoons of the field study period. Prior to the study, there were 3 years of drought (1985, 1986, 1987). The first census was conducted in April 1988 just after the fawning peak of March 1988. The assumption of half the mature female population fawning in March 1988 would not be valid for this fawning peak since the blackbuck were in poor condition. It was assumed that during 1988 March fawning peak, only 1/4 of the mature females fawned.

Mortality

Mortality of older fawns was calculated from censuses. Mortality was the difference between fawns and the number of adolescents in the census 6 months later. Mortality in the first few weeks after fawning was calculated as the difference in number of fawns at the end of the fawning period and the expected number of fawns based on the above assumptions.

A record was kept of all dead blackbuck encountered. Mandibles and maxillae were collected from dead animals whenever possible. These were labeled according to the date of death and sex of the animal when known. The jaws were later aged by criteria of tooth eruption and tooth wear (Mungall 1978:66-68) and comparisons made with a reference collection of jaws of known age blackbuck at the Bombay Natural History Society. During the 3-year study, 127 individual blackbuck jaws were collected and aged. Younger age classes, especially fawns, were under-represented in this sample (Caughley 1976, 1980:85-90, Sinclair 1977:224-229). Thus, mortality for fawns was estimated from consecutive censuses as explained earlier. Mortality rates for all other age classes were calculated from aged jaws as explained by Caughley (1980:85-98).

Long Term Population Trends

No reliable data are available on the age and sex composition for the Velavadar blackbuck population. Reliable information is available regarding total numbers from records of the forest department and censuses conducted by Mungall et al. (1981:50-51) and Ranjitsinh (1989:150). This information from 1969 to 1987 along with census figures from the current study were used to estimate the maximum and minimum numbers between which the Velavadar blackbuck population fluctuated. Regression analysis of natural logarithm of population and time in years were used for estimating various values of r, the realized instantaneous rate of increase (Sinclair 1977:224).

Population Models

For a life-table analysis from mortality data, 2 assumptions are essential:

1) The population has achieved a stable age distribution.

2) The population is either stationary (birth rate = death rate) or is changing (increasing or decreasing) with a constant known r (Caughley 1980:90-95).

Both of these assumption are rarely met by natural populations. The blackbuck population at Velavadar is not hunted and the effect of poaching is insignificant. The population is solely exposed to a natural set of factors influencing natality and mortality. Nutritional factors and predation were considered the most important factors influencing natality and mortality. Nutritional status is dependent on the quantity and quality of food available. This, in turn, depends on rainfall. Rainfall during the study period (1988, 1989, 1990) was above average for the region, and food availability was similar throughout the study period. Predation pressure could also be considered similar throughout the study period (see Results). Thus the population could be considered to have been exposed to a fixed schedule of births and deaths, a prerequisite for a stable age distribution. However, due to the population crash experienced in 1987, a stable age distribution is unlikely to have been achieved. Even if the above assumptions are not strictly adhered to, a life-table analysis is likely to provide insight into the demographic characteristic of a population at a given time (Spinage 1970). The Velavadar blackbuck population was in an increasing phase during the study period. The total numbers during the summer censuses were used to compute an average value of r for the duration of the study. This value of r was used for adjusting the frequency of deaths in all age classes except age class "0" (Caughley 1976, 1980:92-93, Caughley and Birch 1971, Sinclair 1977:225). Age class "0" (neonate to 1 year old) would be under represented in a sample of dead blackbuck recorded due to the tendency of being totally consumed by predators and scavengers and due to a faster rate of decomposition of their fragile skulls (Caughley 1976, Grobler and Jones 1980, Sinclair 1977:225 and Spinage 1972). The mortality rate for fawns (age class "0") was estimated from census data, and the frequency of deaths adjusted accordingly (Sinclair 1977:224-226, Caughley

1970). A life table was constructed from the above-obtained frequencies of death as described by Caughley (1980:91-93), Conley (1978), and Sinclair (1977:224-226). Probit analysis (Caughley 1970, 1976, 1980:92, Finney 1971) was done on the corrected frequencies to obtain estimates of :

1) Median age of adult death,

2) Standard deviation of adult ages at death, and

3) Index of skew of adult ages at death.

A Leslie matrix (Leslie 1945, Taylor and Curley 1988) was constructed from the life table data. The 1990 population figures of blackbuck were distributed according to the proportions computed in the life table in different age classes to constitute the initial population matrix.

In natural populations, schedules of age-specific mortality and fecundity are rarely constant over a long period. Thus, populations always experience stochastic fluctuations. Age specific mortality and fecundity schedules were made variables to incorporate stochasticity in the population model.

Fawn survival depended primarily on predation and nutrition. Blackbuck fawns rely on crypsis like other antelope fawns to avoid predation (Jarman 1974, Mungall 1978a:60-61,70, 1978b and 1991). Fawns lie up in suitable cover and bolt on detection to another hiding place. They are easy prey to a multitude of predators, including wolves, jackals, and pariah dogs. They are specially vulnerable when the ground is bare and there is little cover available. Ground cover in the form of grass patches is dependent on the monsoon rains. Rains are also responsible for the quality and quantity of food resources available to the lactating mother and, after weaning, to the fawns. It can be generalized that in good rainfall years there is higher recruitment from the "0" age class since there is:

1) Greater production of fawns due to good condition of the blackbuck females, and

2) Higher survival due to good cover and a high nutritional plane of both mother and fawn (Kirkpatrick 1975, 1988, Moen 1978). The reverse is true for both of these factors in drought years. Fawn recruitment was estimated in the field for both these conditions. The fawn survival in summer of 1988 was considered to have the lowest survival rate. The highest survival rate was considered to be similar to that observed for the fawning peak of September 1988. In reality, there was no way

to estimate fecundity in the field. The number of fawns surviving through their first months was actually the recruitment per total number of reproductive females. This recruitment is a combination of natality and the fawn survival during the early phase of life. It was not possible to separate these 2 factors under the field conditions. However, recruitment estimates are believed to suffice for the population model. The mortality rates for the age classes other than fawns would fluctuate to a lesser extent and would have smaller coeffecients of variation. The survival of these age classes would also fluctuate with food availability and predation. Thus the mortality rate would be higher in years of poor rainfall with poor availability of food. Therefore, survival of these age classes was made to correlate positively with fawn survival. In poor rainfall years, mortality of both fawn and older age classes increased and vice versa.

Fecundity was made a variable with a mean of 1.5 fawns per year per female aged 2 years and above, and would fluctuate within a range of 0 fawns to 2 fawns per year. Yearling females were considered to breed less frequently (Mungall 1978:84). A mean of 0.25 fawns/yearling female/year was assumed. Fecundity was also highly positively correlated with fawn and adult survival rates.

With these initial conditions a population model was run using the modified Leslie matrix approach. Using the Monte Carlo approach a simulator (Ramasage)(Ferson and Akcakaya 1990) was used to generate 250 stochastic replicates for a run of 50 years. A probabilistic mean path of the population was generated. A confidence zone of population trajectories within 1 standard deviation of the mean was computed and the maximum and minimum trajectories were recorded.

The model was run with different means for fawn survival, with and without density dependence. The maximum numbers of blackbuck during the past 20 years in Velavadar National Park were considered to be near saturation. The model was made density sensitive by reducing fawn recruitment to the population at higher abundance with a Beverton-Holt function (Beverton and Holt 1957). The parameters of the Beverton-Holt function were estimated by fitting a curve to the population data of the past 20 years.

Various parameters like life expectancy at birth, stable age distribution, reproductive value, generation time, and net reproductive rate were calculated from the life table.

Wolf

For the purpose of achieving the objectives of this research project, it was essential to gather data on:

1) Habitat use and preference by wolves,

2) Food habits of wolves, and

3) Population parameters.

Research on endangered species is risky. The researcher, if not cautious, could further endanger the species by the research process. This was especially true in the case of the extremely shy wolf population in Velavadar. The techniques for data collection on the above-mentioned parameters were designed to minimize disturbance to the wolves. This made me rely more on indirect methodology than direct observations.

Habitat Use and Preference

The area in and around the park was intensively searched for wolf signs. Whenever possible, habitat use patterns were determined by observing wolves. Wolves were usually located in the early morning hours on blackbuck kills. They were observed from distances ranging from 2 km to 50 m with the aid of 15 to 60x spotting scope and 8x50 binoculars. The pack was followed initially on foot and vehicle (1988) and later (1989-90) on horseback. It was difficult to keep pace with the pack, on foot, once it was on the move (Fig. 2a). The vehicle was limited to certain terrains. The wolves seemed to be disturbed by the vehicle, especially when it was driven off the roads. Wolves were accustomed to domestic livestock including horses. They seemed to habituate quickly to having a horseman within visible range. They seemingly indulged in normal social activities like scent marking, play, and dominance interactions. Care was taken not to approach the pack too closely

or directly to avoid scaring them. The wolves were followed at distances ranging from 100 m to a 1000 m depending on the habitat and situation. The wolves were followed usually for a few hours (1-5) until they entered cover to lie up for the day (Fig. 2b). The area was circled at a distance to ascertain that the wolves were lying up in it and had not moved past it. The region was located on a map and marked. Each area was later inspected closely to determine exactly where the wolves lay and to record the habitat characteristics of cover, water, and human disturbance.

It was not always possible to locate and follow wolves to their preferred habitat where they would spend the hot hours of the day. I relied greatly on indirect signs as well. Wolves dig out a small hollow in the earth to expose cool moist soil and curl up in it for respite from the noon heat. Presence of wolf hair and sometimes odor confirmed recent use of such dugout resting sites. These were marked on the map and habitats described.

During nights, the wolves covered all regions of the park as evidenced by tracks and spotlight sightings. They occasionally ventured near human dwellings. Wolves, however, followed certain specific routes while traveling at night. They had specific sites for scent marking along these routes. To ascertain which regions of the park were being intensively used by wolves, wolf routes and scent marking spots were cleared regularly of all tracks and scats and then smoothed out in specific areas. Inspection of these locations provided quick information on regions of active use, wolf numbers, and were critical for locating denning areas and rendezvous sites.

Denning Areas and Rendezvous Sites

The above mentioned techniques provided information on regions intensively used during the breeding season. Wolves are extremely shy of human presence and disturbance, and thus areas where denning was suspected could not be intensively searched with the help of several people. This would in all likelihood have caused the wolves to abandon the den. Howling response was used instead to delimit the region being used. Wolves invariably responded to simulated wolf howls near

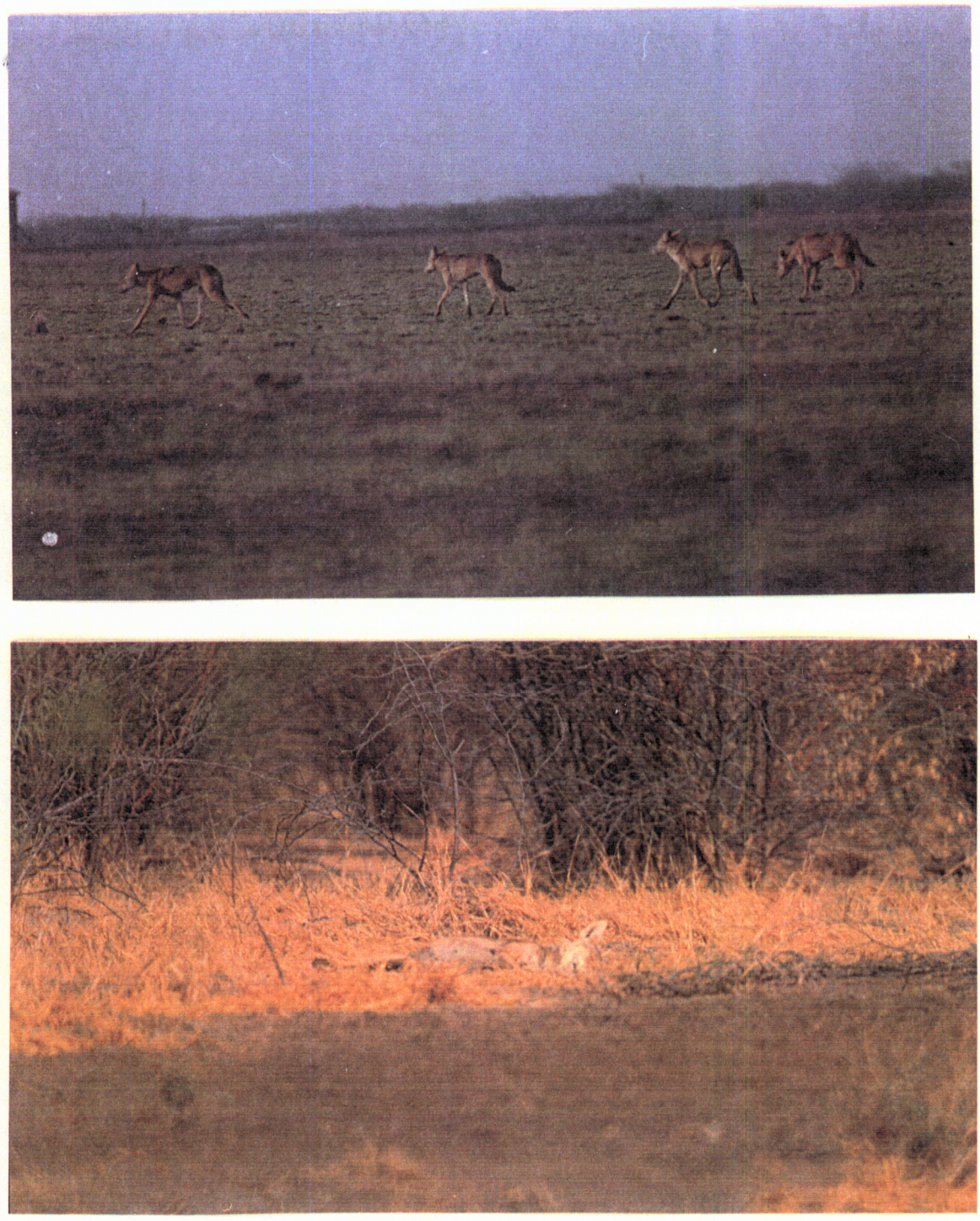


Fig. 2. a) Part of the wolf pack in June 1988 in the grassland. The grasses are beginning to grow after the drought of 1987. b) An adult male wolf resting in the afternoon in the shrubland at a rendezvous site.

their denning area. I would drive up to the suspected area after dark, wait for 10-15 minutes and then howl as described by Harrington and Mech (1978), Joslin (1967) and Pimlot (1960). I had learned the technique personally from Joslin and Peterson, and after hearing the Indian wolves howl had adapted it to mimic them. If the wolves responded, a record of how many and from approximately what location, was made. The next day, during noon hours when wolves are least active, I would cautiously inspect the area leaving minimum human signs. Prior knowledge of the terrain and wolf behavior was of paramount importance in locating dens with minimum disturbance. During the initial months of the study, wolves invariably detected me before I could spot them and they would move away. Luckily the first den located was not abandoned even thought I was detected in the vicinity 2 or 3 times by the wolves (to my knowledge). On subsequent investigations, disturbance caused by my presence was insignificant, since with experience, I could locate resting wolves, search the area, and leave with the pack still lying up in the area.

Once a den was located, a hide was constructed if the terrain was appropriate to allow this without disturbing the wolves. Close approach was avoided and observations were obtained by binoculars and a spotting scope. Dens were photographed, dimensions measured, and habitat parameters were recorded after the pups had moved out to a rendezvous site.

Rendezvous sites were easy to locate due to the pups "enthusiasm" to respond to simulated howls even during early evening hours. Rendezvous sites had wolf trails converging from all directions and the trails being intensively used (Joslin 1967 and Mech 1970:146-148). Scent marking with scats increased around these sites. Such rendezvous sites where the pups remained prior to joining the pack were located on the maps and their habitat characteristics described.

Food Habits

Data on wolf kills were recorded. Fresh blackbuck kills were usually detected in the early morning hours. The feeding activity of the pack, and the observation of aggregation of crows,

vultures, and jackals were the usual clues for detecting fresh kills. If the pack was still feeding on the kill when detected, data collection was suspended until the pack finished and moved away. Whenever possible, I reached the kill remains before most scavengers did. Data on sex, age class, shoulder height, weight of the kill remains, location and date of the kill were recorded. Samples of femur bone marrow, rumen contents, and the mandible and skull material were collected for later analysis. Notes were taken on the proportion and parts of the kill utilized, and method of killing and injury when discernible. Data on 48 such fresh kills were obtained in the course of the study period.

Bone marrow samples were classified into 4 classes (Sinclair and Ducan 1972). Representative samples from each class were analyzed for fat content by ether extraction in a Soxhlet refluxing apparatus (Indian Standard 1976). This index was used to determine the condition of the animal killed. Unutilized weight of the kill, when subtracted from the assumed weight of the killed blackbuck (based on sex and age) was used to estimate the amount of the carcass eaten by the wolves. On occasions, when the number of wolves to have fed on the carcass was known, either by direct observation or by tracks and signs, an estimate of the amount eaten per wolf was possible. When data of this type were available for 2-3 successive kills, it was possible to estimate the amount of meat consumed per wolf per day. This estimate is based on an assumption that blackbuck provided most of the food requirements of the wolves (see Results). This estimate of the amount of food consumed per wolf along with an estimate of the amount provided per day to a breeding pair at Junagadh zoo (Rawal, pers. comm.) was considered to be the amount required by wolves to be on a nutritional plane sufficient for normal physiological functioning.

Wolves have distensible stomachs (Mech 1970:169-172) and can consume large quantities of meat when available. To obtain data on how much meat wolves could consume, 2 goats of known weight were tethered near the denning site. These were subsequently killed and eaten by wolves. Kill remains were collected and weighed.

It was not possible to determine the contribution of smaller prey items to the wolf's diet by mere observation. Therefore wolf scats were collected and analyzed (Korschgen 1980). Scats of pariah dogs and jackals are similar to wolf scats; however, the diameter of wolf scats is larger than

scats of these animals. Wolf scats also have a characteristic odor. Only scats that were from wolves (with reasonable certainty) were collected. Scats that were not of appropriate size or associated with wolf signs were excluded from the analysis (Mech 1970:172, Thompson 1952). Bits of bone, claws, nails, hoofs, teeth, hair, chitin, seeds, etc. obtained from the scat were used as cues to identify the prey being eaten (Gamberg and Atkinson 1988, Johnson and Hansen 1978, and Korschgen 1980). The single most important factor used for determining the prey species represented in the scats was the cuticular structure and sculpture of the hair present in the scats. A reference collection of hair for all possible prey species found in Velavadar region was obtained from skins at the Bombay Natural History Society. Hair from different regions of the animal's body were collected. These specimens were washed and treated (as explained by Koppikara and Subnis 1976) prior to being mounted on permanent microscopes slides. Impressions of the external sculpture of hair was obtained on agar. Photomicrographs of whole-hair mounts and impressions were taken. These, along with permanent slides were used as reference to identify species from hair found in wolf scats (Keogh 1983).

Wolves consume a large amount of hide. Hair in carnivore diets plays a similar role as fiber in herbivore diets (Mech 1970:168-172). Rarely would wolf scats be devoid of any hair. Meat diets are highly digestible; large bits of bone and hair are indigestible (Mech 1970:168-172). Floyd et al. (1978), Gamberg and Atkinson (1988), and Corbett (1989) discussed the biases involved when using "frequency of occurrence" of prey species in the scats. Regression analysis developed by Floyd et al. (1978) was used to estimate the biomass contribution of each prey item. Normally wolf scats contained remains of a single meal (one prey item). When more than one prey item was encountered, the proportional volumetric contribution of each prey item in the scat was used for analysis (as explained by Corbett 1989). Scats were analyzed on a seasonal basis.

Information regarding the food consumption, requirement, and prey composition in the wolf's diet was used to estimate the average number of blackbuck killed per wolf per year. This estimate was used to simulate scenarios with varying number of wolves and the population of blackbuck required to sustain them. This was expressed as a wolf-to-blackbuck ratio (Ballenberghe and Hanley 1985, Fuller 1989a, 1989b, and Keith 1983).

Population Parameters

It was not possible to identify individual members of the pack since none was captured for marking or radio telemetry study. On most occasions, the alpha male was recognized due to his size and dominant behavior. On close observation this male had a scar below his right eye. On some occasions, the alpha female could also be recognized. She was identified by a black spot of fur on her tail. Pack size was determined by direct observation on kills and from tracks. However it was not possible to say with certainty that all pack members were counted or were the same ones seen on prior occasions. Track measurement, behavioral interactions, and a constant number of wolves seen in the pack with same sex and age composition were used as criteria to ascertain members of the pack. It was possible to distinguish subadult and adult wolves from their size, coat, behavior, and facial marking, especially when they were in their winter coat.

Fecundity was determined by the number of pups seen when they emerged from the den. The estimate did not account for mortality that might have occurred in the initial phase of life when the pups were restricted inside the den (Mech 1970:123-126). Consequent survival of the pups up to 9 months of age was estimated for 2 subsequent litters and the litter of 1990 until 5 months of age. Up to this age, dispersal was unlikely (Mech 1987) since the pups were dependent on the adults to provide food. Thus, decrease in the number of pups was considered to have been due to mortality. It was not possible to distinguish between mortality and emigration factors responsible for a drop in the pack numbers of adult wolves. Wolf carcasses, when detected, were examined for possible causes of mortality. Increase in adult pack members was considered to be due to immigration.

Information on other wolf packs was obtained from local villagers and from wolf signs like scats and tracks. Estimates were made of probable numbers of wolves in these packs and of the area being used. The scats collected from these packs were analyzed separately.

Management Options and Optimization Modeling

The exotic shrub *Prosopis juliflora* is considered a pest in most preserves and management is aimed at its eradication (Natarajan et al. 1984, Oza 1986). In the case of Velavadar National Park, *Prosopis* has certain positive values for the major endangered species of the park (see Results) (Muthana and Arora 1983). This property makes the management option of total eradication on this park undesirable. Total eradication of *Prosopis* would be, in any way, extremely expensive, and almost impossible to achieve, due to the rapid rate of recolonization by this exotic shrub (Verma 1987).

Decisions regarding where to cut *Prosopis* and how much area to cut are currently governed by the following :

1) The potential available wood from the stands for charcoal production, and

2) The funds available from the annual budget of the park for hiring labor to cut the *Prosopis* and produce charcoal.

Critical factors such as the following are currently not incorporated into the decision-making process :

1) Cover value of a stand for wolves,

2) Importance of stands as traditional denning areas and rendezvous sites,

3) Soil factors influencing grass production, and

4) *Prosopis* pod production and availability to blackbuck.

The disciplines of management science and operations research are built around a standardization of rational approaches to making decisions (Harris and Kochel 1981). The use of optimization models developed for operations research have been extensively used for natural resource planning (Dykstra 1984). Various forms of linear programming techniques (Hieller and Libermann 1986) were found to be ideal for application to the current situation of conflicting options for managerial decisions for Velavadar National Park.

Optimization Model

Under the current government policy, National Parks are to cater primarily to conservation of natural resources (The Wildlife (Protection) Act 1972). Rarely are any commercially exploitable products harvested from National Parks in India. Thus the economic gain from charcoal sale produced from the cut *Prosopis*, though being an asset to the forest department, is not the primary objective for the management activity. The management activity of cutting *Prosopis* is solely aimed at improving wildlife habitat (National Wildlife Action Plan 1982). The revenue from charcoal sale is not available for the park management but adds to the state government treasury (Majethia, pers. comm). Thus the management activities are aimed at increasing or maintaining the carrying capacity of the park's wildlife, especially its component endangered fauna.

The wolf depends primarily on blackbuck for food (see Results), and thus an increase in blackbuck numbers would be favorable for the wolf population. However, wolves also require some cover for denning and lying up during the day (see Results). Blackbuck are primarily dependent on grasslands for food biomass. Increasing the grassland habitat would increase the available food resource and habitat for the blackbuck. Thus an objective of increasing available food resource for the blackbuck by habitat management would increase the carrying capacity for blackbuck and this in turn should be beneficial to the wolves. The 2 endangered bird species (the lesser florican (*Sypheotides indica*) and the haubara bustard (*Chlamydotes undulata*)), both migrant visitors, would also benefit from the increase in grassland habitat.

The mathematical expression of the objective for increasing the food resource-based carrying capacity called the objective function (Z) of the model is expressed as:

$$\text{Maximize } Z = B_{gc}G_c + B_gG + B_{gc}P_c + B_pP + B_{sd}SD + B_sS + B_{gc}H - D_a - D_{ac}$$

Where the variables are the possible management options.

G_c = number of grassland hectares cleared of *Prosopis* saplings.

G = number of grassland hectares unmanaged.

P_c = number of shrubland hectares cleared of *Prosopis*.

P = number of shrubland hectares unmanaged.

S_d = number of hectares of saline habitat developed by fertilization and plantation to produce shrubland.

S = number of hectares of saline habitat left unmanaged.

H = number of hectares of grassland to be harvested.

D_a = deficit in forage production needed to support a population of blackbuck for a stable wolf : blackbuck ratio (see Results) with a 99 % confidence.

D_{ac} = deficit in forage production associated with the current years rainfall to support the current population of blackbuck in the park.

The B's are values for the mean peak above-ground plant biomass (PAGB = highest recorded standing biomass during the year) (kg/ha) for each habitat with a management option (explained later). The operation of the model to achieve a maximum value for the objective function would thus try to maximize mean biomass by allotting the maximum area to the most "profitable" management options. It would simultaneously strive to minimize forage deficits.

The objective function is then limited to find an optimal solution within a feasible region. This mathematical region (Euclidean space) is defined by several constraints. The constraints were developed according to the limitations within which the management activity could increase food-resource-based carrying capacity for the blackbuck.

Constraints :

1) Area constraint : The total area under the 3 habitat types where management is possible is 2,525 hectares. Thus:

$$G_c + G + P_c + P + S_d + S \leq 2{,}525$$

However due to the dynamic state of these habitats and possible conversion of one to another by management, the areas under each would change from year to year.

$G_c + G \leq$ grassland area

$P_c + P \leq$ shrubland area

$S_d + S \leq$ saline area

The RHS values would thus change due to management activity and would need to be inserted by the manager. The current areas under each habitat type were computed from the digitized map of the park.

2) Forage required to sustain a specified population of blackbuck to achieve a desired wolf to blackbuck ratio.: Mathematically it is expressed as:

$\sum B_i A_i + D_a \geq$ Minimum kg of peak above-ground forage production required for a desired minimum population of blackbuck.

A_i represents the various areas (ha) of grassland, shrubland, and saline region under various management options. Plant productivity in semiarid regions is water limited (Singh and Krishnamurthy 1981). Peak above-ground biomass (PAGB) is a measure of plant productivity above the ground (Singh and Krishnamurthy 1981, Mitchell 1983) and the forage available to the blackbuck. Above-ground primary production in arid and semiarid regions (annual rainfall < 700 mm) is considered to have a linear relationship with rainfall (Coe et al. 1976, Rosenwig 1968, Webb et al. 1978, Whittaker 1970). Regression analysis was used (see Results) to establish a relationship between rainfall and PAGB (estimated from seasonal quadrat sampling). This regression was used to predict PAGB for the past 12 years at Velavadar for the grassland habitat. Variance and mean were computed for the PAGB values for this period. The mean PAGB value was used as the coefficient of the decision making variables in the objective function (B_{gc}). Grassland PAGB was penalized by 10% for areas where *Prosopis* saplings were not eradicated (B_g). As only 3 years of data were available for shrubland and saline region PAGP, regression analysis for these habitats were not attempted. I assumed (see Results for details on PAGB in shrubland and saline regions) that PAGB of the herbaceous component in shrubland was similar to the grassland. However, due to

the thorny shrub and high visual cover, only 50% of the PAGB would be available to blackbuck (B_p). The PAGB of shrublands cleared of *Prosopis* (new grassland) were assumed to be similar to PAGB of grassland.

The average ratio of PAGB of saline regions to PAGB of grassland was 0.24 for the 3 years of the study. It was assumed that this ratio would remain constant over all ranges of rainfall and associated PAGB. Thus, the mean PAGB of saline region was $B_s = 0.24B_{gc}$. If the saline habitat was developed by fertilization and plantation of *Prosopis*, it was assumed to have PAGB similar to the shrubland. From the 12-year rainfall data, a 99% lower bound on the predicted PAGB was calculated. These PAGB values were used as coefficients (B'_iS) for the above constraint.

The right-hand side (RHS) of the constraint (Min Kg) is the amount of forage (PAGB) required to sustain a desired minimum population of blackbuck. Blackbuck are the major prey species for wolves. The number of blackbuck killed per wolf per annum was estimated (see Results). Maximum wolf number in the park was estimated (see Results), the rate of increase of blackbuck was computed, and the number of blackbuck per wolf essential to maintain a stable population was computed using Keith's (1983) model:

$$N = \{K / (\lambda - 1)\} W$$

where

N = number of blackbuck,

K = number of blackbuck killed per wolf,

λ = finite rate of increase of blackbuck, and

W = number of wolves in the park.

Consumption by the blackbuck population (N) was computed from the annual consumption/ $kg^{0.75}$ of captive blackbuck increased by 10% to accommodate higher costs for locomotion (Pennycuick 1979) in the wild. The population (N) of blackbuck was assumed to have a age structure and sex ratio similar to the current population (1988 to 1990) and the N blackbuck were approximately distributed into the various categories (fawn, adolescent, subadult, and adult). The

number in each age category was multiplied by the mean weight of the age category of the same sex (Mungall 1978). The mean weight of a blackbuck was computed for this population. Annual consumption was estimated for the population (N) from the daily mean consumption and mean weight of the blackbuck (similar to Sinclair (1975)).

All of the PAGB is not food for blackbuck. Consumption by ungulates in grassland systems is reported to range from 10% of primary production (Wiegert and Evans 1967, McNaughton 1979b) to over 85% of the standing green biomass (McNaughton 1979b, Sinclair 1975). Estimates in tropical grasslands usually range from 20 to 70% (Cox and Waithaka 1989, Detling 1988, Karunaichamy and Paliwal 1989, Sinclair 1979a, 1979b). Blackbuck like other medium size antelopes are selective feeders (Jarman 1974). The quality of the forage especially in the summer is extremely low (see Results). Although ample quantity may at times be available, actual consumable amount may be very low (Sinclair 1979b). Results from the exclosure studies suggested a consumption of 40% of PAGB by blackbuck (see Results). Thus 30% to 50% range of PAGB seems appropriate as available for consumption by blackbuck.

The right hand side of the constraint would be 3.33 to 2 times the annual consumption by a population of N blackbuck. The variable D_a allows for forage deficit to occur under certain situations. Since D_a is included in the objective function with a negative sign, its value is minimized by the model. However, its inclusion in the constraint allows more flexibility and the option supplying fodder from the storage in the godowns.

3) Grass harvest, storage and forage deficit : In certain years in the past, grass from the park has been harvested and stored in 2 godowns in the park (Mungall et al. 1981). This grass is utilized in years of drought to feed the blackbuck.

Production coefficients (B_i's) for the PAGB for the current year were computed from the regression and as explained earlier. These were multiplied with the current area under each management option and summed to give total forage production of the park. If this amount exceeded the consumption needs of the current population of blackbuck, then there was a surplus which could be potentially harvested. If the forage amount produced was less than needed by the

current blackbuck population, there was a deficit which needed to be bought or supplied from the storage in the godowns. Thus

$\sum B_i A_i - S_p + D_{ac}$ = Forage needs of current blackbuck population.

Thus, in years of good forage production the deficit (D_{ac}) would be 0 and in years of drought the surplus (S_p) would be 0 depending on the blackbuck population.

The previous constraint manages for risk along a time scale considering 99% lower bound "production" and minimum blackbuck population, N, for sustaining wolves. In contrast, the constraint here accounts for the scenario for the current year.

In case of forage deficit (D_{ac}), the stored grass from the godowns would be used to feed blackbuck, if the deficit exceeds godown storage the fodder needs to be bought (D). Thus

$D_{ac} - D \leq$ storage in godowns

In the case of surplus forage production, if budget permits and there is storage space in godowns, then it could be harvested :

$S_p - B_{gc} H \geq 0$

$G_c - H \geq 0$

where H is the area (ha) of grassland harvested.

4) Wolf habitat needs: It would be extremely difficult to determine what would be the minimum *Prosopis* area requirements for wolves. To determine this, it would be essential to start cutting all *Prosopis* stands until the wolves no longer used the habitat any more. It was not possible to conduct such an experiment. Instead an estimate was arrived at by indirect methods. Critical wolf habitat like denning areas, rendezvous sites and lying up sites were marked on a map of the park. Concentric zones were marked around these locations as importance to the wolves increased. In the preliminary runs of the model, these were given increasing costs of shrub removal. However, given

the small size of these areas and the reality of the park's budget, these wolf-used shrub stands were not cut even in the outer zones. Thus, for simplicity, wolf-used areas of shrubland were removed from the optimization process and made a simple constraint:

$P \geq$ shrubland habitat for wolf needs.

Thus, the model would always spare appropriate shrubland area essential for wolf habitat. For spatial resolution of *Prosopis* cutting, a map was prepared showing critical wolf habitat. Cutting should be done as far from such areas as possible (see Results).

5) Budget Constraint : The current budget of the park is between 900,000 to 1,000,000 Rs. and about 500,000 to 600,000 Rs. would be used for habitat management (Chudasama pers, comm.). The various costs of different management activities were obtained from the park records (see Results). The cost of clearing grasslands of *Prosopis* was Rs. 50/ha and the cost of cutting *Prosopis* from the shrubland and producing charcoal was Rs. 5,000/ha. Developing saline habitat and planting *Prosopis* has not been undertaken as a management activity in the park. The estimates for this cost were obtained from the 5,000 to 6,500 Rs./ha. Harvesting grass and storing it in the godown was estimated at 300 Rs./ha.

$50G_c + 5000P_c + 5500S_d + 0.2\ D \leq$ Budget

The model (see Appendix 7) was solved with the simplex algorithm (Dantzig 1963) using LINDO software (Scharge 1991). Runs with the mean AGB coefficients, minimum AGB coefficients, different budgets and management options were made.

RESULTS and DISCUSSION

Vegetation

Description

The grasslands, shrublands, saline regions, and tidal zone account for 92.45% of the total area of the park (Table 1). The rest of the area is accounted for by habitation, roads, waterholes, and agricultural field (Fig. 3).

Appendix 1 lists the genera, species, and local names of the plants found growing in Velavadar National Park. The plant species are further categorized into shrubs, trees, grasses (annual and perennial), forbs, and sedges. Genera represented in the park by a single species are hereinafter referred to by their generic name.

The maximum number of plant species recorded in each habitat by the quadrat sampling was in the monsoon (Table 2, 3 and 4). The high number was due to most annuals (see Appendix 1) completing their life cycle within weeks shortly after the monsoon rains began (Singh and Krishnamurthy 1981). These species contributed as dead biomass (DBM) to the winter and summer sampling. Species that were more homogenously distributed within the habitat type had lower variances in the quadrat samples and thus narrower confidence limits. The opposite is true

Table 1. Area under each habitat type in Velavadar National Park (1989).

Habitat Type	Total Area in Hectares	Percentage of the Park
Grassland	805.34	23.45
Shrubland	935.34	27.24
Saline Habitat	785.17	22.87
Tidal Zone	648.74	18.89

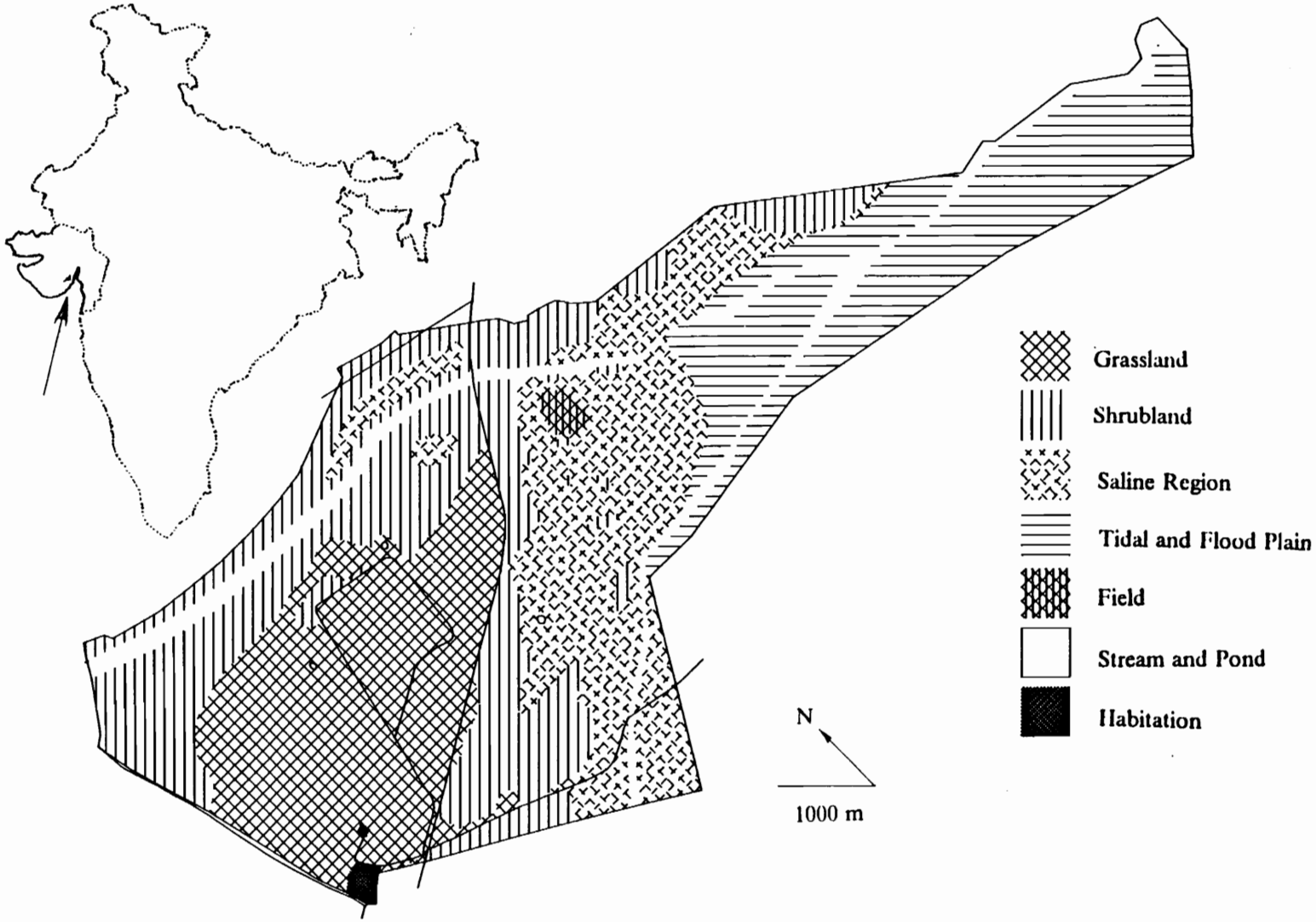


Fig. 3. Areas under the various habitat types in Velavadar National Park in 1990. The inset shows the location of Velavadar National Park within the State of Gujarat, India.

for highly localized species even though their mean dry weight may contribute more than 1% of the total above-ground biomass (AGB) (Table 2, 3, and 4). The total biomass increased up to the summer sampling. This suggests that growth continued well into early summer for the years 1989 and 1990. However, both these years had exceptionally good rainfall (719.5 mm and 566.5 mm) and the conditions may be different in other years.

Dichanthium and *S. virginicus* were the dominant grasses in terms of dry biomass in the grasslands. In 1988 *S. virginicus* contributed 27.56% and *Dichanthium* contributed 21.46% to the total above-ground dry biomass. *Dichanthium* is a favored palatable species (see Food Habits of Blackbuck) and was presumably "hard hit" during the drought years. During 1988 *Dichanthium* was in a "recovery phase". In the consequent years (1989, 1990) its proportional biomass contribution increased to 50.6% and 52.25% respectively to become the major dominant species. *S. virginicus* contributed 16.6% and 16.3% in 1989 and 1990 respectively to AGB in grasslands.

A similar trend was observed in the shrubland habitat. *Dichanthium* initially contributed less than 20% to AGB (1988) but its contribution went up to 60% in 1990 (Table 3). The most dominant species in the shrubland in 1988 was *Chloris*. In the saline region, the succulent halophyte *Suaeda* was the single most dominant species. *Chloris*, *Cyperus*, and *Aeluropis* were the only important forage species contributing to AGB in saline regions. *S. coromandalianus* though growing abundantly in saline regions, contributed less than 1% to the AGB due to its low dry weight.

The primary grass species to colonize saline regions were *S. coromandalianus*, *Aeluropis*, and *Chloris* (Shankarnarayan and Shankar 1984). These were followed by *Dactyloctenium, Cyperus, Paspaladium*, and *Paspalum* species growing in well-drained higher ground of saline regions. *Dichanthium* and *S. maderaspetansis* were the last species to arrive. *S. virginicus* preferred wet grassland areas, presumably with lower pH. This species was not observed to grow in saline regions.

Table 2. Above-ground biomass (gms/m^2)of plant species in the saline habitat in Velavadar National Park.

Species	Monsoon88 n = 60	Winter88 n = 60	Summer89 n = 72	Monsoon89 n = 64	Winter89 n = 64	Summer90 n = 72	Monsoon90 n = 80	Winter90 n = 80
DBM		3.57 (±1.5)	3.67 (±1.9)	7.3 (±3.95)	17.72 (±5)	20.67 (±6.5)		62.72 (±10.1)
Chloris	0.32 (±0.3)	1.78 (±1.1)		4.11 (±2.6)			14.18 (±5.51)	8.32 (±6.5)
Cyperus sp.	7.15 (±5.1)	0.73 (±05)					30.44 (±6.64)	13.44 (±11.12)
Paspalum				0.9 (±0.91)			5.9 (±3.8)	
Dinebra	0.3 (±0.21)	0.33 (±0.4)						
Dactyloctenium	2.9 (±2.1)	0.61 ±(0.6)					1.52 (±0.5)	
Aeluropis	1.47 (±0.3)	0.33 (±0.25)			1.89 (±1.2)		5.136 (±4.12)	5.12 (±3.4)
Suaeda	15.56 (±8.1)	15.32 (±5.58)	16.1 (±4.91	2.08 (±1.5)	3.85 (±1.5)	5.4 (±2.5)	15.5 (±10.12)	44.4 (±21.1)
Cressa				0.71 (±0.5)	o.21 (±0.2		1.63 (±0.48)	3.52 (±1.2)
Paspaladium				0.9 (±o.95)			13.3 (±9.2)	
Panicum	0.45 (±0.3)							
EDWT	37.25 (±10.6)	25.27 (±8.33)	24.00 (±7.51)	20.56 (±11.1)	21.33 (±4.23)	25.1 (±5.95)	123.78 (±22.1)	147.44 (±25.9)
TDW	37.865 (±11.1)	25.55 (±8.5)	24.00 (±7.51)	21.38 (±10.6)	23.66 (±5.4)	26.07 (±6.5)	126.19 (±23.1)	151 (±29.8)

DBM - dead biomass, EDWT - combined dry weight of all edible species, TDW - combined dry weight of all species.
Values in parentheses are 95 % confidence limits.

Table 3. Above-ground biomass (gms/m^2) of plant species in the herbaceous layer in the shrubland habitat in Velavadar National Park.

Species	Monsoon88 n = 72	Winter88 n = 60	Summer89 n = 80	Monsoon89 n = 68	Winter89 n = 72	Summer90 n = 80	Monsoon90 n = 84	Winer90 n = 92
DBM		62.76 (±14)	248.84 (±36)	108.16 (±34)	188.6 (±36)	253.53 (±20)	14.06 (±7.5)	92.08 (±10.11)
Dichanthium	1.5 (±1.51)	7.32 (±2.3)	123.16 (±43)	549.72 (±142)	605.76 (±132)	389.64 (±123)	313.99 (±60.2)	376.24 (±70.1)
Sporobolus virginicus		4.4 (±2.4)	53.48 (±23)	64.2 (±26)	93.84 (±32)	77.76 (±31)	58.33 (±12.12)	90.72 (±20.15)
S. maderaspetansis		18 (±11)	12.52 (±5)	29.76 (±12.1)	5.67 (±3)		36.58 (±19)	15.04 (±8.5)
Chloris virgata	15.6 (±9.8)	102.96 (±32)		75.12 (±23)			25.26 (±7.3)	13.44 (±8.1)
Cyperus spp.	6.6 (±3)	21.5 (±10.2)					11.35 (±3.4)	
Paspalum	1.5 (±1.1)			34.1 (±14)			22.4 (±14.2)	
Dinebra				9.28 (±4.5)				
Dactyloctenium	25.3 (±14)							
S. coromandelianus	7.3 (±4.2)	11 (±5)						
Aeluropis	1.7 (±0.9)							
Aritida spp.	3.27 (±1.4)			8.76 (±4.2)				

Table 3 continued. Above-ground biomass (gms/m^2) of plant species in the herbaceous layer in the shrubland habitat in Velavadar National Park.

Species	Monsoon88	Winter88	Summer89	Monsoon89	Winter89	Summer90	Monsoon90	Winer90
Paspaladium	1.5 (±1)	3.64 (±2.1)					168.96 (±89.2)	
Portulaca sp.	1.9 (±2)							
Panicum	4.83 (±3)							
Brachiraria	3 (±1.9)							
Eriochloa	6.3 (±4.2)							
Digera	4.2 (±2.8)							
Heliotropium	4.9 (±2.4)							
Digitaria	1.2 (±1.1)							
Suaeda			13.84 (±8.9)			12.4 (±5.8)	7.25 (±4.1)	16.88 (±10.2)
EDWT	82.37 (±16)	235.32 (±41.5)	451 (±74)	912.44 (±102)	906 (±185)	737.2 (±132)	699.52 (±119)	625.24 ±75.76)
TDWT	94.56 (±20)	238.28 (±42.4)	451.84 (±74.2)	915.88 (±111.5)	906 (±186)	737.6 (±131)	701.32 (±120)	626.44 (±75.72)

Values in parentheses are 95 percent confidence limits, DBM - dead biomas, EDWT - combined weight of edible species, TDW - total weight of all species.

Table 4. Above-ground biomass (grns/m^2)of plant species in the grassland habitat in Velavadar National Park.

Species	Monsoon88 n = 120	Winter88 n = 90	Summer89 n = 108	Monsoon89 n = 126	Winter89 n = 120	Summer90 n = 130	Monsoon90 n = 126	Winter90 n = 130
DBM	5.2 (±1.2)	97.56 (±16)	175.92 (±23)	37.72 (±13.8)	131.84 (±26.4)	226.44 (±41.5)	38.42 (±10.2)	81.8 (±9.24)
Dichanthium	63.8 (±25.5)	64.88 (±31.2)	68.8 (±18.3)	374 (±112)	461 (±92)	473 (±78)	308 (±44)	437.72 (±58.53)
Sporobolus virginicus	68 (±14)	54 (±16.7)	144.36 (±82.9)	162.6 (±54)	161.6 (±44)	130.2 (±27)	108.56 (±19.8)	120.56 (±22.08)
S. maderaspetansis	3.72 (±1.8)	14 (±10.5)	1 (±0.4)	94.6 (±67)	57.25 (±32.3)	55.96 (±21)	62.6 (±20.2)	63.08 (±24.4)
Chloris		16.68 (±8.5)		25.8 (±15.5)			3.4 (±2)	
Cyperus spp.	2.6 (±2)	21.56 (±15.3)		17.08 (±17.5)			17.6 (±4.9)	
Fimbristylis spp.		12.56 (±12)		16.92 (±13.8)	11.36 (±10.1)		38.52 (±11.4)	38.76 (±16.76)
Striga	1.16 (±0.8)	0.96 (±0.7)		0.24 (±0.21)	0.32 (±0.33)		0.76 ±0.3	
Ischaemum		4.64 (±3.5)		27.8 (±30.1)	38.36 (±32)		17.2 (±8)	211.16 (±27.5)
Iseilema	3.12 (±3.5)	4.48 (±3.1)		9.64 (±5.4)			10.48 (±4.1)	
Paspalum	7.68 (±3.5)			15.72 (±5.3)			9 (±2.4)	
Dinebra				9.88 (±7)			3.88 (±2)	

Table 4 continued. Above-ground biomass (gms/m^2) of plant species in the grassland habitat in Velavadar National Park.

Species	Monsoon88	Winter88	Summer89	Monsoon89	Winter89	Summer90	Monsoon90	Winter90
Phaseolus	5.4 (±2.35)			2.29 (±1.54)			1.32 (±0.3)	
Sesbaenia	5.76 (±8)	22.48 (±20)		10.48 (±11)				
Dactyloctenium	5.24 (±1.23)							
Echinochloa	1.71 (±0.44)			0.17 (±0.2)			0.52 (±0.18)	
Eriochloa	4 (±0.1.2)							
Digera	4.44 (±1.2)							
Sida	2.92 (±0.8)	8.16 (±4.5)						
Themeda	15.08 (±8.1)							
EDWT	203.44 (±40.2)	312.6 (±46)	389 (±92.9)	833.6 (±132)	862.28 (±85)	886.76 (±71.5)	629.76 (±53.76)	768.73 (±57)
TDW	227.84 (±42.2)	344 (±48)	390 (±92)	833.6 (±135)	862.28 (±87)	886.76 (±72)	635 (±54)	770.73 (±60.08)

DBM - dead biomass, EDWT - combined dry weight of edible species, TDW - combined dry weight of all species.
Values in parentheses are 95 % confidence limits.

Soil Analysis

The soils of Velavadar National Park and the Bhal region in general have been described as clayey loams (Ranjitsinh 1982:18-20, 1989:7). The soils of the Bhal region are silt deposits from the several rivers draining into the gulf of Cambay (Dharmakumarsinhji 1978). The textural ratio({clay + silt} / sand) for Velavadar soils is 2.7 (SE 0.069) (Satyanarayana 1985:56). Thus the soils are fine textured and heavy, having a high water-holding capacity of 68.62% (SE 2.16%). This permits moisture retention in the soil in years of good rainfall well into the summer. Ranjitsinh (1989:7) reported soil moisture ranging between 6.38% to 11.35% in the month of April (1982). Preceding this study (Ranjitsinh 1982), the monsoon was exceptionally good in Velavadar with a rainfall of 779 mm (1981-82). Satyanarayan (1985:46-47) reported soil moisture to be as low as 2.8% (SE 0.44%) in the month of February; the rainfall for that year was 441 mm.

A saline alkali soil is defined as one having a conductivity greater than 4 millimhos at 25°C, a soluble sodium content of more than half the total soluble cations and a pH value usually less than 8.5 (Richards 1954). Velavadar soils certainly fit this definition (Table 5). The salinity has been attributed to the origin of the Bhal region from the sea in the late Tertiary and Quaternary (Dharmakumarsinhji 1978) and to its semi-arid climate (Ranjitsinh 1982:23-24, Hess 1971:61-105).

Analysis of variances between habitat types for the study area for pH, EC, SAR and OM showed significant differences ($P \leq 0.01$, Table 5).

Habitat Types

The different habitat types were categorized based on visual differences in plant communities and physiographical characteristics. The analysis of variance procedure used showed significant

Table 5. Soil characteristics in different habitat types of Velavadar National Park (1989).

Habitat	pH	EC mmho	SAR	Percentage OM	N^a	Na^a	K^a	Ca^a	P^a
Grassland	7.83‡ (0.0788)	2.367‡† (0.462)	11.313‡ (2.12)	0.699‡ (0.023)	0.182 (0.029)	0.0392 (0.008)	0.02 (0.0007)	0.0175 (0.002)	0.0031 (0.0003)
Shrubland	8.38‡† (0.6)	5.78† (1.2)	32.63‡† (7.65)	0.581 (0.068)					
Saline regions	7.66† (0.0835)	8.87‡ (1.8)	14.26† (3.89)	0.536‡ (0.029)					

EC - electrical conductivity, SAR - sodium adsorption ratio, OM - organic matter, N - nitrogen.
[a]From Satyanarayana (1985), all values are expressed as percentage.
Nunbers in parenthesis are standard errors
†,‡ Parameters significantly different at $\alpha = 0.05$.

differences in edaphic characteristics (Table 5). One way multivariate analysis of variance procedure showed significant differences ($p \leq 0.0001$) for the above-ground dry biomass (AGB) of major plant species (> 5% contribution of total AGB) between grasslands, shrublands, and saline regions for each season. Two way multivariate analysis of variance to test for differences in total dry above-ground biomass (TDW) and total above-ground biomass of edible species (EDWT) between habitats and seasons showed significant differences ($p \leq 0.001$). However, the interaction between seasons and habitat was significant ($p \leq 0.001$). This suggests that the effect of seasons on plant biomass in each habitat type is different. Such an observation would be expected since the habitats differed in their plant species composition and were likely to react differently to seasonal change. Linear contrasts showed significant ($p = 0.0001$) seasonal differences in TDW and EDWT for each habitat. The 3 habitats also differed ($p \leq 0.05$) in each season for TDW and EDWT. The TDW in the shrubland did not include the contribution from *Prosopis* shrubs, only the grasses and vegetation in the herb strata were included. The habitats thus differed not only in their physical characteristics (soils) but also in vegetation.

Rainfall and Above-Ground Vegetation Production

In water-limited grasslands with a single growing season, peak above-ground biomass (PAGB) would be a reliable estimate of above-ground production (Mitchell 1983). AGB is known to be highly correlated with the actual evapotranspiration (AET) (Arkely and Ulrich 1962, Rosenweig 1968). Ratios between AET and potential evapotranspiration (PET) have been used to predict crop yields (Ramana Rao et al. 1984) and grassland productivity based on drought codes (Shankarnarayan et al. 1985, Ramana Rao et al. 1981). Rosenweig's (1968) predictive equation has been used to compute "carrying capacity" (Phillipson 1975) and biomass of large herbivores (Coe et al. 1976).

In arid and semi-arid regions having a mean annual precipitation of less than 700 mm, AET is considered to be nearly equal to annual precipitation (AP) (Rosenweig 1968, Coe et al. 1976, Webb et al. 1978). The average AP for Velavadar (from rainfall data collected at Bhavnagar) from 1931 to 1960 was reported to be 468 mm. (Ranjitsinh 1982:24). Thus, in Velavadar, this assumption would tend to be true and AET would tend to equal AP.

Singh and Krishnamurthy (1981) suggested a linear relationship between rainfall and above-ground net production for water-limited grasslands (AP < 750 mm). Rainfall for Velavadar was computed as an average of rainfall recorded at Bhavnagar (35 km distance from Velavadar) and Vallabhipur (22 km distance from Velavadar) (Table 6) for the years 1978 to 1990. Peak above-ground biomass (PAGB) values for the grassland habitat were available for the years 1984 (Prasad 1985 and Satyanarayan 1985), 1987, 1988, 1989, 1990 (current study see Table 5 and Table 6). Simple linear regression analysis of PAGB (as the dependent variable) on rainfall (independent variable) (Sinclair 1975, McNaughton 1985) failed to show significant relationship ($p = 0.201$, $R^2 = 0.47$). Multiple regression analysis of PAGB (y) on current year's rainfall (x_1) and preceding years rainfall (x_2) showed a significant relationship ($p = 0.036$, $R^2 = 0.964$ adjusted $R^2 = 0.93$) having a good predictive capability (Webb et al. 1978). The equation was :

$$y = 0.92\ (\pm 0.16)\ x_1 + 0.885(\pm 0.17)\ x_2 - 372(\pm 132)$$

The dominant vegetation in Velavadar grasslands is perennial grasses (Table 5). The AGB production by these species would depend greatly on root reserves, while root reserves would in turn depend on primary production of the previous year. The regression model thus has biological significance with 2-years rainfall explaining 96% of the variation in PAGB. The regression equation was used to predict the PAGB biomass for rainfall of the years 1978 to 1990. Mean PAGB and its 99% lower bound were computed for the past 12-years rainfall (from Table 6).

Table 6. Rainfall and peak above-ground biomass (PAGB) in the grassland habitat in Velavadar National Park.

Years	Rainfall mm	Estimated PAGB (gms/m^2)	SE of estimated PAGB	Predicted PAGB (gms/m^2)	SE of predicted PAGB
1978	397.5				
1979	636			561.6	41.3
1980	549			688.2	41.8
1981	779			809.8	52.4
1982	223			532.4	70.5
1983	727			492.2	60.1
1984	441	628‡	34.2	673.2	51.2
1985	463			452.2	36.8
1986	365			345.8	46.1
1987	90	25†	5.71	30.8	75
1988	719.5	390†	46	374.2	73.3
1989	566.5	886†	36.2	773.1	49.4
1990	776.5	771†	27	822.4	52.5

‡ from Satyanarayan (1985)
† estimated by seasonal quadrat sampling during this study.

Cover

Wolf use of the shrubland was disproportionately greater among cover classes of 40% to 70% cover index than the other cover classes (Fig. 4).

All *Prosopis* plants having a DBH of 2.5 cm or greater were classified as trees. Data from 22 random 25 m x 2 m belt transects and 5 belt transects in shrubland areas intensively used by wolves are summarized in Table 7. Areas intensively used by wolves had significantly greater number of rooted *Prosopis* and a greater number of these *Prosopis* had DBH greater than 2.5 cm.

Prosopis Management

About 80 ha, 40 ha, and 35 ha of *Prosopis* shrubland were cleared for charcoal production during 1988, 1989, and 1990. The average charcoal production per hectare of *Prosopis* cleared was 4100 (SE 189) kg/ha. The average cost of clearing 1 ha of *Prosopis* and producing charcoal from it was Rs. 5000 (Chudasama, pers. comm.). Charcoal was priced at Rs. 65 per 20 kg at the market in Bhavnagar (1989). Fuel wood production as estimated from four 10 m x 10 m clear cut plots was 19833 kg/ha (SE 1600).

All grassland areas were cleared of rooted *Prosopis* saplings every winter. It took about 30 laborers, working at Rs. 25 per day, 50 days to clear the grassland habitat of all rooted *Prosopis* in 1989. Thus the total cost of keeping the grasslands of the park free of *Prosopis* was approximately Rs.37,500 about Rs. 50/ha.

The number of established *Prosopis* per hectare estimated from 15 random 10 m x 10 m plots in the grassland, prior to the eradication activity was 233.3($\pm$112) saplings/ha. The number of established *Prosopis* in overgrazed areas was 9510($\pm$434) saplings/ha. Two sample t-test showed the number of *Prosopis* saplings in overgrazed areas to be significantly ($P = 0.0004$) greater than the

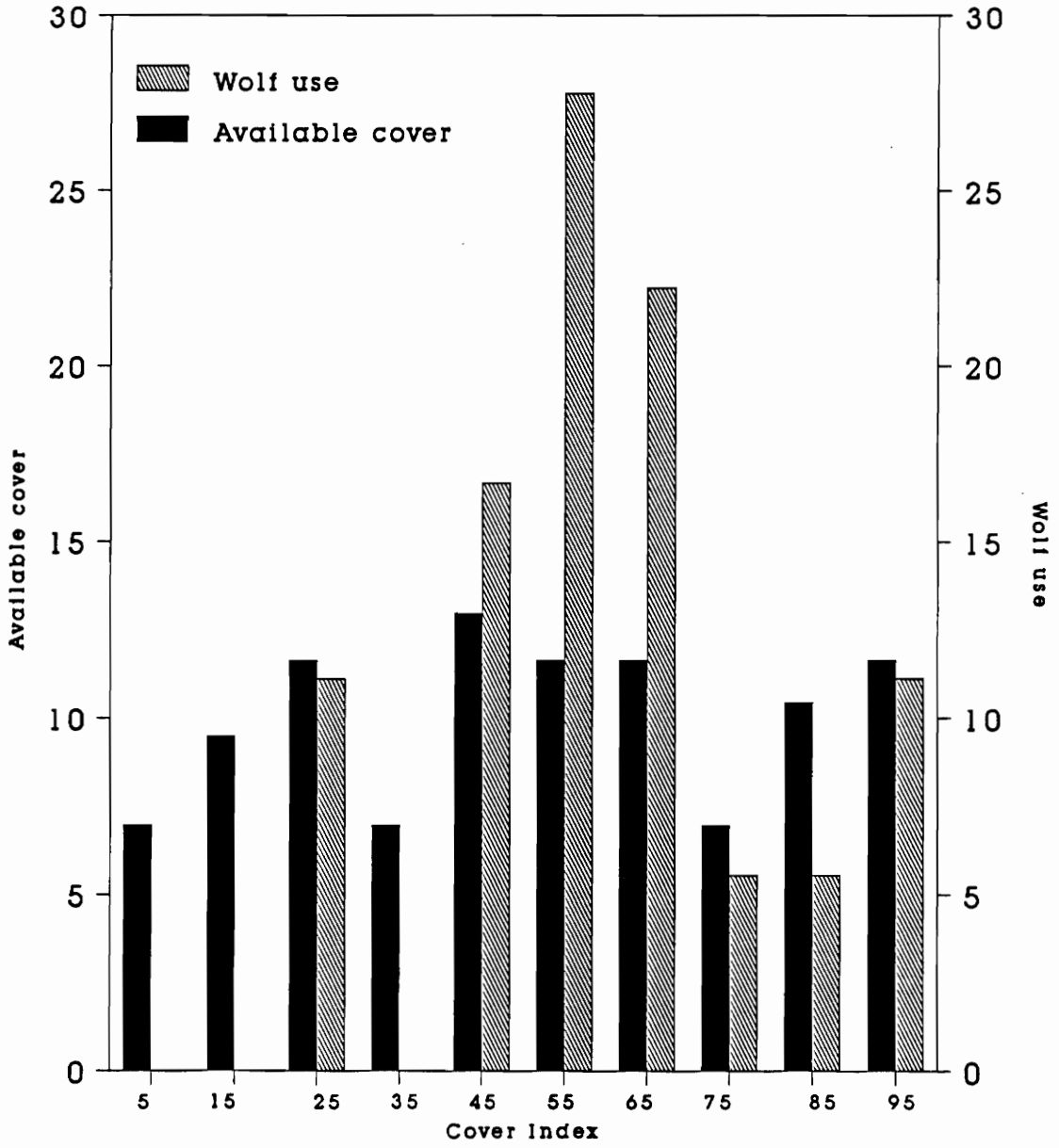


Fig. 4. Percentage of shrubland with various amounts of cover and the percent in each class in areas actively used by wolves. The cover index is percent visibility as estimated by the density board method.

Table 7. Shrubland characteristics in Velavadar National Park (1989-1990).

	DBH cms	Trees/ha DBH > 2.5	Rooted *Prosopis*/ha	Twig Density at 1m	Tree Height m
Random n = 22	3.15 (0.024)	8100† (921)	15400† (1615)	66954 (1225)	4.074 (0.121)
Wolf use n = 5	3.18 (0.03)	13150† (980)	18700† (988)	79100 (5125)	4.68 (0.237)

DBH - diameter at breast height.
Values in parentheses are standard errors.
† Significantly different at $\alpha = 0.05$

rest of the grassland. Heavy grazing appears to encourage *Prosopis* establishment. There are 2 probable factors responsible for the greater number of *Prosopis* saplings in heavily grazed areas. These are :

1) Reduced competition from other plant species, and

2) Greater deposition of *Prosopis* seeds via blackbuck fecal pellets (Fisher 1977, Ghosh et al. 1988, Mauthana and Arora 1983) (Fig. 5a).

During the course of the study, probably related to abundant rainfall, there was heavy infestation of grasshoppers. These insects appeared during the latter part of the monsoon of both years, but the numbers were greater in 1989 and 1990. There was a transition of these insects from the grasslands to the shrublands as the grasses flowered and reached senescence. Grasshoppers were observed on almost all the pod clusters of *Prosopis* trees. Grasshoppers ate the pulp of the pods even before they ripened. The mast crop of *Prosopis* during 1989 and 1990 was a total failure. Grasshoppers, on exhausting the pod resource, concentrated on feeding on the phloem and cambium layers of young *Prosopis* stems and were responsible for several young shoots drying up on almost all trees. Such sporadic infestations of crickets, scorpions, and grasshoppers following good rains are considered normal occurrences in the Bhal by the local farmers (Umarbhai, pers comm.).

The population of Indian gerbils (*Tetera indica*) increased tremendously from 1988 to 1990 (see Wolf Food Habits). These rodents reached such high numbers that by winter of 1990, as the grasses dried out and with a failure of *Prosopis* mast, they probably exhausted their food base. One could hear gerbills gnawing at the roots of *Prosopis* in all shrubland area. The trunk of the trees just below the surface of the ground would be eaten up to the core. Such trees would die and be blown over by the wind (Muthana and Arora 1983). The gnawed surface would look like it had been chiselled (Fig. 5b). Gerbils were estimated to be responsible for killing 8.3% (SE 3.2) of the trees in the winter of 1990. These estimates were obtained from 5 random transects.

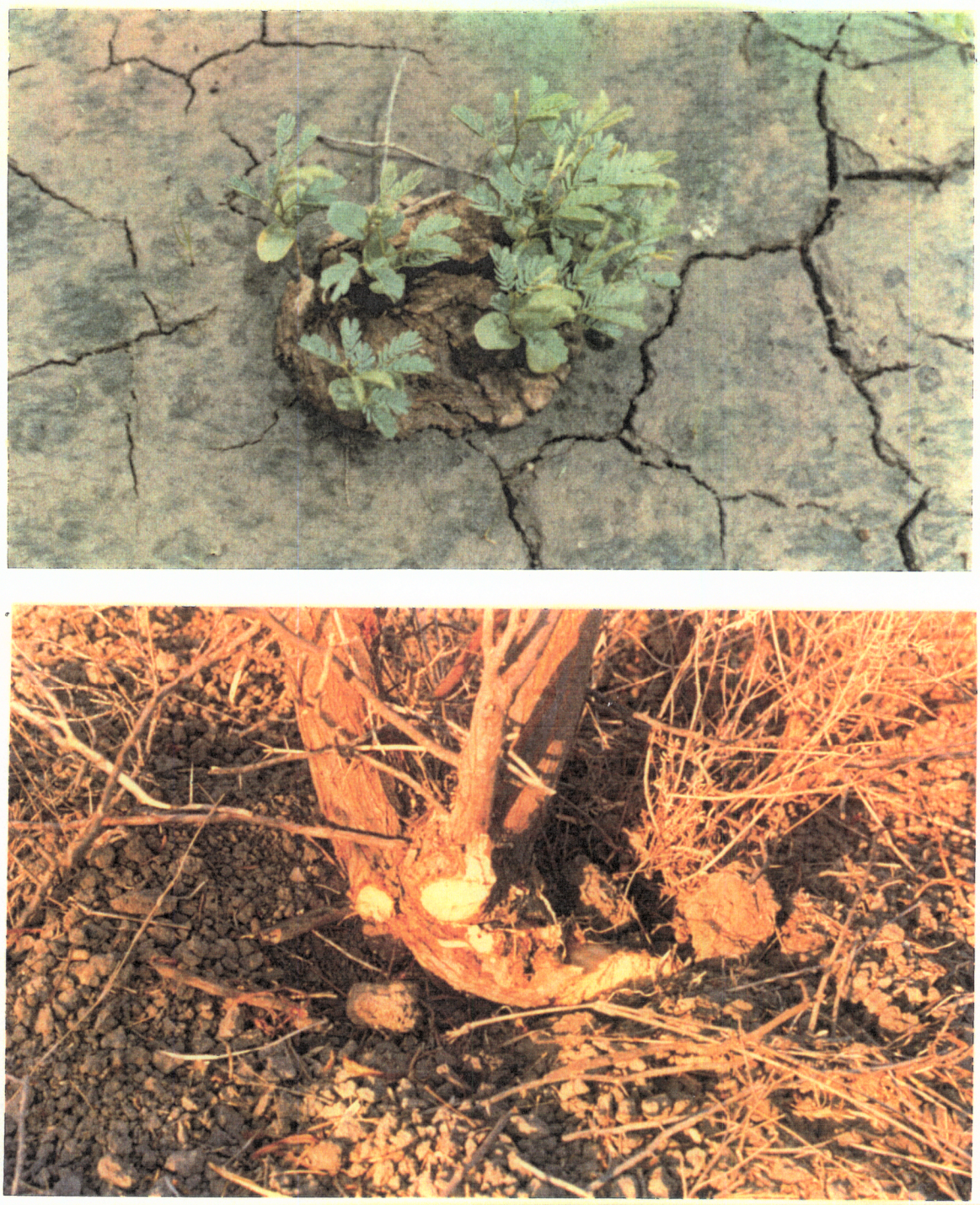


Fig. 5. a) *Prosopis juliflora* seedlings sprouting from cattle dung. b) *Prosopis* killed by gerbils gnawing.

Plant Chemical Analysis

Crude protein (CP) values had a decreasing trend from the monsoon to summer season (Table 8). CP values for several species were below those recommended as minimum for ruminant nutrition in winter and CP values of all species were below recommended levels in summer (Berdon et al. 1963, Milford and Minson 1966, Owens and Zinn 1988, Robbins 1983:148-165, Van Soest 1982:236).

An increasing trend was also recorded in acid detergent fiber (ADF), lignin (L), and acid insoluble ash (AIA) from monsoon to summer (Appendix 2). Some species had highest values for ADF, L, and AIA in winter rather than in summer. This was probably due to the sampling technique, since the dry dead vegetation sampled in summer of each species was analyzed as dead biomass (DBM). The summer samples of perennial species were thus biased towards including only the winter sprouts. The older dry dead matter (which would likely have higher ADF, AIA and L values) was excluded.

The nutritive quality of the plant species was low in winters and extremely low in summers. CP decreased while indigestible components like lignin and AIA increased as the seasons progress from monsoon to winter to summer. Most perennial grasses had lower values for lignin and AIA during 1988 monsoon when compared to 1989 monsoon. Due to a 3-year drought preceding 1988 rains and heavy grazing pressure during that period, most perennial grass swards were killed and propagation in 1988 was primarily by seeds. These newly-established grasses (see Table 5) had lower biomass and less investment in indigestible components for structural support than plants sampled during the rest of study period. In 1989, propagation was predominantly vegetative from perennating organs. Due to good nutrient root reserves (from a previous good productive growth year) there was greater biomass production and higher investment in structural components than in 1988.

Table 8. Percent crude protein content of forage species in Velavadar National Park.

Species	Monsoon88	Winter88	Summer89	Monsoon89	Winter89	Summer90
DBM		3.7 (0.21)	4.55 (0.05)		3.85 (0.35)	4.68 (0.31)
Dichanthium	7.33 (1.4)	2.1 (0.21)	2.53 (0.25)	4.1 (0.81)	3.1 (0.21)	2.6 (0.3)
Sporobolus virginicus	8.2 (1.01)	4.1 (0.05)	3.44 (0.3)	9.5 (0.5)	4.11 (0.12)	2.98 (0.3)
S. maderaspetansis	15.1 (2.1)	5.3 (0.81)	3.4 (0.44)	7.5 (0.78)	5 (0.31)	3.3 (0.51)
Chloris	5.9 (1.01)	1.2 (0.12)	2.1 (0.18)	4.65 (1.7)	2.1 (0.97)	2 (0.09)
Cyperus sp.	5.61 (0.01)			4.91 (0.62)		
Fimbristylis		4.9 (0.25)		6 (0.75)	5.2 (0.91)	
Striga	11.5 (0.5)			12.1 (0.72)		
Iseilema	5 (0.71)			3.26 (0.81)		
Paspalum	9.1 (0.81)			6.3 (0.51)		
Dinebra	4 (0.56)			3.44 (0.72)		
Phaseolus	14 (1.1)			13.2 (0.25)		
S. coromandelianus	8.2 (0.25)	2.5 (0.31)	2.13 (0.35)	7.5 (0.41)	2.41 (0.4)	2.25 (0.61)
Dactyloctenium	6.7 (0.12)			6.25 (0.31)		

Table 8 continued. Percent crude protein content of forage species in Velavadar National Park.

Species	Monsoon88	Winter88	Summer89	Monsoon89	Winter89	Summer90
Suaeda	11.3 (1.25)	10.32 (2.15)	8.7 (2.25)	13.95 (1.71)	11.01 (1.05)	
Eriochloa	12.7 (3.1)			10.25 (3.4)		
Aeluropis	6.59 (1.1)	4.2 (1.5)	3.1 (1.01)	6.9 (2.1)	3.9 (1.9)	2.95 (1.66)
Themeda	7.1 (1.01)			6.2 (1.12)		
Prosopis pods	12.8 (2.5)	13.2 (3.1)	12.7 (2.8)	12.9 (1.25)(0.57)	12.87 (2.6)	14

DBM- dead biomass.
Values in parentheses are standard errors.

The GE values remain fairly high and constant over seasons (Appendix 2). However digestible energy would decrease from monsoon to summer as the contribution by lignin and indigestible parts of ADF to GE increase.

Grazing Impact and Exclosure Studies

Above-ground plant biomass in grazed areas was significantly less than AGB in ungrazed exclosures for all seasons (paired t-test, $n = 30$ pairs in each season, $p \leq 0.01$) in the grassland. There was no significant difference in biomass within and outside the excloures in the shrubland (paired t-test, $n = 20$ pairs in each season, $p \geq 0.05$) and saline region (paired t-test, $p = 8$ pairs in each season, $p \geq 0.05$). In monsoon, winter, and summer seasons the reduction in AGB was 15.9% (SE 4.5), 20.6% (SE 6.4), and 40.0% (SE 6.3) respectively. Blackbuck were primarily the only large ungulate utilizing the grassland in the vicinity of the exclosures. The grazing pressure from small mammals and insects was presumably similar inside and outside the exclosures. The loss in AGB could safely be attributed to blackbuck grazing. The sampling technique recorded only the above ground biomass and did not account for any increase in productivity that may have occurred due to grazing (McNaughton 1979). Neglecting such possibilities, the percentage consumption by blackbuck is within the range of that recorded for large ungulates in the tropical grasslands (Detling 1988, McNaughton 1979, Sinclair 1975). Grazing would affect primary production only in the monsoon and early winter since in most years plant growth was limited to these periods. Removal of AGB in early winter would be beneficial to the grassland since it would facilitate new growth and maintain grazing conditions by preventing development of coarse, less-palatable ecotypes.

The population of blackbuck utilizing the Velavadar grassland was drastically reduced after the drought of 1987, and the rainfall for the duration of the study was exceptionally good. Thus both the grazing pressure was comparatively lower and the primary production was presumably greater during the study period. During the summer of 1988, prior to the rains, the "grassland" had

only 8.4 gms/m^2 (SE 3.6) of AGB in the form of short, coarse grass culms and roots, suggesting low production and a high utilization of primary production by herbivores in years of low rainfall.

Blackbuck

Habitat Selection

Habitat selection by ungulates is a function of several factors, amongst which food availability, mate availability, and predation are of major importance (Jarman 1974). Blackbuck are characteristically known to prefer "open habitats" (Ranjitsinh 1982:63-64, 1989:37, Schaller 1967:150). Blackbuck appear to rely primarily on sight and quick flight to avoid predation as also observed by Mungall (1978:116). Soft muddy ground, especially sticky, clayey soil, tends to stick to their sharp hoofs preventing quick flight. In Velavadar, blackbuck were observed to use all habitat types. Blackbuck rarely venture into the muddy tidal zone except when necessary to cross into agricultural fields or other habitats. Blackbuck were also observed to avoid water-logged areas, and thus, in years of good rainfall they were restricted to the high ground during the monsoon. Most grassland areas were water-logged with 5 cm to 20 cm of water for 1 week to 3 months during the monsoon. During this time blackbuck moved out of the park using the surrounding agricultural fields. Those that remained in the park were restricted to the southern saline region of the park and dry parts of the grassland areas.

Shrubland habitat was often utilized for feeding. The nutritious pods of *Prosopis* were specially attractive (Mungall et al. 1983). Blackbuck were never observed to bed-down after dark in the shrubland. They either congregated in the saline region or the grassland for the night. All the leks of territorial males were observed to be in the short grass grassland habitat or saline regions;

none was observed in the shrubland. Ninety-six percent of the leks were localized in an area of about 50 ha of grassland as also observed by Mungall et al. (1981:25, 1983).

Blackbuck in Velavadar relied primarily on the grasslands for food (Table 9). In winter of 1989-90, the grazing activity concentrated in the saline region and the shrublands. There are 3 possible explanations for this. These are :

(1) Two good monsoons had produced sufficient forage in the saline region to support the blackbuck population and there was an increase in palatable species like *Dichanthium* in the shrubland habitat,

(2) Most of the grassland was covered with grass over 45 cm tall while the shrubland and saline region had shorter grasses, and

(3) The wolf den and first 2 rendezvous sites were located near the "usual" blackbuck congregation sites in the grassland. There may have been greater predation pressure related to low visibility due to the tall grass in the grassland habitat.

Food Habits

The number of bites of each plant species in one habitat type was divided by the total number of bites recorded to estimate the proportion of bites of the species in each habitat. This proportion of bites of a plant species was then multiplied by the proportion of grazing activity in that habitat during that season. (Table 9). This gave an estimate of the proportion of bites of a particular species actually taken by wild blackbuck in that habitat (Tables 10, 11, 12, 13, 14, 15). For example, in the summer of 1989, 5,000 bites were recorded for the grassland habitat of which 592 were of *Dichanthium*. Thus the proportion of bites of *Dichanthium* in the grassland was 592/5000 = 0.118. In the summer of 1989, 66.7% of the grazing activity was recorded in the grassland habitat (Table 12). Therefore the proportion of bites of *Dichanthium* actually taken by wild blackbuck in the grassland would be 0.667 x 0.118 = 0.0787 as shown in Table 12. Similar computations were

Table 9. Percentage of grazing activity of wild blackbuck in different habitats as determined from 36 hours of continuous scan sampling in Velavadar National Park during each season.

	Grassland	Shrubland	Saline region
Monsoon 88	85	9	6
Winter 88	78.3	16.3	5.34
Summer 89	66.7	14.8	18.5
Monsoon 89	80	10	10
Winter 89	5	45	50
Summer 90	42	31	27

done for all species eaten in all the habitat types in each season (Tables 10, 11, 12, 13, 14, 15). The contribution in dry weight by each species to the diet of blackbuck was computed as shown in Tables 10 to 15.

Considering the average annual contribution of different species (average for all seasons during the 2 years) to the blackbuck's diet, *Dichanthium* comprised 35% of the total diet, followed by dead dry matter (DBM 15.8%), *Prosopis* pods (9.5%), *Chloris* (7.4%), *Sporobolus coromandalianus* (6.88%), *Paspalum* (5.22%) and *S. maderaspetansis* (5%). Though species like *Phaseolus* and *Striga* were highly preferred, they contributed less than 1% to the total annual diet due to their low availability.

There was a marked seasonality in species consumption by blackbuck. Most annuals were available only during the monsoon and early winter. These were *Phaseolus* (which comprised 12% of the diet in the monsoon), *Striga*, *Iseilema*, and *Dactyloctenium*. DBM (as dry remains of annuals and fallen dry stems and leaves of perennials) was available only in winter and summer. Most species were grazed heavily when they were green. However, some species like *Chloris* and *S. coromandalianus* were grazed only after they were dry. Such selection could be an influence of secondary plant metabolites like alkaloids (Coley et al. 1985).

Though the *Prosopis* mast crop had generally failed during the study period due to high infestation of grasshoppers, pods still comprised 9.5% of the total annual diet. In seasons when the pods were relatively more abundant (winter 1988-89) as much as 41.4% of the diet was composed of pods. This suggests that pods could be consumed in large amounts and may account for much larger proportions of the diet (when abundant) than observed during this study (Ghosh et al. 1988, Kargaard and Vander Merwe 1976). Pods have a much higher density of digestible nutrients (82.56% digestible dry matter, 80.13% digestible crude protein, and 90.98% digestible ether extract) than grasses (Muthana and Arora 1983 , Leaky and Last 1980, Muthana 1988.). Therefore a 9.5% dry matter contribution by pods to the diet would account for a much greater contribution to digestible energy and protein intake (Muthana 1988). Incidentally, it appears that *Prosopis* mast fails at times due to insect epidemics. However, in low rainfall years, mast seems to be less severely affected. *Prosopis juliflora* flowers in September and the pods ripen and drop in winter (Muthana

Table 10. Computation of blackbuck food habits for the monsoon of 1988 in Velavadar National Park.

Species	A (0.85) x Prop. of bites in grassland	B (0.09) x Prop. of bites in shrubland	C (0.06) x Prop. of bites in saline region	D Proportion of bites in actual diet A+B+C	E Dry wt/bite	F % contribution by dry wt in 100 bites DxEx100	G % contribution in dry wt to actual diet F/ΣF x 100
Dichanthium	0.632	0.0323	0.0009	0.665	0.0945	6.28	45.34
Sporobolus virginicus	0.133	0.00009	0	0.0134	0.1	0.134	0.968
S. maderaspetansis	0.0269	0.00114	0.00106	0.0291	0.241	0.701	5.06
Phaseolus	0.0483	0.00242	0	0.0507	0.118	0.598	4.32
Striga	0.193	0.0185	0	0.212	0.132	2.8	20.22
Paspalum	0.0075	0.0103	0.0015	0.0193	0.1	0.193	1.39
Cyperus spp.	0.0145	0.00828	0.0463	0.0691	0.182	1.26	9.1
Prosopis pods	0	0.0014	0	0.0014	4.6	0.64	4.82
Iseilema	0.0085	0.00558	0	0.0141	0.252	0.355	2.59
Others						0.889	6.192

Table 11. Computation of blackbuck food habits for the winter of 1988-89 in Velavadar National Park.

Species	A (0.783) x Prop. of bites in grassland	B (0.163) x Prop. of bites in shrubland	C (0.0534) x Prop. of bites in saline region	D Propotion of bites in actual diet A + B + C	E Dry wt/bite	F % contribution by dry wt in 100 bites DxEx100	G % contribution in dry wt to actual diet F/ΣF x 100
Dichanthium	0.536	0.0903	0	0.626	0.15	9.39	31.11
Sporobolus virginicus	0.0418	0	0	0.0418	0.1	0.418	1.39
S. maderaspetansis	0.11	0.00104	0.0074	0.118	0.35	4.13	13.68
Cyperus	0.0199	0	0	0.0199	0.3	0.597	1.98
Prosopis pods	0.00997	0.0379	0	0.0479	2.6	12.5	41.42
Fimristylis	0.0555	0	0	0.0555	0.3	1.67	5.35
Suaeda	0	0.0181	0.354	0.0535	0.2	1.07	3.55
Aeluropis	0	0	0.00925	0.00925	0.175	0.162	0.54
Others						0.3	0.98

Table 12. Computation of blackbuck food habits for the summer of 1989 in Velavadar National Park.

Species	A (0.667) x Prop. of bites in grassland	B (0.148) x Prop. of bites in shrubland	C (0.185) x Prop. of bites in saline region	D Propotion of bites in actual diet A + B + C	E Dry wt/bite	F % contribution by dry wt in 100 bites DxEx100	G % contribution in dry wt. to actual diet F/ΣF x 100
DBM	0.457	0.00996	0	0.467	0.173	8.08	49.3
Dichanthium	0.0787	0.00712	0	0.0858	0.145	1.24	7.56
Sporobolus maderaspetansis	0.106	0.00285	0	0.1089	0.105	1.14	6.95
Prosopis pods	0.00319	0	0	0.00319	2.0	0.64	3.9
Suaeda	0	0.0114	0.0126	0.024	0.0814	0.2	1.22
S. coromandelianus	0	0.00854	0.105	0.1135	0.254	2.88	17.6
Chloris	0	0.0626	0.0431	0.1028	0.124	1.27	7.74
Paspaladium	0	0	0.0158	0.0158	0.101	0.16	0.976
Aristida	0	0.0107	0	0.0107	0.09	0.1	0.61
Others				0.068		0.47	2.86

Table 13. Computation of blackbuck food habits for the monsoon of 1989 in Velavadar National Park.

Species	A (0.8) x Prop. of bites in grassland	B (0.1) x Prop. of bites in shrubland	C (0.1) x Prop. of bites in saline region	D Propotion of bites in actual diet A+B+C	E Dry wt/bite	F % contribution by dry wt in 100 bites DxEx100	G % contribution in dry wt to actual diet F/ΣF x 100
Dichanthium	0.298	0.067	0	0.365	0.332	0.12118	62.21
Phaseolus	0.2798	0	0	0.2798	0.143	0.04	20.54
Paspalum	0.0442	0.003	0.04	0.0872	0.112	0.0098	4.62
Cyperus	0.012	0.0071	0.0011	0.02	0.18	0.0036	1.85
Iseilema	0.0748	0	0	0.0748	0.1266	0.0095	4.88
Suaeda	0.0114	0.012	0.0367	0.06	0.0833	0.005	2.567
Striga	0.0293	0	0	0.0293	0.0666	0.00195	1.0
Others						0.889	6.192

Table 14. Computation of blackbuck food habits for the winter of 1989-90 in Velavadar National Park.

Species	A (0.05) x Prop. of bites in grassland	B (0.45) x Prop. of bites in shrubland	C (0.5) x Prop. of bites in saline region	D Propotion of bites in actual diet A+B+C	E Dry wt/bite	F % contribution by dry wt in 100 bites DxEx100	G % contribution in dry wt to actual diet F/ΣF x 100
DBM	0.0027	0.0124	0	0.0151	0.54	0.815	2
Dichanthium	0.0442	0.333	0	0.3772	0.613	23.1	56.21
Suaeda	0	0.0022	0.033	0.0352	0.082	0.288	0.7
Aeluropis	0	0	0.0094	0.0094	0.235	0.22	0.5
Chloris	0.00044	0.047	0.274	0.322	0.3577	11.51	28
Paspalum	0	0.027	0.073	0.1	0.3	3	7.3
Sporobolus coromandelianus	0.0034	0.103	0.106	0.152	1.617	3.9	8.9
Aristida	0	0.015	0	0.015	0.24	0.36	0.87
Others						0.1816	0.4

Table 15. Computation of blackbuck food habits for the summer of 1990 in Velavadar National Park.

Species	A (0.05) x Prop. of bites in grassland	B (0.45) x Prop. of bites in shrubland	C (0.5) x Prop. of bites in saline region	D Propotion of bites in actual diet A + B + C	E Dry wt/bite	F % contribution by dry wt in 100 bites DxEx100	G % contribution in dry wt to actual diet F/ΣF x 100
DBM	0.221	0.13	0.159	0.51	0.175	8.925	43.9
Dichanthium	0.051	0.04	0	0.091	0.15	1.365	6.715
Suaeda	0	0.005	0.015	0.02	0.097	0.158	0.777
Chloris	0	0.059	0.081	0.14	0.124	1.736	8.54
Paspaladium	0	0.001	0.016	0.017	0.103	1.751	8.613
Sporobolus coromandelianus	0	0.03	0.09	0.12	0.251	3.01	14.807
S. maderaspetansis	0.059	0.039	0.001	0.09	0.107	0.963	4.737
Prosopis pods	0.001	0.009	0	0.01	2.1	2.1	10.33
Others				0.011		0.32	1.574

and Arora 1983). In Velavadar, ripe pods were observed at all times of the year, besides the peak fruiting in winter. Thus it appears that the pods may be providing appropriate nutrients at times when the blackbuck need them most.

The total number of bites of each species taken by tame and wild blackbuck in the 1 ha observation plot were arranged in a contingency table (Table 16). A chi-square test suggested no significant difference in diet selection by tame and wild blackbuck grazing in the observation plot.

Data on food habits were collected after the tame blackbuck were habituated to grazing and sustained entirely on natural forage for a minimum period of 2 weeks. Prior to this exposure, blackbuck were observed to "sample" plant species which the wild blackbuck were not observed to eat. Most of such plant species were later avoided by the tame blackbuck, suggesting learned avoidance. These observations stress the importance of exposure to range forage prior to actual data collection using captive animals (Bartmann 1982, Bartmann and Carpenter 1982).

Intake, Fecal Output, and Digestibility

The 4 blackbuck used for this component of the study were growing animals. There was much variation in body weight in each animal as a result of growth and seasonal effects of food in the course of the study. It was not possible to study either the effect of growth or seasonal variation in diet quality in isolation on body mass changes. In 1989 the 2 males and female 1 had reached adulthood. Female 1 conceived and fawned in September 1989 (monsoon 1989). Data on her intake reflect the greater nutritional needs for gestation and subsequent lactation during this period (Table 17). Since the tame blackbuck were feeding on the same forage as wild blackbuck, were exposed to the same climatic conditions, and were socially interacting with each other, dry matter intake (DMI) of wild and tame blackbuck could be considered to be similar.

Table 16. Comparision of bites by tame and wild blackbuck in a 1 ha. observation plot in Velavadar National Park (1989).

Species	Tame blackbuck n = 3	Wild blackbuck n = 8
DBM	582	412
Dichanthium	440	291
Chloris	187	117
Sporobolus maderaspetansis	110	57
S. coromandelianus	220	125
S. virginicus	19	15
Total	1558	1017

$\chi^2 = 5.599, p = 0.6531$

Table 17. Dry matter intake per metabolic weight ($gms/kg^{0.75}$) of captive blackbuck.

	Male 1	Male 2	Female 1	Female 2
Monsoon 88	96.5 (9.167)	143.5 (22.05)	142.61 (15.02)	
Winter 88	92.46 (6.867)	118 (6.937)	136.9 (8.14)	
Summer 89	22.38 (1.23)	19.22 (1.03)	18.36 (1.04)	17.72 (1.15)
Monsoon 89	97.79 (6.34)	119.22 (7.23)	143.92 (8.37)	134 (8.163)
Winter 89	77.7 (5.68)	79.19 (4.77)	147.99 (5.48)	119.5 (6)
Summer 90	26 (1.3)	22.44 (1.22)	21.48 (1.28)	22.1 (1.156)

Values in parentheses are standard errors.

A universal trend of a drop in DMI is observed in summer (Table 17). DMI increased in monsoon and winter. These changes in DMI were accompanied by fluctuations in body weight clearly seen in adult animals, but masked in growing animals (Appendix 3a).

Highest nutritive values of forage as well as highest digestibility coefficients were recorded in the monsoon of 1988 (Table 18). These conditions were a consequence of preceding drought years followed by heavy rains in 1988. Most forage species were restablished from seeds in monsoon 1988 and were thus shorter, more luxuriant, with fewer structural (less digestible) elements than in 1989. Digestibility decreased from the monsoon to the summer season (Table 19). The negative apparent digestibility of proteins in summer (Table 19) suggests that the animals were losing more protein via feces than they were acquiring through DMI. It would be to an animal's advantage to reduce intake of such low-quality forage so as to minimize loss of endogenous nitrogen via feces and maintain its body "reserves" of nitrogen (Dunbar 1979, Sinclair 1975). Due to a positive digestible coefficient for dry matter and GE, albeit very low for summer (Table 19), the blackbuck would obtain 1.087 kcal of digestible energy from every gm of DMI for summer 1988. Thus DMI in summer would depend on the energy needs of the blackbuck, the energy costs of foraging, body energy reserves, and protein "reserves" of individual blackbuck.

Digestibility coefficients for lignin (as determined by AIA as internal indicator) were high for the monsoon and winter of 1988. Lignin was almost indigestible in summer 1988 and winter and summer of 1989 (Table 19). Lignin from immature young grass is reported to be partially digestible (Merchen 1988, Van Soest 1982:51). This was observed for the newly established grasses in 1988. Thus lignin could not be used as an internal indicator for estimating DMI. The use of lignin as an internal indicator in summer when the forage has matured would give similar results as AIA.

Digestibility coefficients of other forage components (EE, GE, and ADF) were positive in all seasons, generally greater in monsoon and winter, and low in summer (Table 19). With extremely low intake (Table 17) and digestibility (Table 19) of forage in summer, the blackbuck face a severe energy and protein deficit in summer. They would rely greatly on body reserves during this period. Body condition should cycle through the year, improving in monsoon and winter, and dropping in summer. Blackbuck's external physical indices of body condition were observed to conform to the

Table 18. Nutritional analysis of the composite forage (Fo) and wild blackbuck feces (Fe) from Velavadar National Park.

		EE	CP	CF	Ash	ADF	L	AIA	GE
Monsoon 88	Fo	4.3	10.2	26.3	9.2	33	5.3	2.438	3.92
		(0.08)	(0.11)	(1.1)	(0.31)	(1.2)	(0.5)	(0.2)	(0.3)
	Fe	3.9	8.94	22.1	20.19	44.8	9.4	14.39	3.91
		(0.1)	(0.5)	(2.1)	(1.02)	(1.22)	(0.61)	(0.32)	(0.05)
Winter 88	Fo	2.54	8.212	27.33	11.24	40	5.61	4.02	3.89
		(0.09)	(0.15)	(2.1)	(1.81)	(1.81)	(0.71)	(0.11)	(0.32)
	Fe	3.52	7.42	20.6	22.86	46.9	9.7	15.1	3.75
		(0.13)	(0.32)	(1.09)	(2.01)	(1.39)	(1.02)	(0.25)	(0.15)
Summer 89	Fo	1.83	3.75	27.4	11.736	45	5.65	8.6	3.87
		(0.1)	(0.1)	(1.45)	(1.21)	(1.64)	(0.65)	(0.1)	(0.21)
	Fe	2.07	6.85	19	19.94	47	9.75	11.8	3.82
		(0.06)	(0.4)	(1.1)	(0.97)	(2.11)	(1.04)	(0.19)	(0.035)
Monsoon 89	Fo	2.66	8.67	27.85	11.52	34.00	5.3	5.00	3.94
		(0.064)	(0.2)	(2.11)	(1.56)	(1.9)	(0.8)	(0.21)	(0.31)
	Fe	3.87	8.375	20	24.24	53.3	16.4	15.5	3.8
		(0.14)	(0.29)	(1.95)	(1.6)	(3.34)	(1.5)	(1.01)	(0.16)
Winter 89	Fo	2.21	6.00	28.29	12.5	32.00	4.87	4.21	3.89
		(0.106)	(0.27)	(2)	(1.61)	(1.03)	(0.28)	(0.11)	(0.18)
	Fe	2.9	7.6	16.12	20.57	54	15.8	14	3.9
		(0.11)	(0.18)	(0.98)	(1.97)	(3.5)	(1.5)	(1.01)	(0.19)
Summer 90	Fo	1.95	3.5	27.00	14.00	39.00	9.00	8.9	3.86
		(0.09)	(0.1)	(1.89)	(2.1)	(1.53)	(1.1)	(0.8)	(0.12)
	Fe	2.09	7.1	20.1	20.89	55	15.5	14.1	3.83
		(0.03)	(1.01)	(1.75)	(2.2)	(2.69)	(2.02)	(0.59)	(0.11)

EE - ether extract, CP - crude protein (6.25 x % nitrogen), CF - crude fiber, ADF - acid detergent fiber, L - lignin, AIA - acid insoluble ash, GE - gross energy.
Figures in parenthesis are standard errors, values are expressed as percentage, GE is in kcal/gm.

Table 19. Percent digestibility of the components of the blackbuck diet in different seasons in Velavadar National Park.

	DDM	DCP	DEE	DADF	DGE	DL
Monsoon 88	82.4	84.6	84	76.1	82.4	63
Winter 88	74.8	77.3	65.9	71.2	76.2	57
Summer 89	27.1	-33.1	17.9	22.3	28.1	0.1
Monsoon 89	70.6	72.3	57.3	53.9	71.6	8.9
Winter 89	70	61.7	58.7	47.1	68.6	0.26
Summer 90	36.8	-28.2	32.4	12	37.4	0.2

DDM - dry matter digestibility, DCP - digestible crude protein, DEE - digestible ether extract, DADF - digestible acid detergent fiber, DGE - digestible gross energy, DL - digestible lignin.

above pattern. Further evidence was obtained from bone marrow fat index of wolf-killed blackbuck (see Mortality, Table 20). However this sample may be biased towards poor-condition animals due to differential predation.

The TFO estimated by the Cr_2O_3 method had wider confidence intervals (Appendix 3) than TFO estimated by total collection for the 2 males in winter 1989. There was no significant difference between TFO, DMI, and digestible dry matter (DDM) ($P \leq 0.01$) estimated by external and internal indicator techniques and those by actual measurements of DMI and collection of TFO.

There was much variation in TFO due to uneven excretion by the blackbuck (as measured by total collection). A sampling period of 6-8 days in each season during which 2 grab samples of feces were collected each day was considered satisfactory to accommodate for this variability and provide good estimates of the mean. Variation in the estimate of AIA, the internal indicator, was very little (see Appendix 3b and 3c). However both these variances (TFO and AIA) would affect the estimated DMI. I considered the estimates of DMI from AIA and TFO to be accurate since they did not differ ($p = 0.01$) from the actual DMI for the 2 male blackbuck determined by measuring actual consumption in winter of 1989 for 4 days each.

Fecal Indices

Fecal nitrogen was significantly correlated with CP content of forage ($r = 0.89$, $p = 0.017$), DDM ($r = 0.796$, $p = 0.074$) digestible GE ($r = 0.797$, $p = 0.058$), digestible CP ($r = 0.772$, $p = 0.075$). Fecal EE was also correlated with DDM ($r = 0.928$, $p = 0.008$), digestible GE ($r = 0.938$, $p = 0.006$) and digestible CP ($r = 0.945$, $p = 0.007$). Correlations of digestibility with fecal ADF and fecal lignin were not significant.

Regression analysis of percentage fecal nitrogen (FeN) on percent forage nitrogen (FoN) gave the following relationship :

FeN = 0.957 (±0.075) + 0.257 (±0.066) FoN

(R^2= 0.793, adjusted R^2 = 0.74, p = 0.017)

The intercept of the above equation would be metabolic fecal nitrogen (MFN) which in the case of blackbuck is 1 gm for every 100 gms of feces excreted. True digestibility of CP (N x 6.25) (Van Soest 1985) is calculated as follows (Schwartz and Hobbs 1985):

True digestion coefficient = {CP intake - [CP in feces - (MFN x 6.25)]} / CP intake

Linear regression of percent nitrogen in the forage versus percent nitrogen in the feces gave the following relationship :

FoN = 3.08 (±0.787) FeN - 2.73 (±0.976)

The relationship had a good predictive ability (R^2 = 0.792, adjusted R^2 = 0.74 p = 0.017) and could be used to estimate forage quality from fecal nitrogen. Fecal EE (FeEE) had a stronger linear relationship to CP content of the forage than fecal nitrogen. The relationship was :

Percent CP in forage = 3.23 (±0.28) FeEE - 3.16 (±0.9)

(R^2 = 0.97 adjusted R^2 = 0.96, p ≤ 0.0001)

Fecal nitrogen and fecal ether extract are relatively easy to sample and inexpensive to estimate. Thus by estimating either of these characteristis from wild blackbuck feces, insight into the quality of the forage available at that time would be obtained. By using the above relationships for predicting diet quality from fecal indices (FeN and FeEE) a tedious study on food habits, and chemical analysis of several plant samples could be avoided. The limitations of using fecal indices especially FeN for predictive purposes, have been discussed by Arman et al. (1975), Robbins (1983: 152-157), Hobbs (1987), Leslie and Starkey (1987). Blackbuck are primarily grazers with grasses predominant in their diet. Thus the effects of tannins and secondary plant compounds (Hobbs 1987, Robbins 1983:156) are likely to be minimal. The above relationships are designed to be used for a

single species and population inhabiting the same (similar) habitat subsisting on forages similar to those found in Velavadar National Park, and comparing "nutritive quality" between years in the same season (Leslie and Starkey 1987).

Population History and Rate of Increase

The blackbuck population in the Velavadar region was down to about 400 individuals when the preserve was established in 1969 (Ranjitsinh 1989:56).The population then increased rapidly (within 4 years) to about 1840 individuals (see Appendix 4 for population data and sources). A summary of the total population from 1969 to 1990 is given in Fig. 6. The y axis is in natural log of total numbers, thus the slope of the regression fitted for these data points provides an estimate of the realized rate of increase, r, for the population over its 20-years history. The slope of the line fitted for the data from 1973 to 1987 (Fig. 6) was 0.009 and was not significantly different from zero ($p = 0.44$). The population could be considered to be "stationary" during these 14 years, with a mean total population of 1,850 individuals (the y intercept of the regression). The population fluctuated about this mean due to environmental factors like cyclones in 1976 and in 1982 (Dharmakumarsinhji 1978, Majethia, pers. comm.) and droughts. After major crashes, the population takes 4 to 5 years to recover. A similar recovery period is reported for the recovery of the blackbuck population in Texas after sever winter mortality (Mungall 1978:87)

Due to low rainfall in 1985, 1986, and extreme drought in 1987, the population experienced a crash in 1988 (Fig. 6). The crash was not as much due to mortality within the park as it was due to emigration. The population experienced a phase of increase from 1988 to 1990 (Fig. 6) due to exceptionally good rains and associated forage production. The rate of increase (r) for these years was computed to be 0.18 (i.e., $\lambda = 1.197$).

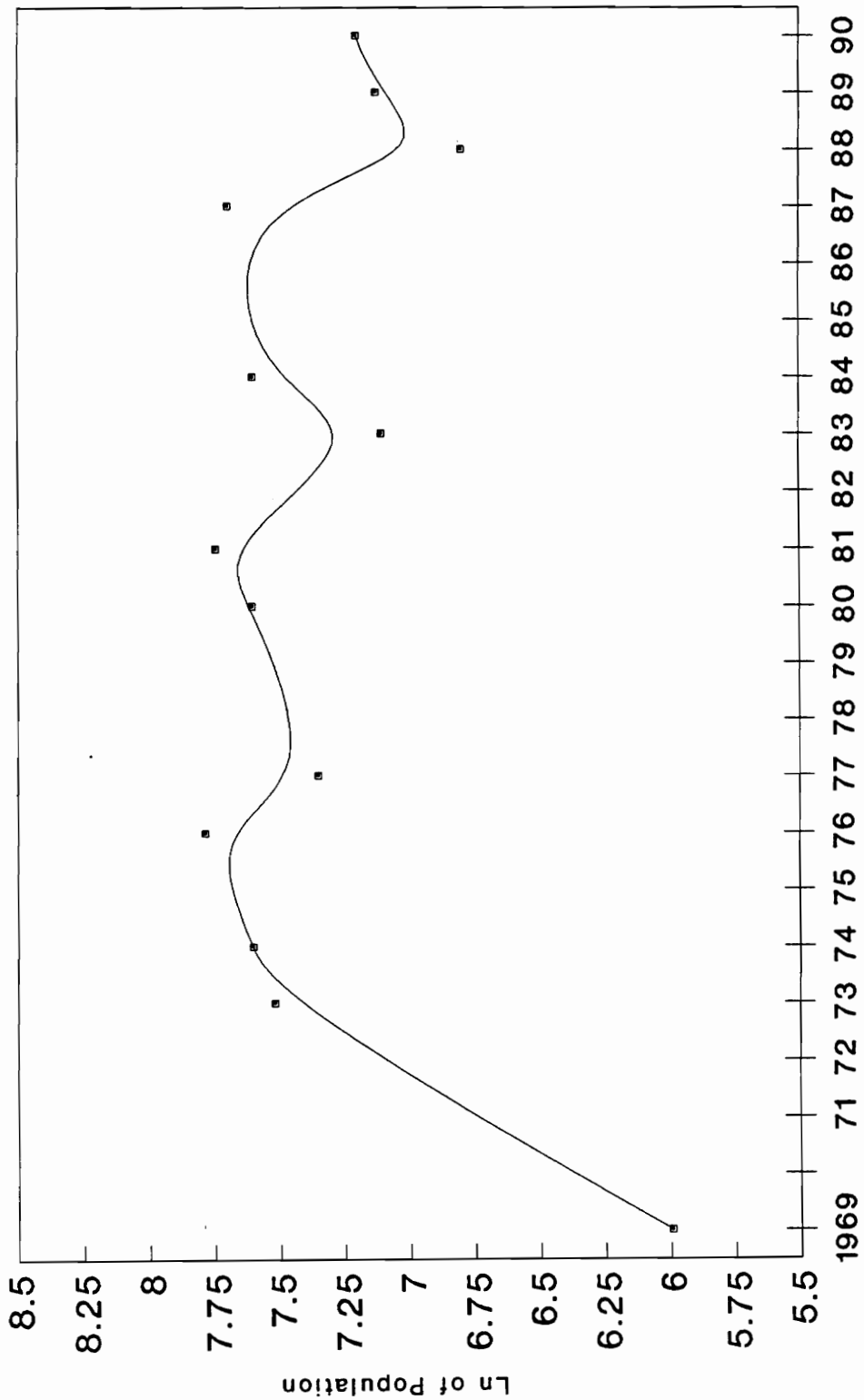


Fig. 6. Blackbuck population trends at Velavadar National Park from 1969 to 1990 expressed as natural logarithm of blackbuck numbers.

Mortality and Survival

The major cause of known mortality among blackbuck was wolf predation. Among 48 fresh carcasses examined in the course of the study, 43 were killed by wolves (85.5%), 2 were killed by poachers (4%), 2 by dogs (4%), and for one the cause of death could not be ascertained. The condition of the blackbuck killed by predation was examined and categorized into 4 classes based on the bone marrow fat index (Table 20) (Cheatum 1949, Sinclair and Duncan 1972). Seventy-five percent of the examined carcasses were over 5 years of age and of these 76% were in poor condition (class 3 and 4). This suggests that though predation was the proximate cause of death, age and condition may have predisposed the individuals to predation (Peterson 1977, Theberge and Gauthier 1985, Thompson and Peterson 1988). Amongst the males killed by predation, 78% were in poor condition (class 3 and 4, Table 20). Of these, 95% were killed during the rutting season. The average age of these males was 8.6 years (SE 0.634), the youngest was 6 years, the oldest 13 years. The age distribution, condition, and season during the deaths of these males suggest that energy investment for breeding (primarily establishing and maintaining territories) predisposes males with depleted body reserves to predation (Flook 1970).

Mortality for the first 6 months of life was estimated (from census data, Appendix 4) at 36% (SE 15.7%). The mortality for the next 6 months was estimated from the number of mandibles collected and aged. This was estimated at 5%. Thus, mortality for the first year of life would be 39%. The frequency of deaths in other age classes (> 1 year) were corrected for an increasing population by multiplying by e^{rx},(r = 0.18 and x = age in years). Sex of some blackbuck from which jaws were recovered could not be ascertained and thus the total sample size of frequencies of death (> 1 year) was larger for the whole population (n = 110) than for females (n = 50) and males (n = 53).

Using these corrected frequencies of deaths as the f'x column, life tables were computed (Caughley 1977:92) for the male, female, and for the combined data set (Appendix 5).

Table 20. Bone marrow index of wolf-killed blackbuck in Velavadar National Park (1988 to 1990).

	1 Solid white	2 White opaque gelatinous	3 Red/pink opaque gelatinous	4 Transluscent yellow/pink gelatinous
% of Blackbuck n = 43	17.8	21.4	25	35.8
% of Males	11	11	33	45
% of Females	30	40	10	20
Mean % fat† n = 3	95.46 (3.4)	68.2 (4.9)	26 (4.2)	4.3 (3.5)

Numbers in parentheses are standard errors.

† A random sample of 3 bone marrow samples from each category were analyzed for fat content by ether extraction.

The 61% survival of the "0" age class was probably an estimate on the higher side due to exceptionally good forage and cover. Mortality pattern is bimodal amongst males; mortality increases between the ages 7 to 9 years and then decreases (Fig. 7). This age group seems to be under intense predation pressure (as seen earlier) especially during and after the rutting season. Males in this age group would probably try to maximize their breeding effort and would be exposed to intense sexual competition (by acquiring and defending territories). These activities require high energy expenditures and are likely to deplete body condition predisposing the animals to predation and other causes of mortality (Flook 1970). The maximum age recorded for males was between 12 and 13 years and for females 16 years. The survivorship curves of females and males were similar to each other and to those recorded for ungulates (Fig. 8) (Caughley 1977:226).

Probit analysis (Caughley 1970, 1976, 1977:96-97 and Finney 1971) was done on the total population data for adult deaths. Regression analysis of :

$$\text{Probit } (f_x/f_1) = a + b^{xi}$$

where f_x is the corrected ($f'_x e^{rx}$) frequency in age class x ($x \geq 2$); f_1 is the corrected ($f'_1 e^{rx}$) frequency in age class 1; a = the regression intercept, b = regression slope, and i = a function of skew.

The median age adult death was

$$M = (5 - a/b)^{1/i} = 7.92 \text{ years.}$$

The standard deviation of adult death was

$$S = \frac{1}{2}\left[\left(\frac{4-a}{b}\right)^{1/i} - \left(\frac{6-a}{b}\right)^{1/i}\right] = 3.296$$

The skew of the frequency distribution of adult mortality was

$$-\log_e i = 0.105.$$

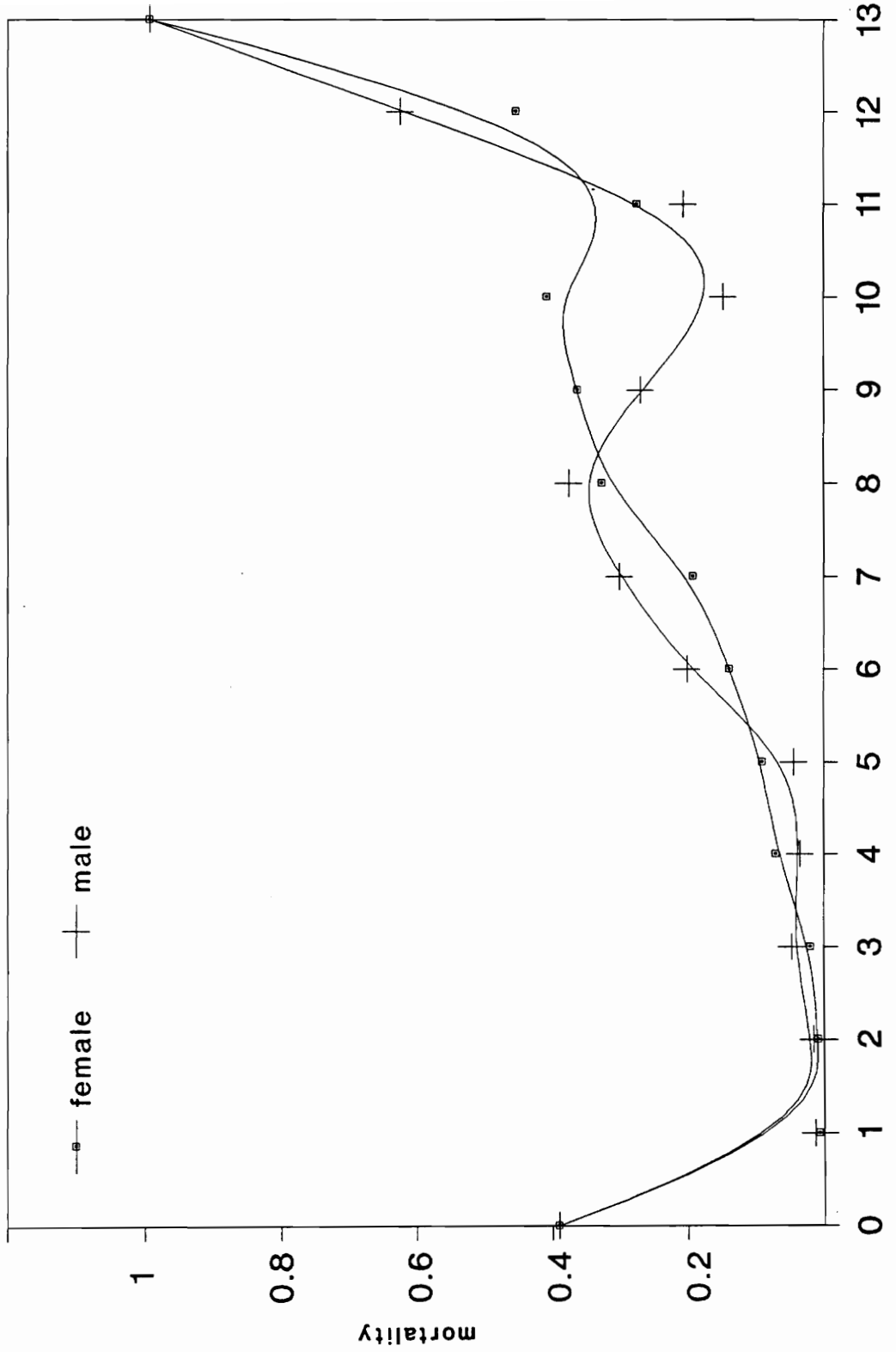


Fig. 7. Mortality curve of blackbuck in Velavadar National Park (1988 to 1990).

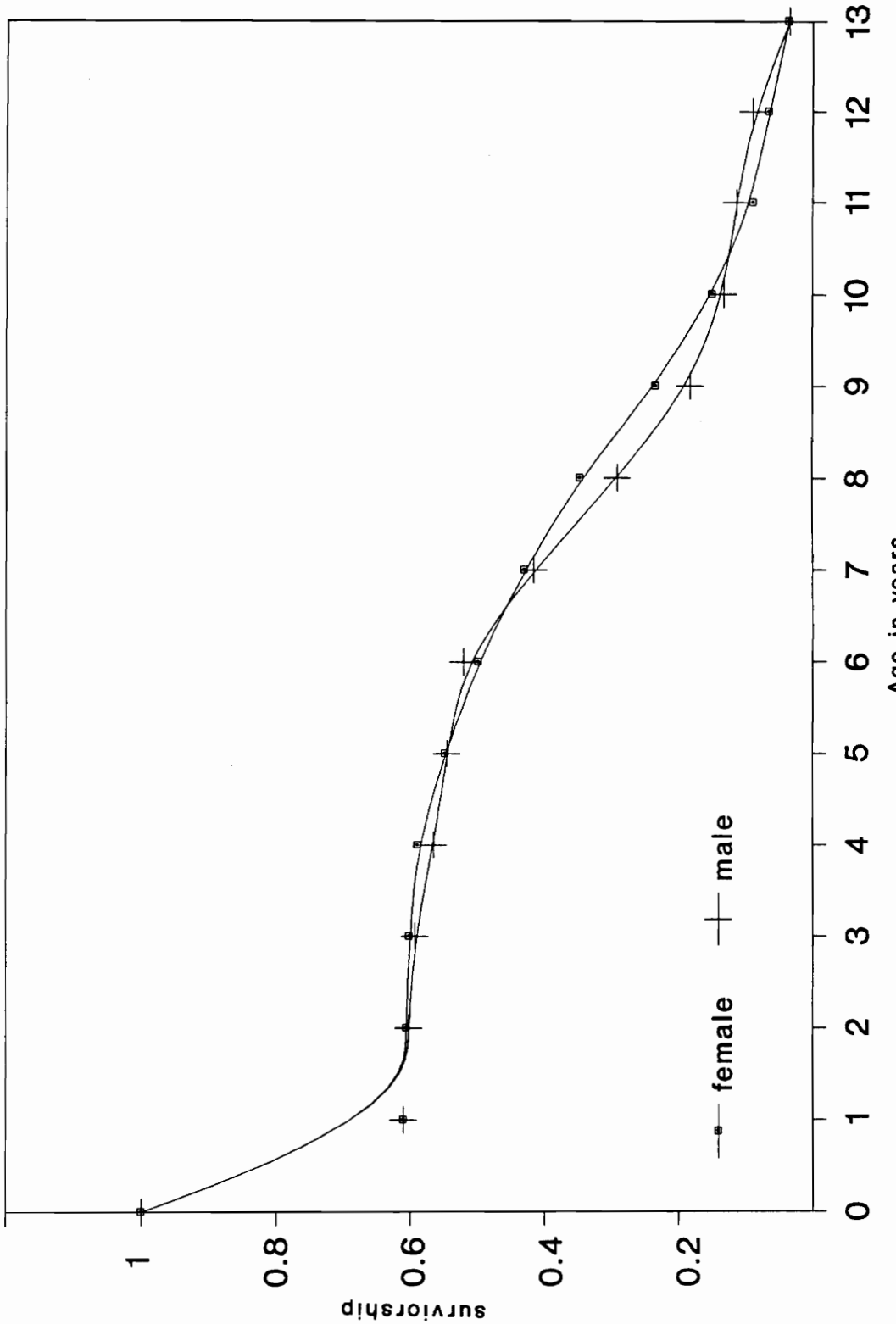


Fig. 8. Survivorship curve of blackbuck in Velavadar National Park (1988 to 1990).

Skew is positive at low rates of increase, disappears at a moderate rate, and becomes negative at a higher rate (Caughley 1976). The standard deviation reflects the change in skew; it is greatest when skew is zero and contrasts with a change of skew in either direction. The median age at adult death is least affected by the rate of increase (Caughley 1976).

Sex Ratio

Sex ratio of all age classes above fawn stage was 55 males to 100 female blackbuck considering the pooled data from all censuses. A sex ratio of 43 males to 100 females was reported for the blackbuck (above fawn stage) that perished in the 1976 cyclone (Mungall 1978:91). Daniel (1967) reported a sex ratio of 71 males to 100 females amongst younger age groups and a sex ratio of 55 males to 100 females for adult blackbuck at Point Calimere. Adult sex ratio is known to be biased towards females in mammals (Emmel 1976). The deviation of the sex ratio from 50 : 50 suggests differential mortality or emigration of males from the population. Further examination of the census data by age class showed that the sex ratio was (a) close to 1 among adolescent blackbuck (82 males to 100 females), (b) highly skewed towards females for the subadult age group (22 males for 100 females); and (c) skewed towards females for the adult blackbuck (68 males to 100 females), but greater than the ratio observed for the subadult age group.

Increased mortality of adult males due to increased vulnerability to predation would account for the skewed sex ratio in the adult age group (Flook 1970, Sinclair 1977:129). Evidence for higher mortality among subadult males was not obtained. It seems more likely that at this age males disperse to join bachelor herds in "marginal" habitats outside the park as observed in impala (*Aepgceros melampus*) and other antelopes (Jarman 1974, Jarman and Jarman 1974). These males are more likely to be poached since they would not experience the same protection offered within the park. Subadult males that survive to adulthood are likely to return to the park to compete for territories for breeding.

Demographic Characteristics

Fecundity pattern in ungulates is characterized by an initial steep rise over the first few years of life, followed by a long plateau, which often has a slight negative slope (Caughley 1976). For the purpose of population analysis, little precision would be lost from calculating a single fecundity rate for adults as the weighted mean of plateau fecundity (Caughley 1976). Fecundity schedules were obtained from the literature (Mungall 1978, Rangitsinh 1982) and various parameters like the net reproductive rate (R_o), mean generation time (G), and intrinsic rate of Increase (r_m) were calculated from the life table (Appendix 5). The results were as follows :

$R_o = \sum l_x m_x = 3.218$

$G = \sum l_x m_x x / \sum l_x m_x = 5.308.$

$r_m = \log_e R_o / G = 0.22$

Population Model

Life table analysis assumes schedules of survival, mortality, and fecundity to be fixed and therefore yields deterministic results. In natural populations, age-specific survival and fecundity are seldom stationary for long periods (Caughley 1966, 1970). Stochasticity is more the general rule.

The parameter most affected by environment fluctuations is the survival of the young. This survival seems to be primarily responsible for major population fluctuations (Sinclair 1973). Mean fawn survival during the course of the study was 61% but ranged from 25% to 95% (see Appendix 4). The coefficient of variation for fawn survival was computed to be 30%. Adult survival rates were

obtained from the life table and were considered to be less variable than fawn mortality (Sinclair 1973). Fecundity reportedly is the least affected of the 3 key parameters (adult survival, fawn survival, and fecundity) responsible for population changes in closed populations of tropical ungulates (Caughley 1970:84, Sinclair 1973). A reproductively mature blackbuck female could produce a maximum of 2 fawns in a year. In poor years, only one or no fawns may be produced. Considering a 1:1 sex ratio at birth, the coefficient of variation for female births would be 0.33 (for model parameters see Appendix 6).

From the past 21 years of population data, it seems likely that the blackbuck population of Velavadar has been regulated at a dynamic equilibrium (Fig. 6). To incorporate a regulatory process in the model, a Beverton-Holt function (Beverton and Holt 1957, Ferson and Akcakaya 1990) was used (see Appendix 6). The function acts by regulating recruitment to the population in a density-dependent manner. In reality several mechanisms would be responsible for population regulation. It is likely that adult survival and fecundity would also be density dependent and may be important for regulation. It is also entirely possible that environmental catestrophies like droughts, floods and cyclones might be responsible for the apparent steady state (Andrewartha and Birch 1954:655-656). The purpose of incorporating density dependency in population recruitment is for simplicity of the model based on empirical evidence, and implications about the regulatory mechanisms are not intended.

The purpose of the model was to understand the stochastic behavior of the population, given the variability in fawn survival, adult survival, and fecundity derived from field data with a possible density dependent regulatory mechanism (Caughley 1981). Fig. 9 represents the trajectory of the female population for a period of 50 years obtained from 250 stochastic replicates. The standard deviation and maximum and minimum values recorded suggest wide variation, but a clear pattern is apparent. Given these parameters for the model, there is a 1% probability that the population will fall below 700 blackbuck in the next 50 years and has an almost 0% chance for extinction. The model also predicts only a 5% chance for the population to increase above 3000 individuals (see Appendix 6).

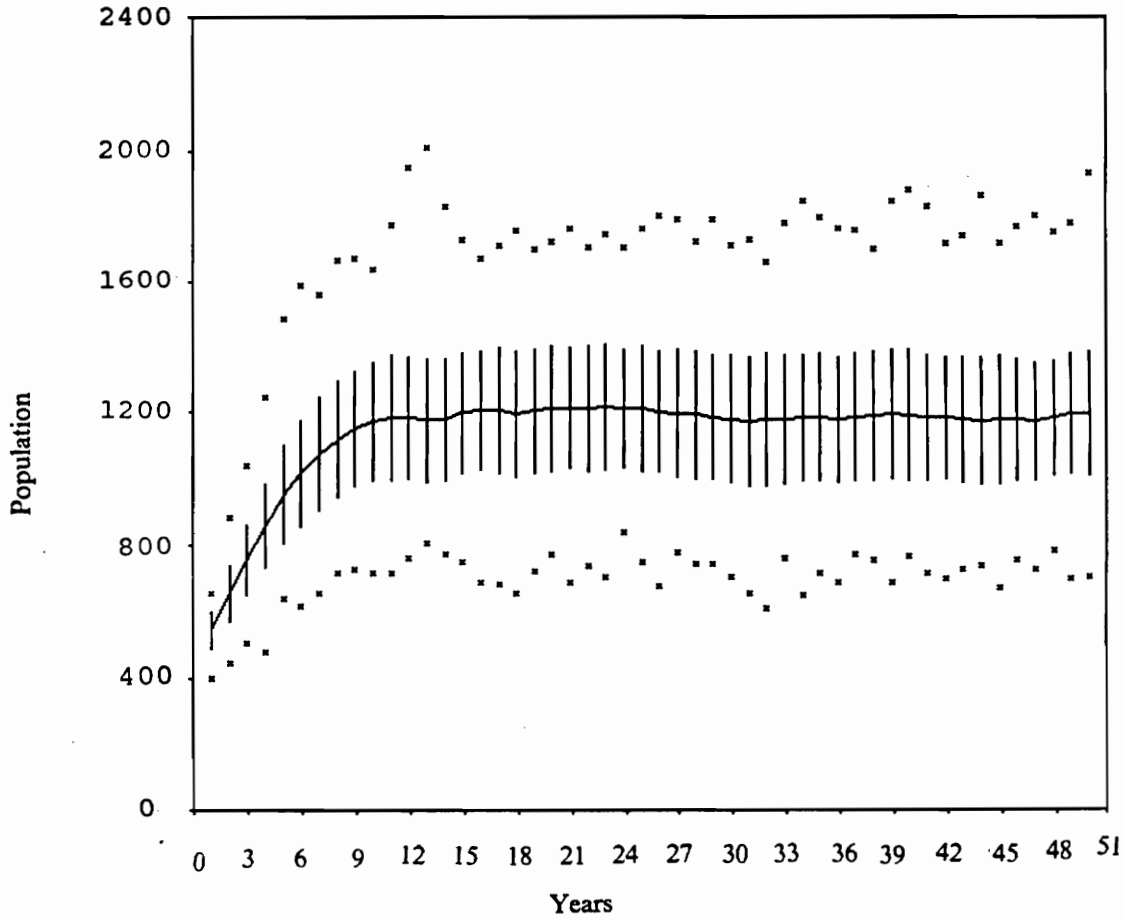


Fig. 9. Results of 250 simulations of the blackbuck population at Velavadar National Park. The mean population trajectory, the standard deviation, and the range within which the blackbuck population is likely to fluctuate are shown.

Wolf

Habitat Use and Preference

From data on observed tracks and from actual observations, the pack seemed to cover an oblong area of about 150 sq km. The long axis of the area extends in a north-south direction from the vicinity of Gangawada and Adhelai villages to Gokulpara village grounds, a distance of 16 km. The east-west axis was short between the muddy flats of the tidal zone at the eastern edge, and Velavadar village at the west. Two packs of wolves were suspected to have territories adjacent to the Velavadar pack. The pack in the south was composed of 4 individuals in 1988 (Chikotara pack) and the pack on the north western side (Mithapur pack) had 2 wolves in 1988-89. Though the pack ranged outside the park, the majority of its activities were concentrated within the park boundaries. This was probably due to :

1) High prey concentration in the park,

2) Availability of suitable habitat for lying up during the day, and

3) Minimal disturbance from humans.

Wolves were rarely observed to be on the move after the day temperature rose. They inevitably sought cover to spend the hot hours of the day. On locating appropriate cover, the pack would lie up in an area until evening. Wolves would normally dig out a hollow in the ground to a depth of 7-14 cm, expose the cool soil from under the heated surface and curl up in it. Pack members would lie adjacent to each other or as far apart as 100-200 m.

Activities gradually decreased as temperature rose. If water was available in the vicinity, wolves would occasionally go and drink and dip themselves in it. Even tidal pools were utilized for dipping and cooling. From tracks and spot-light sightings, the wolves did not seem to be limited by habitat choice at night. The alpha male was once observed to approach a blackbuck herd from behind 2 cottages on the outskirts of the Velavadar village, and the pack was observed on several

occasions at night near my cabin. However, during the daytime, the pack was restricted to certain habitat types.

The pack was rarely observed to use the grassland or saline habitat between 9 am to 4 pm during the course of this study. The shrubland thus seemed critical to provide cover during the day for the wolves. The dugout hollows for lying up (locally called akhalis) were often located under shady low canopy *Prosopis* quite close to the trunk (Fig. 10). Certain areas of the shrubland were repeatedly used (Fig. 11). Often the same dugout hollows were used. If disturbed, even during the noon hours, the pack would leave the area and travel a few to several km before lying up again. The smallest *Prosopis* grove repeatedly used by wolves for lying up and also as a rendezvous site was less than 50 m in diameter. However the location of this grove was "remote" with almost no human activity within a radius of 2.5 km.

Surprisingly, wolves were observed on 3 occasions lying up in one of their favored spots (rendezvous site) in thick cover within 800 m of a team of 15 laborers working on constructing a check dam. The laborers were unaware of the wolves. Disturbance to wolves was apparently minimal due to thick intervening cover of *Prosopis*. Construction sounds and human voices were barely audible (to me) near the wolves.

There were 2 locations of lying up sites and one rendezvous site outside the shrubland habitat (Fig. 11). Two of these sites in the grassland habitat were located in a clump of 6 to 8 *Prosopis* trees. These trees (4 m tall) had been trimmed of their lateral branches to produce a canopy for the purpose of producing mast for blackbuck. There was hardly any visual cover available but the canopy offered ample shade from the sun. The lying-up site in the saline region was on well-drained high ground. It was used during the cold winter season and in the monsoon. This location had no "cover" and was near and on the top of an embankment of a pond. The wolves used it to bask in the sun and to keep dry.

During winter and monsoon, wolves were active and used the open habitat (grassland and saline region) later into the morning and earlier in the evening than during summer. The above observations suggest that wolves rely on the shrubland not only for visual cover but also for protection from the sun.



Fig. 10. a) Wolf lying-up sites in a stream bed in the summer of 1989. b) Wolf pups in the cool shade of *Prosopis* in the stream bed of Utavli at a rendezvous site in March 1990.

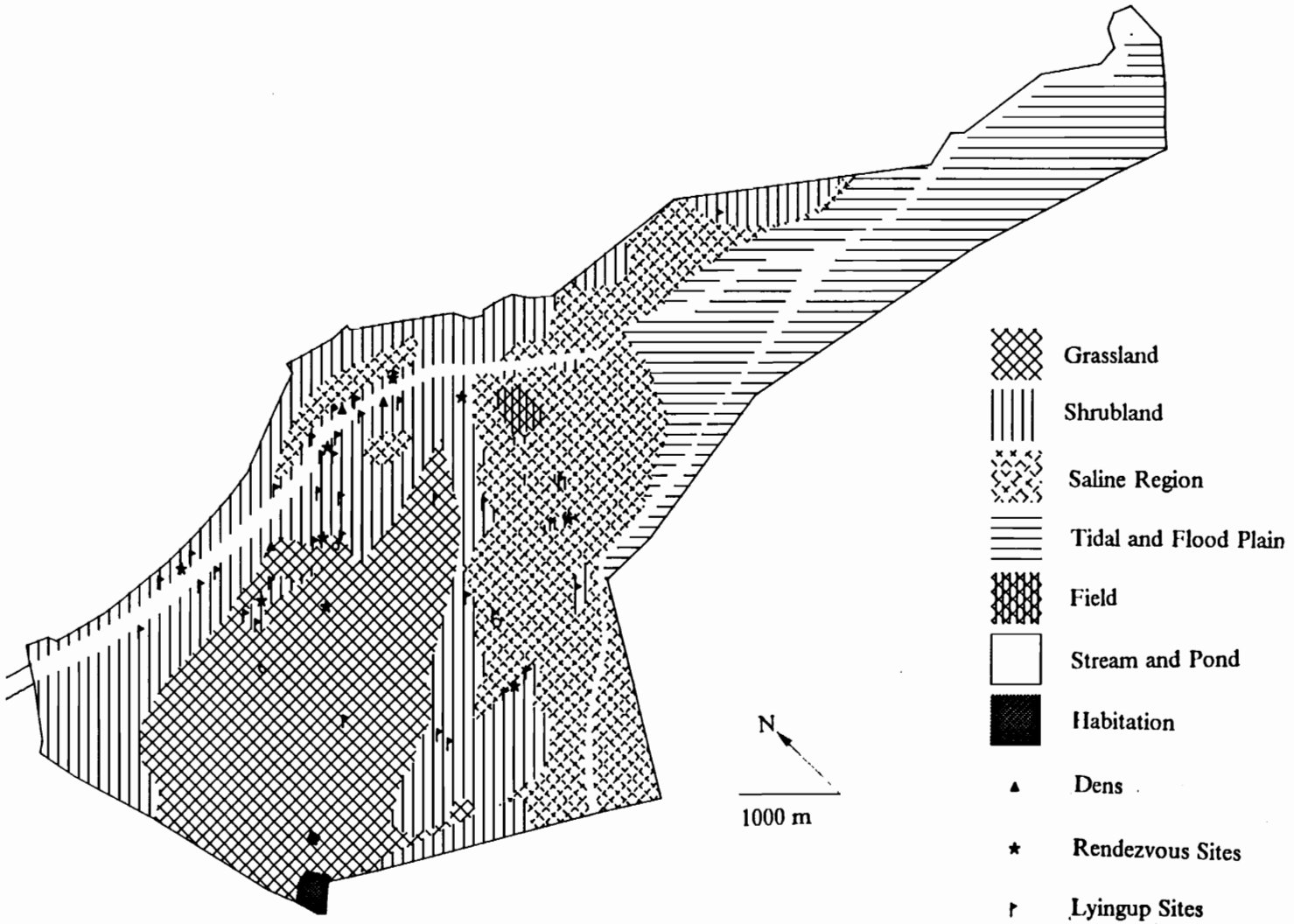


Fig. 11. Habitat types and locations intensively used by wolves in Velavadar National Park during 1988 to 1990.

Dens

The litters of 1988 and 1989 were born in the month of December. The dens made in 1988 and 1989 were both excavations and enlargements of fox holes (Fig. 12) The den used in 1987 was located in May 1988. By this time it was in a dilapidated condition and was half caved in. All 3 dens were within of 1.2 km from each other (Fig. 11). The 1987 and 1988 dens were dug out in the steep bank of the rivulet Utavali. A check dam was built down stream of the denning site in 1989. Due to good rains and the checkdam, the denning area remained flooded in December 1989. The 1989 den was about 1.2 km from the 1987 and 1988 den site.

The soil excavated from all the dens was moist and the texture was clayey. The 1988 den had a single entrance with a vertical diameter of 30 cm and a horizontal diameter of 35 cm. The tunnel progressed upward at an angle of 5 ° with an angle of 30 ° to the stream bank. The tunnel bent sharply at 3 m depth into a 0.5 m chamber. *Prosopis* roots protruded into the chamber from the trees on the bank; these were gnawed and scratched. The clayey texture of the soil and the *Prosopis* roots were probably important for preventing collapse. The 1989 den was on the border of the shrubland habitat. It was devoid of any shrub cover in the immediate vicinity and was in a patch of dry *Chloris* grass about 35 cm tall. The den was discovered on observing the wolf bitch disappear into this patch of grass. The camouflage provided by the dry grass was very effective. The original fox hole was a complex of tunnels with 5 entrances, the wolf bitch had enlarged only one entrance and tunnel and constructed a chamber at its end. The entrance measured 35 cm and 91 cm in diameter and was oblong. The tunnel was 3.3 m long. The roof of the tunnel was at an average depth of 32 cm from the surface. The chamber had a length of 110 cm, breath of 70 cm , a height of 25 cm, and was at a depth of 58 cm from the surface.

The possibility of using the same den over the years as observed elsewhere (Jhala, in prep., Mech 1970:121) was remote in Velavadar since during the monsoon the denning area was flooded, especially in the vicinity of the rivulet Utavali. However dens were excavated in the same region for all 3 years suggesting a tenacity to the site (Fig. 11). The region during December to February had:

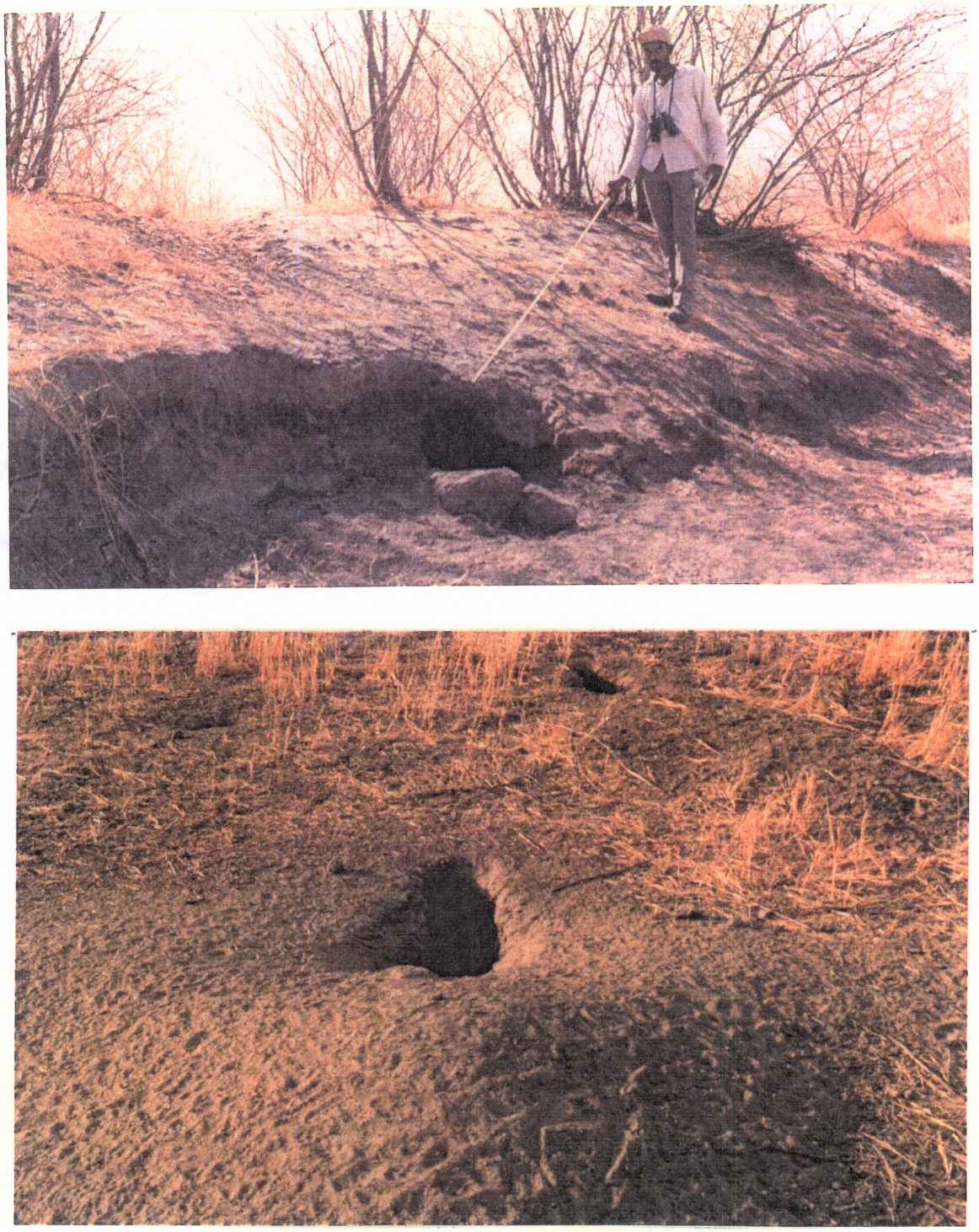


Fig. 12. Wolf dens. a) Den of 1988-89 in the Utavli stream bed in the shrubland habitat. b) Den of 1989-90 in a patch of dry grass.

1) Fresh drinking water within a radius of 3 km in all 3 years,

2) Good cover in the form of *Prosopis* shrubs and cool shade under the rivulets embankment,

3) Almost no human activity in the vicinity, and

4) Probably the right texture of soil that would allow excavating a den.

These could be probable reasons for the intense use of the area for denning.

Rendezvous Sites

Nine rendezvous sites were recorded as used by the pack over 2 breeding years (Fig. 11). A location was considered a rendezvous site if the pups remained in the vicinity for over a week.

By the time the pups left the den site in both years, it was late February or early March. The summer heat had begun. During the summer, the rendezvous sites in and around Utavli stream bed were intensively used. The pups would spend the hot hours of the day in cool depressions dug out in the stream bank (see Fig. 10). The depressions were often 25-30 cm deep and 25-50 cm wide. These were also used by adult wolves for lying up. During the early months, the pups were restricted to an area of 250 m radius at their first rendezvous site. Wolf tracks converged from all direction along well-used trails. The area smelled strongly of wolf odor and urine. Pup and adult wolf scats accumulated in and around the area. Kill remains like bones and hide were often strewn around. The description of rendezvous sites of timber wolves in North America (Joslin 1966, Mech 1970) matches extremely well with the Velavadar sites.

As the pups grew, they explored larger areas, especially at night, and often visited nearby kills. As the rains started (mid June) the pups were 6 months old. The pack utilized the higher dry saline region with small groves of *Prosopis* within which to lie up. At this age the pups visited almost all the kills, yet they were fed by adult wolves which regurgitated food and brought chunks from kills to these rendezvous sites. Nearing August, pups (about 8 months old) joined the pack. Although

they were often fed by adult wolves, it was not possible to identify a central location for the pack activity.

The pack ranged over larger distances during this time of the year, often outside the park boundaries. In September-October of both years the pack was rarely spotted with all its members together. Wolves were often seen alone or in groups of 2 or 3. Track records also suggested that group numbers decreased during this time of the year.

There was thus a seasonal trend in the use of different areas of the park by wolves. The shrubland habitat seemed critical for lying up and for rendezvous sites. The shrubland habitat along the Utavli rivulet was extremely important for denning and rendezvous sites in summer. In the monsoon *Prosopis* patches in the higher saline region were intensely used (Fig. 11).

Food Habits and Consumption

Active dogs require about 189.2 kcal/$kg^{0.75}$ /day (Whitney 1949). Considering the average weight of *Canis lupus pallipes* to be 18 kg (Joslin 1982, Mendelssohn 1982, Shahi 1982) and if wolves have similar metabolic rate as dogs, they would require 1,652 kcal/day for maintenance. This amount of energy would correspond to 0.99 kg of meat/day (at 1,668 kcal/kg meat) about 5.5% of the wolves body weight for maintenance. Wolves were observed to have a much higher intake in the wild (Fuller and Keith 1980, Mech 1970:184-185, Peterson 1984, and Peterson et al. 1988). Captive wolves at Junagadh zoo were maintained on a diet of 0.85 kg of meat/day (Rawal pers. comm.). This pair bred and produced a litter of 4 pups.

From the several observations on wolf kills (43) only a selected few were used for analysis of biomass consumption by wolves. The criteria for selecting kill observations for analysis were as follows :

1) The number of wolves to have fed from the kill were known with reasonable certainty,

2) The interval between consecutive kills was known,

3) The amount eaten was estimated by the difference between kill remains and estimated weight of the killed blackbuck (based on age and sex),

4) There was no loss due to scavenging, and

5) The wolves were not disturbed on the kill. (They left the kill remains on their own accord and not due to human disturbance.)

Data from 13 such blackbuck kills along with data on consumption of 2 goats of known weight were used to estimate the maximum intake/wolf and average intake/wolf/day.

Wolves have distensible stomachs (Mech 1970:181-185) and gorge themselves on large quantities of meat when undisturbed on the kills. Meat diets have high digestibility (Mech 1970:181-185). These 2 factors allow wolves to consume large quantities of meat when it is available. The average consumption by wolves was estimated to be 4.62 kg (SE 0.109 kg, n = 13). The average kill interval was 3.5 days (n = 16, SE 0.5). Considering that wolves consumed on the average 4.62 kg of food at each kill and made a kill on the average of every 3.5 days, the food intake by the wolves would be 1.328 kg/wolf/day or 0.0738 kg/kg of wolf per day. Wolves were assumed not to have fed during the inter-kill period. This assumption would be realistic because the contribution to the diet of wolves by prey other than blackbuck was small (see below).

Wolves had a varied diet (Table 21). Though several prey items were recovered from wolf scats (including an intact leather shoe) only 3 prey species, blackbuck, rodents and hare (*Lepus nigricollis dayanus*) constituted the majority of the diet (Table 21 and Table 22).

Due to the heavy rains, the number of scats collected in the monsoon was small and it was combined with the winter sample for analysis. The frequency of occurrence of prey (Table 21) was calculated by the number of occurrences of each prey type divided by the total number of scats analyzed and expressed as a percentage (Leopold and Krausman 1986). The total percentage exceeded 100% due to occurrence of more than one prey item in some scats. Biomass contribution by different prey types to the wolf's diet was estimated using Floyd et al.(1978) regression equation:

$y = 0.38 + 0.02x$

Where x is the average weight (in kg) of individuals of each prey type and y is the kg of prey per collectible scat.

Table 21. Food habits of wolves as estimated by the frequency of occurrence method in Velavadar National Park (1988 to 1990).

	Blackbuck	Rodent	Hare	Goat	Fox	Cattle	Insect	Nilgai	Dog	Sheep	Pods	Bird	Unidentified
S 88 n = 98	85.57		4.08	12.24		2.04							3.06
W 88 n = 145	91.03	4.14	2.76	4.14	2.07		12.41			1.38	1.37		2.06
S 89 n = 181	89.5	3.87		1.66	1.66			2.76	3.31				
W 89 n = 177	72.88	30.5	15.25	5.08	4.52		1.69		1.69		1.13	1.13	
Total n = 601	84.36	11.15	5.82	4.99	2.33	0.33	3.49	0.83	1.5	0.33	0.67	0.33	1.00

S = summer, W = winter.

Table 22. Contribution by weight (kg) of prey items to the wolf's diet in Velavadar National Park (1988 to 1990).

	Blackbuck			Rodents	Hare	Goat	Fox	Cattle	Nilgai	Dog	Sheep	Total
	Fawns	Others	Black males									
Mean weight	5.5	25	36.75	0.3	2	15	2.5	60	60	15	18	
y	0.49	0.84	1.115	0.386	0.42	0.68	0.43	1.58	1.58	0.68	0.74	
Summer 88	19.6	23.672	16.2		0.378			3.223				63.073
n = 98	(31.1)	(37.35)	(25.68)		(0.6)		(5.1)					
Winter 88	19.6	19.589	22.253	1.197	0.302		0.344				0.99	64.275
n = 145	(30.49)	(30.48)	(34.62)	(1.9)	(0.45)		(0.54)				(1.5)	
Summer 89	19.6	24.446	21.89	0.926	0.252	1.054	0.71		4.36	2.25		75.488
n = 181	(25.96)	(32.38)	(29)	(1.23)	(0.33)	(1.4)	(0.94)		(5.78)	(2.98)		
Winter 89	19.6	14.502	23.484	7.141	5.506	1.612	1.944			1.149		74.938
n = 177	(26.15)	(19.35)	(31.34)	(9.53)	(7.35)	(2.15)	(2.59)			(1.53)		
Total Sample	78.4	82.209	83.827	9.264	6.438	2.666	2.998	3.223	4.36	3.399	0.99	277.774
n = 601	(28.22)	(29.6)	(30.18)	(3.34)	(2.32)	(0.96)	(1.1)	(1.16)	(1.57)	(1.22)	(0.3)	

Numbers in parenthesis are percentages; y is the amount (kg) of prey consumed per scat.

It was possible to distinguish hair of adult black male blackbuck in the scats. Blackbuck males were considered to have an average weight of 35 kg in the summer of 1988, 38 kg in the winter of 1988 and 1989, and 36 kg in the summer of 1989 (Mungall 1978:86). Average weights of blackbuck killed by predation would be lower than the average of blackbuck in this group in the population since wolves were observed to prey on black males in poor condition (see Mortality under Results). It was not possible to differentiate between the remains of subadult blackbuck, adolescent blackbuck, and adult non-black males and adult females in scats. Fawn remains in scats were distinguished from this group by hair coloration and presence of bones and hoofs in scats. These criteria were likely to under-represent fawn remains, especially when bones and other structures were absent in scats and fawns had coat color similar to the above group. Minutely detailed analysis would be needed to detect them. To avoid this bias, 40% of blackbuck scats were assumed to be from fawns (40% was estimated by detailed analysis of 127 random scats with blackbuck remains). Fawns were assumed to have an average weight of 5.5 kg while the combined blackbuck group was assumed to have a mean mass of 25 kg. Y values for all prey types were computed (Table 22). Visually estimated proportions of each prey type/fecal sample were summed (seasonally) and multiplied by the corresponding y value (kg of prey per scat) to obtain the biomass consumption of a particular prey type (Table 22).

The frequency-of-occurrence method and the estimate of biomass consumption (Tables 21 and 22) rated the importance of the major food items as blackbuck, rodents, and desert hare. These 3 prey items together accounted for 93.66% of the wolf's diet in terms of biomass. Due to a 3-year drought prior to this study, the population of rodents and hare was extremely low in summer 1988. No rodents were encountered on night drives in the park and hares were spotted rarely during 1988 summer. By the winter of 1989 an average of 21.5 (SE 5.1, n = 23) rodents were spotted on a 6 km road used as a transect. Rodent remains were not differentiated into separate species for analysis. The majority of the remains (> 90%) were of Indian gerbils (*Tatera indica*), a species of field mice (*Mus booduga*) and metas (*Millardia meltada*) also occurred in the park and in the scats. The population of hares also increased presumably due to good rains in 1988 and 1989. The wolf's diet in winter reflects the greater availability of these 2 prey species. A 17% contribution by hare and

rodents to the wolf's diet in the winter of 1989-90 compared to only a 1.5% contribution during the rest of the study period, suggests a reduction in predation on blackbuck during the winter of 1989-90. However, due to small size of these 2 prey species in comparison to blackbuck a very large number of rodents and hare would have to be consumed by wolves for a significant prey switch to occur (Murdoch and Outen 1975).

Nilgai (*Boselophus tragocamelus*), cattle, and sheep were rare occurrences in the wolf's diet and occurred only in one season. These occurrences suggest that these species were possible remnants of a single kill or scavenging incident. Thus they would be relatively unimportant to the food habits analysis (Corbett 1989).

Considering an average pack size of 6 wolves with a mean consumption of 1.328 kg/wolf/day, the total annual consumption by the pack would be 2908 kg of meat. Blackbuck, hare, and rodents would contribute 2782 kg of this amount.

During the few incidences (5) when wolves were observed to hunt blackbuck , they seemed to rely on stalking as well as a chase. Most (98%) kills were made during the night. During night, the flight distance of blackbuck seemed to decrease. Wolves seemed to rely greatly on stalking at night to get close to blackbuck before rushing. Blackbuck are diurnal, and rely primarily on sight to avoid predation by quick flight (Mungall 1978). They are likely to be at a disadvantage to nocturnal hunters. Wolves were successful in killing adult blackbuck when hunting in packs or individually. The method of killing by the pack was primarily an attack on the rear end and then evisceration. The blackbuck likely died due to blood loss and shock. The technique of killing by a single wolf was a bite on the throat or base of the skull. Wolves killed goats by a bite on the throat and clasping on until the animal died of asphixia.

Wolves invariably opened the carcass from the rear end. They preferred to feed first on the visceral organs and the rump. The rumen would be left unruptured and dragged a few meters away from the kill. Often wolves would defecate on or near the rumen. The fore limbs and the neck region were the next to be consumed. Head and the skull were the last to be eaten, in the case of adult males the head could nearly always be recovered from the kill.

Adult blackbuck kills were rarely fully utilized by wolves. Wolves were not observed to continue feeding on a kill made in the grassland or saline habitat later than 8:30 am. Wolves rarely returned to a kill. Normally scavengers including jackals (*Canis aureus*), fox (*Vulpes bengalensis*), dogs (*Canis familiaris*), crows (*Corvus splendens*), vultures (*Gyps bengalensis, Gyps fulvus, Neophron percnopterus, Sarcogyps calvus, Aegypius monachus*) and eagles (*Aquila rapax nipalensisu*) finished off kill remains within a few hours. A kill was considered fully utilized if all the edible portion of the kill was consumed by wolves. Utilization of kills was dependent on the time at which the kill was made. If wolves killed the blackbuck early in the night, it was likely to be almost 100% utilized, otherwise, the pack left the unconsumed kill remains in the morning. Of all the fresh kills observed only 16% were 100% utilized. On the average, blackbuck kills were 57% (SE 6.6%, n = 43) utilized. Underutilized kills were more likely to be located in the morning due to the feeding activity of the pack and the aggregation of scavengers. This conspicuousness may have been a source of bias towards underestimating kill utilization. Underutilization would cause the pack to kill more often. The number in Table 23 for adult blackbuck kills would need to be inflated by about 43% to account for underutilization of kills. Thus a pack of 6 wolves would kill between 59 to 84 blackbuck and about 150 fawns (considering fawns to be 100% utilized). The actual number of blackbuck killed per wolf would range between 35 and 39 per year.

Considering an average fawn mortality rate of 39% for the study period and a average of 828 fawns produced in a population of 1200 blackbuck (46% reproducing females with a fecundity of 1.5 fawns/year/female (see Blackbuck Population under Results and Appendix 4), then wolf predation on fawns would account for 46% of fawn mortality. This seems reasonable since jackals, dogs, and jungle cats (*Felis chausu*) also preyed on fawn and would easily account for the other 52% of fawn mortality. Considering an annual finite rate of increase (λ) for blackbuck in the absence of predation to be 1.246 (see Blackbuck Population under Results) and using Keiths's (1983) model, the number of blackbuck required per wolf to maintain a stable blackbuck population is as follows:

$$N = k/(\lambda - 1)$$

Where

Table 23. Annual consumption of different prey items by a pack of 6 wolves in Velavadar National Park (1988 to 1990).

	Blackbuck			Rodents	Hares	Other prey
	Fawns	Others	Black males			
Kilograms	821	861	878	97	67	184
Numbers	149	35†	24†	324	33	

† Under-estimated due to under utilization of kills. See text for details.

N = blackbuck numbers per wolf,

k = annual blackbuck kill per wolf (39),

λ = annual finite rate of increase for blackbuck with adequate food and no predation by wolves (1.246). Multiplying N by the number of wolves in the pack gives the number of blackbuck required to maintain a stable population and sustain wolf predation. The number is 845 to 951 blackbuck (i.e., N x 6).

Wolf Population

Wolves are reported to attain sexual maturity at the age of 2 years (Mech 1970:143). It was extremely difficult to differentiate between adults and wolves over 1 year of age in the field. Three age groups were distinguished in the current study : (1) pups < 6 months, (2) subadults between 6 and 12 months, and (3) adults over 1-year old.

A definite date for parturition could not be fixed for 1988 since continuous observations were not obtained. The den was in the bank of river Utavli and the terrain was not suitable to construct a hide without disturbing the wolves. In 1989 a continuous record was kept on the den from a hide constructed about 850 m away. Parturition is believed to have occurred in the second week of January 1990. The pups emerged from the den for the first time on February 4, 1990. The mean litter size for the 2 years was 5.5 pups, assuming that no mortality occurred before the pups emerged from the den. It is likely that birth occurred earlier in the year for the litter of 1987 since the young wolves observed in the pack in April 1988 were much larger than the subsequent litter of 1988 and 1989 in April. For the young wolves of the pack during summer 1988 the difference between pups and subadults could not be distinguished (probably due to my lack of experience at that time) (Table 24). The alpha breeding pair could be recognized throughout the study. A third wolf could also be identified from the winter of 1989 onwards. The alpha bitch was the only female which reproduced in 1988 December and 1990 January and presumably also in 1987.

Table 24. Numbers and sex composition of the Velavadar wolf pack (1988 to 1990).

	Adult		Subadult		Pups	Total
	Male	Female	Male	Female		
Summer 88	1	1	2	2		6
Monsoon 88	1	1	1	1		4
Winter 88	1	1	1		5	8
Summer 89	2	1			4	7
Monsoon 89	2	1	1	2		6
Winter 89	2	1	1		6	10
Summer 90	2	2			5	9

Mortality could be estimated only for the pups since pups were unlikely to disperse (Mech 1987). Mortality for the litter of 1988 was 40% in their first 6 months and mortality for the litter of 1990 was 16.6% in their first 5 months. The average mortality for the pups would thus be 28.33%. The cause of mortality for the pups could not be determined since carcasses were not recovered. Two wolf deaths were recorded and carcasses were examined. A subadult male wolf in June 1988 was found lying moribund in the vicinity of my cabin. It was in an emaciated state and diseased (distemper was suspected). After being revived by administration of intravenous glucose and atropine, it readily consumed 1.5 kg of meat which was offered. It died the next day. A carcass of an adult male wolf in prime condition was located in December 1989. The wolf was a young animal judging from its tooth wear (Mech 1970:140-143). There were no injuries on the head and thorax region and the abdomen was ruptured. This injury could be a result of subsequent scavenging on the carcass. Subadult and adult wolf numbers in the pack dropped in the late monsoon (September-October) and winter. It was not possible to ascribe reduction in numbers to emigration or mortality except in the above 2 cases. The pack size dropped from their summer numbers by an average factor of 0.464 during the winter. This drop in number suggests that if dispersal occurred, it was after the age of 9 months. The fate of dispersed wolves could not be traced. It is unlikely that these members returned to reintegrate into the pack (Mech 1970:52) since increase in wolf numbers in the adult and subadult categories was accountable by recruitment from pups (Table 24). During 1988 there was 1 subadult male assisting the alpha pair in winter. In 1989-90 there were 2 wolves, one adult male and another subadult female assisting the alpha pair in pup rearing (Table 24).

The average pack size, excluding pups younger than 3 months for the entire study period, was 5.57 (SE 0.782). The wolf numbers in the pack for the 3 consecutive summers were 6, 7, and 9, thus registering an increase of 50% in 2 breeding seasons ($r = 0.2$, $\lambda = 1.22$).

Management and Optimization

Coefficients and Model Parameters

The regression model developed for PAGB and rainfall was used to predict a peak above-ground biomass (PAGB) for the past 12 years of rainfall. The mean of the 12 predicted values was used as the coefficient (B_{gc} = 5463 kg/ha) for grassland habitat in the objective function. A 99% lower bound for the PAGB for the 12-year predicted data was 3654 kg/ha. This value was used as the coefficient of grassland PAGB in the constraint to ensure sufficient forage availability for "a minimum" number of blackbuck. The coefficients for other management options (habitats) were estimated as explained in the methods. Sensitivity analysis of the model (see Appendix 7) showed that the model solution was not sensitive to a 55% change in the coefficients of PAGB production in shrublands and saline regions.

Using a conservative estimate of 39 blackbuck killed per wolf per year and the maximum number of wolves in the park to be 12, then the number of blackbuck essential to sustain a stable population would be about 1,900.

Assuming that the blackbuck population, over time, would be distributed in the different age and sex categories similar to the current blackbuck population (as estimated by summer census) then the total blackbuck biomass would be 49,000 kg (Table 25). The average blackbuck in the population would weigh 25.8 kg (11.447 $kg^{0.75}$). Considering an average annual consumption of 0.095 kg/$kg^{0.75}$ body weight/day for the blackbuck (see Intake in Results) a population of 1,900 blackbuck would consume 754,157 kg of forage/year. Assuming a 30% utilization of PAGB the PAGB production should be 2,513,857 kg to suffice for the blackbuck needs. This assumption seems realistic and conservative since blackbuck were observed to consume more than this proportion (40%) from the exclosure studies. Though over 70% of AGB was consumed during the 1987 drought, the blackbuck were in very poor condition and were given supplementary fodder.

Thus it appears that although blackbuck can harvest a large portion of PAGB, most of it is of poor quality due to low CP values and low digestibility and blackbuck cannot maintain body condition on it (Sinclair 1975). A 30% utilization should ensure an appropriate quantity so that selective feeding on quality forage could maintain body condition. To ensure the above minimum production of PAGB from the grassland habitat with 99% confidence, an area of 700 ha of grassland would suffice.

The inclusion of the constraint on minimum forage production incorporates the risk of low rainfall and ensures maintenance of blackbuck and wolf numbers in a stochastic environment prone to droughts. With the current situation in the park, the areas in the different habitats provide the minimum forage requirements. However, if in the future the budget of the park is reduced, then the grassland area may be reduced due to *Prosopis* invasion. In such a situations this constraint (see constraint 5, Appendix 7) would still result in adequate forage that would allow a appropriate size herd that is relatively stable, even under the pressure of wolf predation, over a long period.

Constraint 6 (Appendix 7) specifies current conditions for making management decisions. The coefficients for the habitats and management options are obtained from the regression of PAGB with the rainfall of the present and last year as independent variables. The model was run with mean coefficients and the lowest value of grassland AGB predicted by the regression for the past 12-year rainfall data. The right hand side (RHS) of the constraint (3,041,788 kg) was considered to be the forage requirement of an hypothetical population of 2,300 blackbuck (the highest number attained in the past 22-years).

The RHS of the area constraint (constraints 1 to 4, Appendix 7) for the 3 habitats were the areas under these habitats in 1990. They could be changed according to the management activities of changing one habitat type to another. Thus the model is flexible and needs to be initialized with the appropriate areas under each habitat. If the total area of the park is increased, RHS of the first constraint would need to be changed. The model was run with the current (1989) area estimated from the digitized map and again with the grassland and/or shrubland areas increased (as an hypothesized consequence of management at some future date).

Table 25. Average percentage of the blackbuck in different age classes (1988-1990) and their biomass at a desired population in Velavadar National Park.

	Fawns	Adolescent	Subadult ♂	Subadult ♀	Adult ♂	Adult ♀	Total
Percentage	3.8	20.2	3.3	13.8	21.1	37.9	
Numbers	72	384	63	262	401	720	1902
Mean Weight	5.5	15.75	28.75	20.25	39	27.5	
Biomass (kg)	396	6,048	1,811.25	5,305.5	15,639	19800	48,999.75

Average blackbuck in the population weights 48,999.75 / 1902 = 25.8 kg.
At 0.095 kg consumption / $kg^{0.75}$ body weight, an average blackbuck consumes 1.087 kg / day.

From the data on wolf habitat use I assumed that, as a minimum, wolves would need a shrubland area with a radius of 50 m for lying up sites, 150 m for a rendezvous site, and 200 m for a denning site. All the intensively-used wolf sites marked on the map (Fig. 13) were encircled with zones of appropriate radii. These added to a total of 70 ha. To err on the side of conservation the absolute essential requirement for a pack of 6 wolves was assumed to be twice this amount (140 ha) of shrubland, i.e., 23.3 ha/wolf. The mean pack size of the Velavadar pack during the 3 year study was 6 wolves. Wolves are considered to be socially regulated (Packard and Mech 1980) by mechanisms such as : (a) disproportional partitioning of food at kills between dominant and subordinate animals, (b) disinclination of well-fed dominant wolves to hunt again after a meal, and (c) limits on meat availability at a kill due to size of the prey. These are viewed as likely factors to cause dispersion (Mech 1977, Messier 1985, Packard and Mech 1980, Peterson et al. 1984, Peterson and Page 1988). Pack size and mean prey size are highly correlated (Nudds 1978, McNab 1983). Considering an average blackbuck to weigh 26 kg, and a consumption rate of only 4 kg / wolf at a kill, then an average blackbuck would barely meet the needs of a pack of 6 wolves. During pre-independence (1947) days, a population of about 9,000 to 10,000 blackbuck were believed to have existed in the Bhal region (Dharmakumarsihnji 1978, Nirmalkumarsinhji, pers. comm.). Wolves were then common in the Velavadar area. The pack size observed during those days ranged between 5 to 8 individuals (Nirmalkumarsinhji, pers. comm.). Similar observations have been made for other packs (Jhala and Giles 1991).

Wolf numbers increase in the pack as pups start to travel with the pack prior to dispersal (see Wolf Population Results). The maximum number of wolves that Velavadar could possibly have at any one time was considered to be 12. This could arise from recruitment prior to dispersal or by 2 packs using parts of the park. Thus the minimum shrubland habitat needed would be 280 ha. (Constraint 12, Appendix 7).

The optimization was done with the budgets of Rs. 500,000 and Rs. 900,000 (the upper and lower limits of current budgets available for management of the park); and with Rs. 5,000,000 (about $ 250,000), an amount 10 times that currently available.

The model was also run with and without the option of developing saline habitat. This management activity is currently not practiced but represents a major possibility of increasing forage production and wolf habitat without increasing the total area of the park.

Model Results and Management Options

All the model runs recommend managing the grassland by continuously eradicating *Prosopis* saplings. The constraint on minimum blackbuck population (1,900) forage needs with a 99% confidence was not binding, given the current areas of the different habitats. As long as the grassland habitat covered more than 700 ha, there would be sufficient forage production to sustain a minimum of 1,900 blackbuck. However if the area of grasslands dropped below 650 ha by *Prosopis* colonization and the shrubland habitat was not available for grazing (due to being too dense), the carrying capacity of the park would drop below the desired level.

All the area constraints were binding. Thus by increasing the total area of the park or by converting less productive habitat types (S, P, and G) to more productive habitat types (S_d, P_c,G_c) the mean carrying capacity as measured by forage production, would be increased.

Within the budgetary range of Rs. 500,000 to 900,000 the model did not recommend developing saline habitats. Eradicating *Prosopis* is a more profitable activity than saline region development in terms of optimizing forage for blackbuck. When the budget is increased 10 times, the model exhausts cutting all the shrubland (except the minimum required for wolves) and then develops the saline habitat. However, the model does not incorporate the value of developed saline regions as wolf habitat into the maximization function. Wolf habitat needs are built into the model as a minimum requirement constraint. Thus the model does not strive to increase wolf habitat. This is one of the limitations of linear programming where the decision making variables of the objective function need to be in the same units (kilograms of forage in this case) (Hiellier and Libermann 1986). This limitation should be remembered while making decisions based on the model's

recommendations. Even with a budget of Rs. 500,000 (current lower limit) all shrubland habitat (except minimum wolf needs) would be cut in over a decade. The model would then allot money to "develop" saline habitat. Thus a prudent management practice would be to invest in developing saline habitat to shrublands simultaneously while cutting the shrubland to ensure that wolf habitat never drops to the minimum requirements.

The management activity of cutting the *Prosopis* and producing charcoal should be done as far away as possible from the critical wolf habitat shown in Fig. 13. Any kind of habitat alteration activity should be avoided in and around the traditional denning area and rendezvous sites used by the wolves near the rivulet Utavali (Fig. 11).

Harvest and Grazing

During most years, the storage capacity of the godowns is the limiting factor for harvesting surplus fodder. Cattle grazing could be looked upon as a way of harvesting surplus fodder. If in the future the management policy changes to allow controlled cattle grazing or selling harvested grass, the model could be altered to incorporate such activities. The model in its present structure calculated the potential surplus each year.

Cattle grazing, though currently illegal (Wildlife (Protection) Act 1972) often occurs in the park. Blackbuck were observed to use grassland areas grazed by cattle (cows and buffalos) for grazing more often than ungrazed areas. In the monsoon of 1989, heavy (50% reduction in AGB) grazing by cattle was recorded in about 200 ha of the northern section of the park. Blackbuck rarely used this area of the grassland in 1988. In the winter of 1989-90, 72% of the blackbuck population concentrated their grazing activities in this area. Cattle grazing had reduced the grass height and encouraged tillering of young nutritious sprouts. The evidence supports the hypothesis of grazing facilitation by cattle as observed in the Serengeti by grazing activities of zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) (Gwynne and Bell 1968, McNaughton 1976). It is likely that

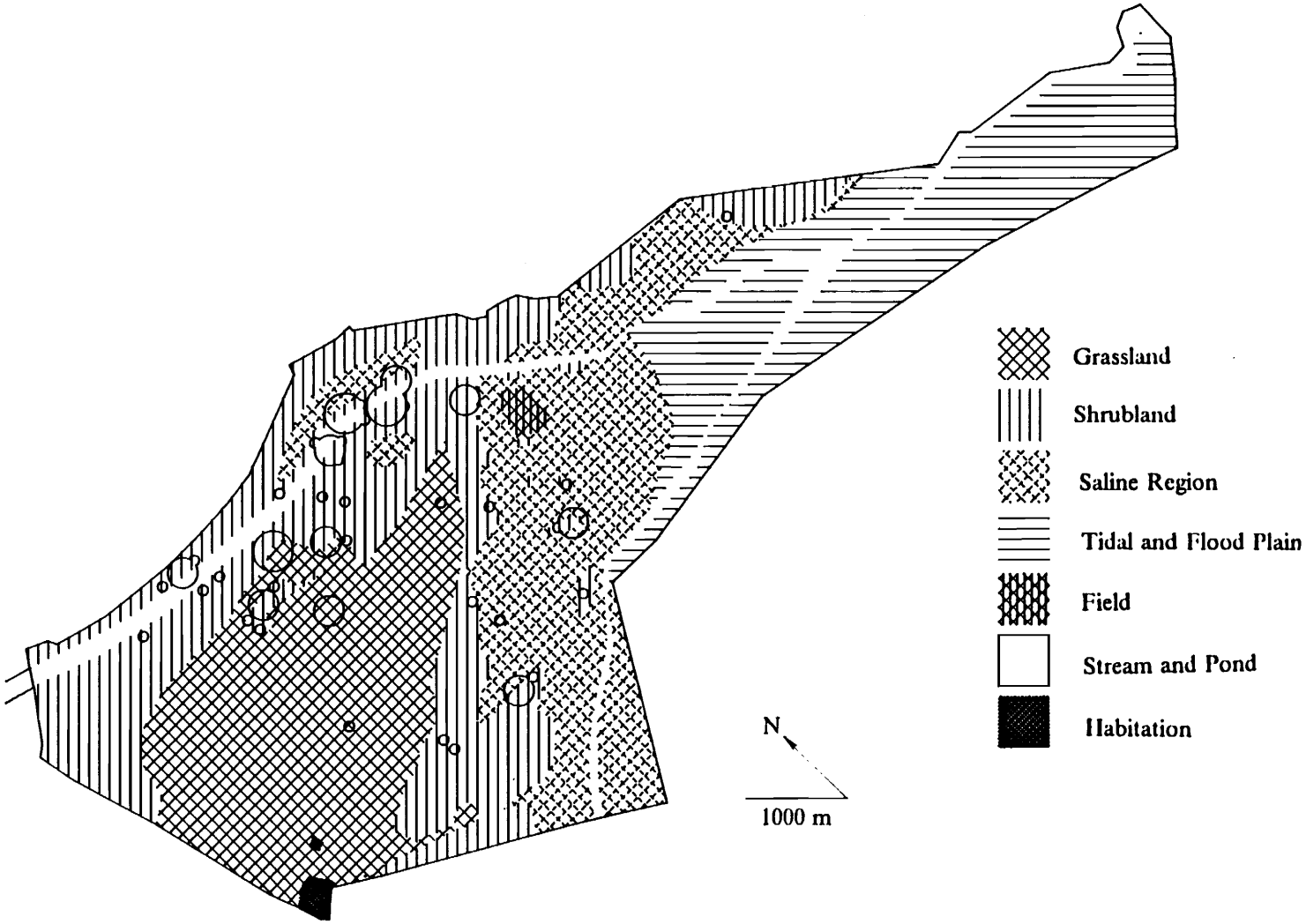


Fig. 13. Suggested wolf habitat management areas are marked. These are based on wolf observations during 1988 to 1990 in Velavadar National Park.

there is an optimal grazing pressure to maximize AGB production and nutritive quality of the grasses as suggested by McNaughton (1979a and 1979b) and the grasses at Velavadar could be "obligate grazophils". The impact of cattle grazing would depend on the rainfall (moisture content of the soil), grazing pressure and phenological stage of the grasses (McNaughton 1979a, 1979b, Sinclair 1975). Thus, in good rainfall years, cattle grazing would be beneficial for the blackbuck and the grassland, while in years of poor rainfall, cattle grazing could severely reduce the carrying capacity of the park for blackbuck. Harvesting would mimic grazing by reducing AGB, however, it may not have several beneficial effects of actual grazing on productivity (Detling 1988, McNaughton 1979b, Owen and Weigert 1976, 1982, Reardon et al. 1972, Stenseth 1978).

If grazing is allowed or grasses are harvested, either should be done just after the monsoon (October) prior to the flowering phase of the perennial grasses. This grazing and/or harvesting schedule would likely : (1) reduce trampling of young shoots in the soft mud by the heavy hoofs of buffalo, (2) promote new growth since the soil would still have high moisture content, (3) make the nutritive quality and AGB optimal for economics of harvest and storage, and (4) provide a new nutritive flush of grass in winter when the blackbuck are building up body reserves for the "resource lean" summer. Cattle grazing and harvest should be avoided in years of poor AGB production.

The model, when run with the least PAGB production coefficients in 12 years, exhausted its budget in purchasing forage and maintaining the grassland habitat. In such severe drought years, the park can support only 400 to 800 blackbuck (depending on the proportion of PAGB utilization) without forage being supplied. If the areas under the grassland, shrubland, and saline region are altered to 1,600 ha, 500 ha, and 425 ha respectively, then the park could support about 1,000 to 1,200 blackbuck at a 50% utilization of PAGB in a worst-case scenario.

Although the 99% lower bound on PAGB estimates forage production sufficient to meet the needs of over 2500 blackbuck, such high numbers of blackbuck were rarely attained in the 22 year history of the park. It seems more likely that the occurrence of severe droughts (as observed in 1986-87), even though infrequent, seem important in regulating blackbuck numbers in Velavadar National Park.

Prosopis pods could form a major portion of the blackbuck diet when available (see Food Habits under Results). *Prosopis* has a long tap root system and can obtain moisture from great depths (> 20 m) (Bokil and Rao unpub. data, Leakey and Last 1980, Muthana and Arora 1983). In drought years when grasses can no longer produce AGB with their shallow root system, *Prosopis* pods may form a very important energy and protein source for the blackbuck. Increasing the production and availability of *Prosopis* pods by managing *Prosopis* clumps would be a way to increase the carrying capacity of the park. All trees with a large canopy are ideal for : (1) producing mast, (2) offering shade to both wolves and blackbuck, and (3) allowing grass growth beneath them. Well distributed clumps of such trees should be spared while clearing shrubland, appropriately spaced vigorous stems selected, and all managed by trimming lateral branches.

CONCLUSIONS

The major contributions of this study towards achiving the objectives stated in chapter 1 are as follows:

(1) A regression model developed for predicting peak above-ground production from 2 years precipitation data is useful for estimating annual forage availability an estimate needed by managers. The regression model emphasizes the influence of the primary production during the past year on forage production in perennial grasslands. Most regressions for estimating production are developed using mean rainfall of the region. Though these models may predict mean production of a region reasonably accurately they do not have the fine resolution for estimating annual production. Above-ground production may fluctuate drastically about the mean in semi-arid grasslands. Management decisions need to be made on an annual scale. Thus the regression model developed answers the important question of "How much forage is available this year?"

(2) The forage quality fluctuates in an annual cyclical manner in Velavadar. The quality (as measured by crude protein content and digestibility) is high in the monsoon and extremely low in the summer (see Results). Blackbuck adapt to this situation by increasing their dry matter intake of good quality forage (in the monsoon and winter) and reducing intake in summer. Rumen fill and the rate of passage are the likely factors limiting intake of low quality forage in the summer. *Prosopis* pods comprised a significant portion of the blackbucks diet. Due to their high protein and sugar

content, their high digestibility, and availability when other forage quality is low, pods are an important source of food.

(3) The regression models developed to estimate forage quality (crude protein and digestibility) from fecal ether extract and fecal nitrogen now allow range managers to assess seasonal forage quality reasonably quickly and economically.

(4) Though blackbuck used shrublands for foraging, they relied primarily on the grasslands to obtain their food. Blackbuck were not observed to use the shrublands for lying down during the day or at night. No male territories were established in shrublands. Blackbuck prefer "open" habitats for all activities and use shrublands only for foraging.

(5) The major cause of blackbuck population fluctuations were natural calamities like floods and droughts. The population at Velavadar seems to take 4-5 years to recover from such population crashes. The mean carrying capacity of the blackbuck population at Velavadar National Park for the past 20 years is about 1,850 animals.

(6) The demographic characteristics of the Velavadar blackbuck population as estimated from census data, life table analysis, and probit analysis of adult deaths were as follows.

Sex ratio = 55 males : 100 females.

Reproductive rate R_o = 3.22

Mean generation time G = 5.31

Intrinsic rate of increase r_m = 0.22

Median age of adult death = 7.92

Standard deviation of adult death = 3.296.

(7) Shrublands were critical wolf habitat. Wolves used shrublands for visual cover and for shade. Cool moist areas with shade were important for rendezvous sites in the summer.

(8) Wolves relied primarily on blackbuck for food (88% of their diet). Rodents and hare were other important prey items.

(9) Wolves consumed on the average 7.38% of their body weight in food in a day. A daily intake of 1.328 kg of food/wolf was estimated. A ratio of 141 to 158 blackbuck to one wolf was considered essential to sustain a stable blackbuck population.

(10) The mean wolf pack size in Velavadar National Park was 6 wolves. Wolves denned and produced a litter in December and January. During the period from November to February disturbance in terms of tourism or management activities should be minimized in wolf habitats. The mean litter size was 5.5 pups and pup mortality was estimated at 28%.

(11) The optimization model developed here incorporates the major biological processes governing the grassland-blackbuck-wolf system. It considers the real economic limitations of the park budget. An objective function of maximizing the forage based carrying capacity for the blackbuck was developed. Prey and habitat needs of the wolves were incorporated as constraints. The feasible optimal solution obtained specifies: a) Maintaining grasslands free of *Prosopis*, b) the amount of shrubland areas to be cleared, c) the area of saline regions that are to be developed as shrublands, and d) the amount of surplus grass that needs to be harvested in years of good forage production. The model has shown that a stable wolf and blackbuck population can be achieved. However, management is essential to maintain these populations. The optimal allocation of resources done by the model is readily applicable to the current management of the park. The model is robust to the various assumptions, and is flexible for expansion and update. Concepts on the formulation of the objective function and the biological constraints incorporating risks involved in a shochastic environment and prey-predator ratios could be adapted to formulate similar management oriented models for other parks and preserves.

GENERAL DISCUSSION

Soil and Vegetation

The major part of the saline region of the park borders the tidal zone and appears to have resulted from flooding of the area during extremely high tides in recent times. The transition from shrubland and grassland to saline region is abrupt and distinct. There is scarcely a transition zone separating these habitats; a continuous undulating line invariably distinguishes where transition occurs. The above observations, along with high salinity (EC, Table 1) lend support to the hypothesis of tidal flooding.

Prosopis juliflora plantations are reported to improve saline soils by reducing pH and salinity, increasing OM, and by fixing nitrogen (Hoglund and Brock 1987, Metha 1983:172, Sharma 1984, Verma 1987, Yadav and Singh 1970). It was not possible to conduct an experiment *a priori* by estimating soil parameters before and after *Prosopis* establishment. Contrary to the above reports, pH and SAR values were significantly greater in the *Prosopis* shrubland than grassland and saline regions, while OM and EC values were intermediate. *Prosopis juliflora* has deep root systems (Leakey and Last 1980, Muthana and Arora 1983). Deep soil strata (> 1.3 m) in the Bhal region have high sodium content and the subsoil water has high SAR (Pathak, unpub. data). Deep-rooted

plants in semi-arid regions are reported to recycle cations and bring them to the surface (Brady 1990:226). *Prosopis juliflora* is considered to be salt tolerant (Leakey and Last 1980), and it is likely to take up salts and to have high tissue concentrations of Na^+ (Shrama 1984, Leakey and Last 1980). It seems likely that high pH and SAR recorded for shrublands are due to Na^+ recycling by *Prosopis*. A carefully designed study of soil characteristic at various depths before and after *Prosopis* plantation and growth, or sampling in different aged stands seems to be needed to provide a good understanding of the processes involved. Currently, data support the hypothesis that *Prosopis* is likely to increase pH and SAR, at least in a short time (3-8 years). On a longer time scale, soil pH and SAR are likely to drop with the accumulation of OM, with nitrogen fixation, and with leeching and drainage of salts as reported by Metha (1983:172). For soil improvement, a longer duration of *Prosopis* growth (> 10 years) at a site is desirable prior to cutting in Velavadar National Park.

Increasing the productivity of saline regions would result in an increase in the carrying capacity of the park. Reclamation of saline soils is extremely costly and labor intensive (Bradly 1990:247, Metha 1983). The optimization model recommends investing funds in this activity only after exhausting other management options (see Appendix 7 , and Results). Most of the saline habitat borders the tidal and flood plane (see Fig. 3). It is likely that tidal water might cover parts of the area during storms and cyclones. Thus saline areas away from tidal influence should be given priority for management. Besides certain halophytic species like *Suaeda* , *Aeluropis*, *Sporobolus coromandialis* and *Chloris*, other palatable grasses would take a long time to colonize these habitats (Shankarnarayan and Shankar 1984). A quick transition to grassland seems to be possible via encouraging transition through the shrubland habitat type. Appropriate treatment with gypsum, farm manure, and improving drainage (Brady 1990:247) would enhance shrub establishment. *Prosopis juliflora* and the endemic salt-tolerant *Salvadora* sp. could be encouraged. *Salvadora* would provide excellent cover and shade for wolf (pers. observation in other wolf habitat), browse for blackbuck, and fruit for avifauna. Grasses grow readily in areas where shrubs become established and where they are later removed. All species of grass found in Velavadar were observed to grow beneath *Prosopis*. Wind-blown branches of small bushy shrubs of *Prosopis* tend to sweep and shade the ground thereby preventing other plant growth (Muthana and Arora 1983). Once these shrubs

grow tall and the canopy is not too dense, grasses readily grow beneath them (Muthana and Arora 1983). *Prosopis* groves should thus be thinned to allow access to blackbuck and pruned to produce a tall canopy. Such "trees" are likely to yield more mast, better wood for charcoal, provide more shade and allow more grass growth than unpruned stands. A shrub rotation schedule (Duffey et al.1974) of 25 to 30 years for these clumps will tend to preserve them for their many benefits over the long run. During low-rainfall years and severe grazing pressure, grasses like *Dichanthium* survive and flower only in the thorny protective "bush" of young *Prosopis*. Such clumps may serve as an essential refuge for grasses to survive and to flower to produce seed for the next year.

Information obtained from older local people suggests that the coastal region once had flourishing mangrove forests. Research should be done on the historical composition of mangrove species that grew in the region. These should be planted in the tidal zone. Such plantations are likely to add to the faunal diversity of the park. They would also tend to block tidal flooding of saline regions and improve wolf habitat. Wolves are observed to use mangroves in other parts of Gujarat (Jhala, unpub. data).

Grasslands were observed to be extremely resilient to droughts. After a continuous drought for 3 years and heavy grazing pressure, several perennial grass swards were killed. During the early monsoon of 1988, the grasslands were dominated by species of unpalatable forbs (*Digera*, *Sida*, *Heliotropium*, *Rungia*, *Euphorbia* sp., and *Phyllanthus* sp.), and anunal grasses (*Dactyloctenium*, *Paspalum*, *Digitaria*, *Panicum*, *Brachiaria*, and *Urochloa* sp.). These species completed their life cycle within weeks to a few months. The perennial grasses (*Dichanthium*, *S. virginicus*, *S. madraspetansis*) were re-established from seeds and constituted the bulk of the biomass by the end of the monsoon of 1988, and the rest of the study period. It seems likely that occurrence of severe droughts gives forbs and annuals (the therophytes) an upper edge over dominant perennial species (cryptophytes) (Misra 1983). With reduced competition from perennials, these species would flourish and produce large amount of seeds during favorable periods after droughts. These species would survive by sheer magnitude of seed production during such periods and occasional establishment in normal years (Misra 1983). Droughts thus seem to help maintain the species diversity of the grasslands. For a study of species dynamics in the grasslands, a monthly sampling

schedule would be essential to record short-lived species during the monsoon. Such a study was not attempted due to time limitations and the importance of other objectives. Droughts may also serve to increase genetic variability in perennial species by reducing competition from asexually propagating established grass swards and by allowing establishment from sexually reproduced seeds. Velavadar National Park is arguably the only natural grassland preserve in Gujarat (Dharmakumarsinhji 1978). With increasing demand of land for agriculture and industry, and remnants of grazing lands deteriorating from overgrazing and erosion (Dunin 1987, Misra 1983, Oza 1986), Velavadar may be a critical source of genetic stock of endemic grasses in the future. Grasslands should be preserved in Velavadar, not only for the endangered fauna which depend on them, but also for their own merit.

Any form of plantation (exotic grasses or shrubs) should be avoided in the grassland habitat. Grassland habitat should be maintained by *Prosopis* eradication as suggested by the results of the optimization model. It is possible to distinguish 2 ecotypes of perennial grasses in heavily grazed and moderately grazed regions of the grassland. Short, prostrate, matted forms with flowering culms parallel to the ground are typical of grazed areas, while erect tussoks with thick fibrous bases are typical of ungrazed and moderately grazed areas (Ghosh et al. 1988). If such ecotypes are a result of genetic differences (McNaughton 1979b), then the total protection from grazing would, in the long run, eliminate these genotypes (obligate grasophils). Cattle grazing seems to facilitate foraging for blackbuck (Gwyne and Bell 1968, McNaughton 1976, Sinclair 1983) (see Results). Uncontrolled cattle grazing (cows and buffaloes) results in range deterioration (Misra 1983) as is evident on the grazing grounds of Velavadar as well as Bharbhil and Kanatalav villages. McNaughton (1979a, 1979b) suggested an optimal grazing pressure at 25% removal of green AGB to maximize above-ground net primary production (for the Serengeti ecosystem). Thus, controlled cattle grazing (in time, space and grazing pressure) (Detling 1988) is likely to benefit the ecosystem as a whole. Currently, though cattle grazing is illegal within the park, enforcement is difficult. Cattle do graze at varying intensities within the park, especially at night. Villagers later come and gather the dung for fuel. Dung collection should be totally prohibited since manure from dung is critical for lowering pH and improving alkali soils (Omaliko 1984). A study to test the hypothesis regarding cattle

grazing generated here is essential before management decisions are made. Exposure of select grassland areas to controlled grazing pressure at an appropriate season (late monsoon) (see Results) complimented with long term-exclosure studies should answer these questions conclusively.

The construction of a looped raised road in the grassland for tourists (see Fig. 3) has created a water-logged area. Less palatable species like *Ischimum*, *S. virginicus*, and *Fimbristylis* are encouraged due to water logging. By controlling drainage from this region, it would be possible to favor palatable species like *Dichanthium*. In years of low rainfall, drainage should be blocked to prevent runoff and increase soil moisture thereby encouraging green growth well into winter. In years of heavy rainfall, good drainage should prevent tall fibrous species from becoming dominant.

Rainfall and Above-Ground Production

The regression model with 2 years of rainfall explaining 97.2% of the variability in PAGB suggests the simplicity of mechanisms involved in the production of the grassland ecosystem in semiarid regions and the extreme dependence of such lands on precipitation. A regression model using a squared function of previous years rainfall (x_1) including an interaction term (x_1x_2) and a log transformation on PAGB (y) was significant ($p = 0.0152$) and gave a better fit $R^2 = 0.9999$ adjusted $R^2 = 0.999$. The regression coefficients were :

$\log \text{PAGB} = 2.26 (\pm 0.05) + 586 \times 10^{-8} (\pm 19 \times 10^{-8}) x_1^2 + 5.545 \times 10^{-3} (\pm 0.1 \times 10^{-3}) - 4.049 \times 10^{-6} (\pm 0.27 \times 10^{-6}) x_1 x_2$

Due to a small sample size (5), transformation may be unwarranted and the simpler model was preferred for predicting PAGB (see Results). If future studies in Velavadar yield data on PAGB, it would be possible to validate either of the models developed here. As PAGB values reflect net above ground primary production (Mitchell 1983), similar models could be developed to predict primary production in semiarid grasslands. The regression models developed here would be

appropriate for predicting PAGB of herbaceous vegetation in shrubland habitats and saline regions. The coefficients of the models would differ due to difference in species composition and total AGB production in these habitats.

Shrub Management

Historically, the Bhal region has been a mosaic of agricultural fields, grazing grasslands, saline wastelands, and marshes mostly devoid of trees (Dharmakumarsinhji 1978). Occasional stunted *Acacia nilotica*, *A. arabica*, and *Salvadora* bushes managed to survive. Shrubs like *Tamerix* and mangrove species grew in rivulets and tidal zones. Wolves have always been a part of the ecosystem in the Bhal, and the region is still a major stronghold for the species in Gujarat (Jhala and Giles 1991). The advent of *Prosopis juliflora* and consequent availability of thick cover has been a recent development (about 40 years). This would lend one to believe that cover may not be a critical requirement for wolves. The Bhal region was devoid of metalled roads just 2 decades ago. There were vast areas of "waste land" and grazing lands which are currently agricultural fields with intense human activity. Wolves were observed to use scant cover in the form of 1-2 shrubs of *Prosopis* provided that the area was remote with no human activity within view. Such areas are now rare around Velavadar National Park and the Bhal in general. Management activity within the park is also currently a source of disturbance to wolves. Wolves use areas near human activities only when thick cover intervenes. With increased road density (Mech et al. 1988, Mech 1989) and human presence, wolves are unlikely to use an area having only the shade of a few shrubs with no visual cover. The estimates for minimum wolf cover needs (see Results) should always be provided within the park as habitat outside the park is rapidly deteriorating. Management activities, tourism, or other human presence should not be allowed near the denning areas. Such protection is essential since wolves are extremely shy and likely to abandon a den if they are disturbed often. The practice

of chasing wolves from kills, when sighted by park staff, or by tourists should be prohibited. Wolves are likely to get accustomed to human presence once they are not persecuted. Tourism could then (and only then) be encouraged (carefully) to rendezvous sites and dens. Viewing from hides and by telescope may enable, with great care, the human use of this endangered resource.

If total eradication of *Prosopis juliflora* is ever desired, an appropriate area with endemic shrub species (*Salvadora, Acacia, Ziziphus* sp., etc.) should be developed for wolf habitat prior to total *Prosopis* removal.

Extremely thick growth of *Prosopis* is undesirable since such areas are not used by wolves or blackbuck. Tall trees with large canopies should be spared to provide shade and pods. Such trees would also serve as roosts for a variety of raptors like Eastern steppe eagle (*Aquila rapax nipalensis*), emperial eagle (*Aquila heliaca*), short-toed eagle (*Circaetus gallicus*), kesterel (*Falco tinnunculus*), blacked-winged kite (*Elanus caeruleus*) and harriers (*Circus cyaneus, C. macrourus, C. pygargus, C.aeruginosus*) which use the park at different times of the year. An increase in the short grassland would also benefit the endangered lesser florican which breeds here. The endangered haubora bustard utilizes saline habitats with *Suaeda* and *Chloris* as dominants. Thus such habitats should not be totally converted to shrublands. About 2000 harriers and 300 to 500 white storks (*Ciconia ciconia*) use the grasslands in winter for foraging and roosting (harriers). Hundreds of common cranes (*Grus grus*) and demoiselle cranes (*Anthropoides virgo*) visit in winter and utilize the saline region and tidal zones for roosting. Sarus cranes (*Grus antigone*) nest in water-logged grassland which turn into swamps. Flamingoes (*Phoenicopterus roseus*), painted storks (*Mycteria leucocephala*), spoonbills (*Platalea leucorodia*) and gray herons (*Ardea cinerea*) feed in the tidal zone. All habitat types found in Velavadar National Park are used by at least some species. Habitat management should be done, keeping all these species in perspective. The model in its current formulation caters to the blackbuck and wolf needs; habitat needs of the other fauna are not formally incorporated. If future research provides estimates for these parameters for the minimum habitat needs of these species, then the model could be expanded to incorporate them in the optimization process. Since models are, in essence, abstractions of reality and could not possibly include all the components and processes of ecosystems; they should not be followed blindly, but

instead used as guidelines to rationalize decisions. According to Jeffers (1978): "Any tendency to regard (mathematical programming) as an alternative to clear thinking ought to be condemned." The current formulation of the model allows the manager to preserve critical areas in their unaltered state by providing sufficient flexibility in choosing areas for active habitat manipulation.

Forage Quantity, Quality, and Food Habits of Blackbuck

A profound seasonality is observed in forage availability for temperate ungulates. During favorable seasons, a plethora of good quality and quantity of food is available (Geist 1974, Jordan 1971). Temperate ungulates adapt to this situation by lipogeneis and fat storage which are consequently used to survive the resource-lean winter (Kirkpatrick 1988, Mautz 1978, Moen 1978). It is generally believed that in the tropics, forage production does not fluctuate as severely as it does in cold regions (Giest 1974). Tropical forages are considered to have lower caloric density than temperate and arctic forages (Jordan 1971). The situation in Velavadar conforms to the above pattern to some extent but has some major differences. Not only is the quality of the forage comparatively much lower than temperate forages but there is also a marked seasonality in both quality and quantity of forage availability. Most studies of tropical ungulate grassland systems have focused on the African scenario (Coughenour 1985, Coughenour et al. 1985, Edroma 1989, Gwyne and Bell 1968, McNaughton 1976, 1979b, 1983, 1984, 1985, 1986, 1989, Sinclair 1975, 1977, 1979, Wallace et al. 1984, 1985). The Bhal grasslands systems are remarkably similar, but they have one major difference. The East African savannas receive precipitation in 2 wet seasons (November to January and March to May) thus the longest dry spell is about 6 months (Sincair 1979b). Contrary to this situation, there is a single wet season (monsoon, mid June to early September) with a dry spell for nearly 9 months in Velavadar. Green grasses are preferred by ungulates to mature and dry forages since they have higher digestibility and nutritive quality (Aflayan and Fafunsho 1978,

Dulphy et al. 1980, Gupta 1985, Schwartz and Hobbs 1985, Sinclair 1975, 1977:78-79, Thakur et al. 1985). In the non-growing season, in grasslands, there is a general tendency for proteins and carbohydrates to be transported from above the ground plant parts to the roots (Hanks 1981). Crude proteins values of the Serengeti grasses have been observed to have low values similar to those recorded in Velavadar (Sinclair 1975). Wildebeest in Serengeti managed to maintain an intake of forage with 4% crude protein (Sinclair 1975) while dry matter digestibility dropped to 40% in the dry season (Sinclair 1975). Even though blackbuck are probably more selective grazers than widlebeest, they could maintain CP intake of only 3.63% (SE 0.13) in summer and the dry matter digestibility was as low as 31.95% (SE 4.85) in summer in Velavadar National Park. Thus it appears that blackbuck are subjected to lower quality forages than Serengeti ungulates and for a much longer duration (9 month dry season compared to 6 month). Body "reserves" of energy and proteins would seem to play a more vital role in blackbuck than in other tropical ungulates. Though there is sufficient forage available (quantity) for most years, the quality (digestibility and CP) drops below the minimum amount necessary to maintain body condition. With low CP intake as well as low digestibility in summer, it is likely that proteins may be more limiting than energy (Sinclair 1975). There is strong evidence to suggest that catabolism of body proteins may play a critical role in providing energy and maintaining ruminal flora by urea recycling through the rumen in summer (Jhala et al. 1991, Owen-Smith 1982, Riss 1983, Robbins et al. 1974, Swick and Benevenga 1977). A study on protein metabolism and turnover rates (Garrett and Johnson 1983, Macrae and Lobley 1986, Waterlow 1984, White et al. 1988) would be essential to understand the physiological mechanisms involved in coping with such low protein and energy intakes and the levels at which they may become critical for survival. Among temperate ungulates, the physiological mechanisms for adjusting forage intake to seasonal forage quality are well known (Moen 1978). These include changes in ruminal volume (Milne et al. 1978, Suttie et al. 1983), decreasing metabolism, and increasing insulation of pelage (Mautz 1978). A cyclic nature of DMI is observed among tropical ungulates accompanied with cyclical changes in body condition (Sinclair 1977:183-192, Stanley Price 1977, 1978). Drop in dry matter intake and body condition in dry season among tropical ungulates is usually explained by low quality of the forage (Dunbar 1979, Kay et al. 1980, Sinclair

1975). It also seems likely that blackbuck and other tropical ungulates may have evolved physiological mechanisms that reduce voluntary DMI and metabolism in summer (Ghosh et al. 1987, Jhala et al. 1991, Kay et al. 1980, Stanley Price 1977, 1978, 1985) as a response to avoid excess loss of body proteins that results from ingesting such low quality diets.

Even though in most years forage quantity seems to meet the needs of blackbuck, the Bhal region is prone to droughts (Dharmakumarsinhji 1978). During severe droughts, there is hardly any above-ground biomass production and the blackbuck are maintained by stall feeding. In the past, the Bhal region was known for its large blackbuck population (Dharmakumersinhji 1978). It is likely that there were large migrations of blackbuck in search for forage and water in years of drought (Rogers 1988). During the 1987 drought, several blackbuck emigrated and established new populations. Large migrations of blackbuck are not possible today due to habitat discontinuity, habitat deterioration (Oza 1986, Oza and Gaekwad 1973), and poaching of dispersed blackbuck. In years of extreme drought, there seems to be no other alternative than stall feeding. With 2 years of poor rainfall and a third year drought (1985, 1986, 1987), Velavadar grassland seemed to have deteriorated due to heavy grazing in the summer of 1988. With consequent good rainfall (1988, 1989) the grassland showed great resilience with no sign of any trends in vegetation (Walker and Noy-Meir 1982). This suggests that this system has evolved under conditions of droughts and heavy grazing pressure. Severe droughts would reduce blackbuck numbers under natural conditions and may be a requisite for re-establishing perennial grasses from seeds. Stall feeding is likely to prevent reduction in blackbuck numbers on the range. However this may lead to range deterioration. An increase in browse species like *Acassia nilotica*, *A. arabica*, *Salvadora*, and *Ziziphus* sp. would provide forage in drought years due to their deep taproot systems. Due to limited foraging area and inability of blackbuck to migrate, it seems likely that *Prosopis* pods may have become critical for providing essential proteins and energy. Rumen contents of wolf killed-blackbuck in the summer of 1988 contained a large number of *Prosopis* seeds, suggesting the importance of pods in drought years to blackbuck as also observed in other blackbuck areas (Goyal et al. 1988).

Blackbuck Population

There seems to be a "stable equilibrium" for the blackbuck population of Velavadar National Park at around 1,850 animals (see Fig. 6 and Results). The question of why the blackbuck population does not increase beyond the numbers observed in the past 20 years needs to be answered. Several factors can be considered to have a "regulatory" role on the blackbuck population, or rather several processes would presumably be respossible for an equilibrium (Caughley 1981b), in the Velavadar ecosystem.

Social factors

Temperate ungulates, in general, are not considered to be socially regulated; rather, they appear to be regulated by a nutritional carrying capacity dictated by their habitat (Caughley 1970, 1981a, 1981b, Keith 1974). Social factors among temperate and tropical ungulates are likely to cause dispersal of certain age classes or to increase the vulnerability of others to predation (Estes 1974, Flook 1970, Jarman and Jarman 1974, Sinclair 1971, 1977:129). Among blackbuck, as in other ungulates, it is only the subadult males that disperse to "marginal habitats" and again only adult males may be experiencing great predation during rutting season. Thus, though these social factors may act to reduce male numbers and skew the sex ratio, they would not be regulatory since the female population and recruitment would not be affected.

Wolf predation

Based on Keith's (1983) model and using 39 blackbuck killed per wolf per year, the blackbuck-to-wolf ratio necessary to archive a stable equilibrium was computed to be 159

blackbuck per wolf (see Results). The number of 39 blackbuck killed per wolf per year was computed from 2 years of field data. During this time blackbuck contributed 88% to the biomass consumption by wolves. However, in 1988, predation on blackbuck was greater, and they contributed about 95% to the biomass consumption by wolves probably due to the scarcity of alternate prey (hare and rodents). This would correspond to 42 blackbuck killed per wolf per year. Wolves were also observed to kill more than 1 blackbuck in 1 night and eat only preferred portions from the kill (on 3 occasions). During drought years when blackbuck vulnerability to predation increases due to poor body conditions, and availability of alternate prey for wolves is low, it seems likely that the number of blackbuck killed per wolf would increase. On recomputing the blackbuck-to-wolf ratio (with 42 blackbuck killed per wolf), 171 blackbuck per wolf seem essential to maintain a stable blackbuck population. For a pack of 6 wolves a population of 1,026 blackbuck would be essential. If the wolf numbers in the pack increased to 10 (a number quite likely to be reached, see Results) a population of 1,710 blackbuck would be required. This number is that of a population quite close to the historical "carrying capacity" of the park. Though previous studies in Velavadar National Park considered the wolves to be occasional visitors and wolf predation as rare events (Mungall et al. 1981, 1983, Ranjitsinh 1982:110-112), wolves have always been present in the Bhal region (Nirmalkumarsinhji pers. comm. also Ranjitsinh 1982:26). Local villagers have several stories and myths about wolves killing cattle, livestock, and even people. Unless there were specific attempts to look for evidence, it is likely that wolf predation on blackbuck could be easily over-looked due to the wolves nocturnal habit and secretive nature. It is also possible that the wolf territory established in Velavadar National Park may be a "recent" development, since wolves were probably likely exterminated locally in the Velavadar area during the 1960's (Ranjitsinh 1982:26). It seems possible that though wolf predation was historically present on blackbuck populations in the Bhal, the Velavadar population may have not experienced it regularly in the "recent" past (Ranjitsinh 1982:110-112, Mungall et al. 1983).

The wolf-to-blackbuck ratios during the study period were close to the numbers derived from the model for stable equilibrium. The similarity suggests that wolf predation may be able to control the blackbuck population under certain situations. The fact that the blackbuck population

continued to increase throughout the study period shows lack of control during these years. However, wolf predation would definitely slow the rate increase. Predation by jackals and pariah dogs on fawns and adult blackbuck would augment predation by wolves.

Climate

Velavadar National Park is prone to floods and droughts (Dharmakumarsinhji 1978, Rashid 1977). Due to the lower elevation of the park than its surroundings, the area is prone to flooding. In 1976 and 1982 cyclones struck the coast of Saurashtra. The accompanying rain and flooding caused the death of at least 923 blackbuck in 1976 (Dharmakumarsinhji 1978, Rashid 1977) and over 350 blackbuck in 1982. The low rainfall of 1985, 1986 and the drought in 1987 reduced the blackbuck population by 1,300 (by 59%). It seems possible that frequent occurrence of such floods and droughts could maintain a population within limits (Anderwartha and Birch 1954:655-656). Natural calamities like droughts and floods certainly explained the drastic fluctuations observed in the blackbuck population (Fig. 6). However, Fig. 6 suggests evidence for a density dependent regulatory process which would reduce survival and/or recruitment to the population at higher densities (Keith 1974).

The simulation model, though not consonent with the biological processes, serves a useful predictive purpose (Caughley 1981a). The model incorporates the likely limits and the stochastic nature of the schedules of survival and fecundity at Velavadar National Park. However it does not incorporate catastrophic mortality. Though the population is predicted to fluctuate within limits (Fig. 9), the major cause of these drastic fluctuations seen in the natural population (Fig. 6) was a result of these catastrophic deaths. Droughts and floods seem to be acting similar to severe winter kills in Texas (Mungall 1978). These factors would preclude a population from maintaining and/or attaining a stable age distribution and a equilibrium with its biotic and abiotic environment.

Nutritional Factors

Water-driven, semi-arid grassland ungulate systems are less predictable than temperate systems (Caughley 1981b) and cannot be modeled as a simple "prey-predator" relationship (Caughley 1976). Complex interactions like grazing optimization, (McNaughton 1979, 1983, 1989) and possible coevolution (Coughnour 1985, Detling et al. 1986, Owen and Wiegert 1976, 1982) further complicate the issue. It seems likely that given the stochasticity of semi-arid grassland systems and their extreme resilience (Laws 1981), vegetation and ungulates would not show the typical oscillations seen in temperate systems. The Velavadar region was known to support a much larger population of blackbuck in the past than has ever been achieved since the creation of the preserve (Dharmakumarsinhji 1978). The prime grassland area of the late Maharaja's private grazing grounds which supported the highest concentration of blackbuck are now converted to agricultural fields (Nirmalkumarsinhji pers. comm., Shivbhadrasinhji pers. comm.). The remaining grassland area is further reduced by *Prosopis* encroachment. Thus reduction in grassland area seems to be the major cause of a low blackbuck population when it is compared to the population of the pre-independence era (1947).

The majority of the grazing activity (60%) by blackbuck was observed in the grassland habitat. Before the introduction of *Prosopis*, grasslands would have been the most critical habitat in which to procure forage, especially in years of low rainfall. It seems possible that due to the extremely low quality of forage in summer in Velavadar, blackbuck would have to be highly selective in feeding to obtain adequate intake of nutrients. Due to a limited area available for grazing and a continuous grazing pressure, a point would be reached where selective feeding would have reduced the density of palatable forage to such low levels so as to make its consumption "unprofitable" (Hanks 1981).

Such situations seem to occur annually in summer. The negative digestibilities of CP and extremely low digestibilities of dry matter and GE in summer of 1988 and 1989 lend support to the above hypothesis. In average and poor rainfall years, this annual nutritional "bottle neck" would

be more severe than in the study period. Only blackbuck in good condition with appropriate body reserves are likely to survive and reproduce, while others would succumb to predation and other causes of mortality (Hanks 1981, Sinclair 1975).

Due to a limited area for foraging (blackbuck do graze in the surrounding agricultural fields, but in summer the crops are harvested, and the grazing condition is poorer than within the park) the nutritional factors seems to act in a density-dependent manner. The greater the grazing pressure (from a larger population) the lower the food availability to an individual blackbuck. The equilibrium would be determined by forage production and quality, available area and grazing pressure. At the equilibrium, theoretically, recruitment and emigration would equal mortality and immigration. Due to the stochastic nature of forage production, the equilibrium would be a dynamic one and the population would fluctuate about the mean. Considering 1,850 blackbuck to be near the equilibrium for the current area of Velavadar National Park (Fig. 6) (density of 0.73 blackbuck/ha of habitats used by blackbuck, i.e., grasslands, shrublands and saline regions) and presuming that the proportional grazing activity in each habitat represents proportional forage provided by that habitat (Table 9), then the grassland would account for 60% of the forage, shrubland 21%, and saline regions 19%. Further, assuming for the sake of analysis that these proportions also represent proportional contribution of nutrients, then, the grassland habitat alone would support population of 1,110 blackbuck, the shrubland would support 389 blackbuck and the saline region would support 352 blackbuck. Considering the current areas in the grassland, shrubland and saline regions to be 805, 935, and 785 ha respectively (Table 2), the equilibrium blackbuck densities work out to be 1.4 blackbuck/ha grassland, 0.42 blackbuck/ha shrubland and 0.46 blackbuck/ha saline region. During the study period, due to sufficient rains, there was ample forage production in the saline region and the *Prosopis* pod crop had failed due to heavy grasshopper infestation. Thus the density estimates of saline region are likely to be overestimates while grassland and shrubland densities would be underestimates.

In view of the above discussion, 2 major factors seem to limit blackbuck numbers in Velavadar. These are; limited area of grassland for grazing and extreme low quality nutritional bottlenecks during some years. To increase the blackbuck population beyond the current

equilibrium point to a higher equilibrium (Sinclair 1981, Walker 1982) it would be essential (1) to increase the area of the park (foraging area), and/or (2) to increase production of forage having high nutrient density which would be available to the blackbuck when the grass nutrient quality drops (summer).

The first alternative could be achieved by increasing the total area of the park. This would be extremely desirable, since this would benefit not only the blackbuck but also the wolves and other fauna. "Wasteland" and grazing grounds towards Gokulpara and Mevasa villages south of the park are continuous with the park boundaries and have no agricultural fields. This area harbors a substantial blackbuck population and is often used by wolves. Due to uncontrolled grazing by livestock and trampling by buffaloes, the area is severely degraded (Ghosh et al. 1988). The area should be given the status of a sanctuary. Such a status would allow livestock grazing, while livestock numbers, season, and area grazed could be controlled by the range manager (Heady 1986). Addition of the area to the park is likely to improve the range to benefit both wildlife and the local villagers (Njoka 1986). One agricultural field (about 15 ha) is within the the boundries of the park (see Fig. 3). The field is not productive due to the saline soils and crop damage caused by blackbuck. The farming activities and access roads are a major source of disturbance to the wildlife (wolves use nearby areas as a rendezvous site). The area needs to be accquired by paying appropriate compensation costs and be made a part of the park. The land owners are willing to sell the land due to conflicts with the wildlife and park authorities.

Another simultaneous approach would be to convert saline region and shrubland habitat to grasslands as done with the optimization model. The management of *Prosopis* trees and groves would produce more mast and permit accessibility to blackbuck. Plantation can be made of indigenous browse species (*Acacia nilotica*, *Salvadora* spp.) and managing the grasslands by controlling (1) livestock grazing, (2) harvesting grass and (3) controlling drainage (already discussed earlier) would increase the density of nutritious forage and shift the equilibrium to a greater population (Sinclair 1973, 1981, Walker 1981, Walker and Noy-Meir 1982).

In reality, climate, predation and nutritional factors act in synchrony to maintain the population in a dynamic equilibrium. Though these factors have been discussed separately, for the

sake of simplicity in understanding, it is not likely that any single factor alone is responsible for regulation. The interaction of the blackbuck population with any of these factors would be different in time and space. Thus, predation would act to regulate blackbuck populations during conditions of population lows and when the population reacts to the environment with a low rate of increase. However, predation may not be regulatory at the same low density if there is good food availability and the population reacts with a large rate of increase. Thus a single factor like predation would act differently under different conditions of nutrition and climate. The same argument is applicable to the other factors discussed. The existence of multiple equilibria (Sinclair 1981) is possible for the Velavadar ecosystem. During population crashes due to climatic catastrophes, predation may take the regulatory role at low population. At higher population densities, nutritional factors would be regulatory (Sinclair 1981). If *Prosopis* is not managed, it would so invade the grasslands that they will be converted shrublands and the blackbuck population will be forced to lower numbers at another equilibrium. At this new equilibrium the blackbuck population may be stable or unstable depending on other factors like predation, disease, and natural calamities (Walker 1981, Walker and Noy-Meir 1982).

Wolf Food Habits, Population, and Conservation

The Velavadar wolf pack subsists almost exclusively on wild prey (Tables 21, 22), a rare case for wolves in India (Shahi 1982). With blackbuck composing 75 to 95% of the wolves diet and blackbuck-wolf ratios capable of approaching low levels, it is likely that wolf predation could control the blackbuck population (Bergrud and Ballard 1988, 1989, Fuller 1989, Gasaway et al. 1983, Keith 1983, Mech 1970, Pimlott 1967). In a case like the one under study in which (1) the predator (the wolf) and the prey (the blackbuck) are both endangered (Saharia 1981), (2) the predator is probably capable of reducing prey numbers substantially, and (3) the system is

maintained by human inputs, then serious thought needs to be given to management decisions. When the blackbuck population is at the nutritional equilibrium, wolf predation is likely to be compensatory (Theberge and Gauthier 1985) and would serve a useful function, i.e., "the sanitation effect" (Mech 1970:265). However when the blackbuck population is low and blackbuck-to-wolf ratio below 142 blackbuck/wolf (about 3,692 kg of prey/wolf), it is likely that wolf predation would be noncompensatory and the blackbuck population could be controlled by wolves.

There is strong evidence for social regulation among wolf populations of North America at densities dictated ultimately by prey availability (Fritts and Mech 1981, Fuller 1989a, Packard and Mech 1980, Packard et al. 1983). Wolf predation alone has not been responsible for rapid declines in ungulate numbers on any mainland ecosystems (Connolly 1978, Cowan 1979, Mech and Karns 1977, Raush and Hinman 1977). Pack size and territory size are regulated by mean prey size and prey density (McNaab 1983, Moehlman 1989, Nudds 1978, Walthers et al. 1981). It seems likely that due to the small size of the major prey (blackbuck, mean weight in the population being 26 kg) pack size in Velavadar would not increase substantially beyond that observed during the study period. Due to the small size of Velavadar National Park (34 sq km.) it seems unlikely that more than 2 packs would use the area simultaneously. Additionally there is little alternate prey available in the region to sustain high density of wolves at periods when the blackbuck population is low (due to droughts or floods). Thus wolf predation should not be considered a potential threat to blackbuck survival in the region.

The Velavadar pack was identified as different from the Chikotra and Mithapur packs due to numbers of wolves in the pack, presence of 2 or 3 identifiable wolves, sex composition of pack members, and differences in food habits as observed from remains in scats. Mech (1970:166) discussed the biases involved in using these criteria to distinguish between packs. However, in absence of capture marking or a radiotelemetry study, more reliable data were difficult to obtain. Relatively few scats were collected from the Chikotara and Mithapur packs (n = 72) and 68% of these had remains of domestic livestock. Blackbuck populations in these regions were very low compared to Velavadar. Most wolves in Gujarat and Rajasthan subsist on domestic livestock generating human-wolf conflicts (Jhala and Giles 1991). Packs like the Velavadar pack are a rarity.

It is unlikely that protecting and preserving single packs like these would save the wolf, though it would be one of the primary steps to a National conservation strategy (Jhala and Giles 1991). Problems of inbreeding (Laikre 1991, Wayne et al. 1991) are unlikely to arise due to the wolf's dispersal ability (Mech 1987) and an almost continuous distribution of wolves in Saurashtra and parts of Rajasthan (Jhala and Giles 1991).

The home range estimate of the Velavadar pack was made primarily by following the wolves from kill locations, sightings at night, and inferences from track observations. Besides the inherent biases involved in these crude estimates, it is likely that the area covered outside the park could be an underestimate since:

1) Most wolf kills were located within the park, and wolves with full stomachs would probably be disinclined to travel large distances,

2) Wolves could not be followed at night, during which time they were most active, and

3) Wolves were not located for several days, especially in the monsoon. During this time they were likely to be using areas outside the park.

The Velavadar pack is believed to be a typical wolf pack though it is not a true representative of the majority of wolf populations in India. It is rather a close representation of a pristine natural population. Detailed study of wolf biology in areas like Velavadar where wolves subsist on natural prey and in other areas where the primary prey are domestic livestock are essential to answer questions on home range, dispersal, survival and habitat needs. These are the minimum essentials for a recovery plan.

Wolf Interaction with Dogs

Pariah dogs are common in Velavadar National Park and were considered as the major predators on blackbuck (Mungall et al. 1981, 1983, Ranjitsinh 1982, 1989). These dogs live in the surrounding villages, come into the park mostly during the daytime and course blackbuck. The dogs

hunt individually or in packs and are successful in killing fawns as well as adult blackbuck. Ranjitsinh (1982:112) believed dogs to be responsible for killing 2 to 3 fawns per day during peak fawning periods. During the course of this study, 23 dogs were shot within the park. Of 48 fresh (adult) blackbuck carcasses examined, 2 were dog kills. Dogs are prolific breeders and there is a continuous "supply" from the surrounding villages.

Occurrence of dog hair in wolf scats suggests that wolves did prey on dogs as also reported by Fritts and Paul (1989). In Velavadar, dogs are not an important prey item for wolves and composed about 1.22% of the wolf's diet. In March 1989, a large male dog carcass was discovered partly consumed by wolves at their first rendezvous site. The dog had apparently been killed by a bite at the base of the skull. Three dog wolf interactions were observed during the course of this study. The following descriptions are from my field notes.

April 22, 1988, (6:45 am:) 5 wolves were spotted in the grassland near the Machhan trotting towards the shrubland across the main road. On looking in the direction from where they had come, 3 jackals were seen waiting 25 m from a male blackbuck carcass on which a wolf was still feeding. ***(6:55 am:)*** The 5 wolves crossed the main road and entered the *Prosopis* shrub on the eastern side of the park towards the Hanuman deri. One defecated near a milestone on the road. The sixth wolf, a subadult male, continued feeding. The 3 jackals occasionally "played" by pouncing on one another but kept a distance of 15-20 m from the wolf and the carcass. ***(7 am)***: A large bay-colored male dog was seen approaching the carcass from the side of the Velavadar village. The dog continued towards the wolf and the blackbuck carcass without hesitation. When the dog was within 20 m from the wolf, the wolf stopped feeding and looked up towards the dog. The dog slowed down to a slow walk but still continued to approach. The wolf took a small bite from the carcass, hesitated, turned and trotted off in the direction of the pack. ***(7:05 am)***: The jackals approached within 5-6 m of the carcass as the dog started to feed. ***(7:10 am)***: I approached the kill. The jackals ran off initially but stopped and lay down at a distance of 85 m from me and the kill. The wolf crossed into the *Prosopis* about 500 m away from the spot where the pack had entered the shrubland. The dog circled around at about 10-25 m despite my efforts to chase him off while I collected samples and data from the kill remains. ***(7:25 am)***: I left the carcass; the dog and the jackals closed in. ***(9:30 am)***: I returned

to the kill location. Two Egyptian vultures and 1 white-backed vulture were gleaning the hide and bones for meat remnants.

August 9, 1989, (6:20 pm): I was riding past the rendezvous site which the wolves had been using for the past 2 weeks. The rendezvous site was in and around a patch of *Prosopis* in the saline region on the Eastern part of the park. A black-and-white-colored dog was seen 60 m away, behaving in an unusual manner. The dog would run a short distance, circle back, and prance about apparently "playing". I dismounted and, using the mare and shrubs as cover, approached within 35 m. The dog was "playing" with 2 wolf pups. The pups were "quizzically" watching the dog, with ears erect and sitting on their haunches. The "play" continued with the pups as "interested" onlookers for about 4-5 minutes. A big wolf ("the baby sitter") approached from the *Prosopis* thicket 15 m away. The dog stopped, looked at the wolf, walked up to a dry *Prosopis* stump and did a raised leg urination on it. Without looking back, it then trotted away in the direction of Bharbhil village. The wolf walked up to the stump, sniffed the dog's urine, and performed a raised leg urination on it. The (adult male) wolf then approached the pups and the 3 of them dozed off lying down in the grasses***(6:45 pm)***.

February 2, 1990, (Observations from the hide) (5:30 pm) : The alpha female was sleeping in the shade of a *Prosopis* tree 25 m away from the den entrance. The adult male "helper" was resting at the edge of the shrubland 80 m from the den.***(5:38 pm)*** : A brown dog was observed trotting towards Kanatalav village. It crossed a saline patch out of view of the wolves. ***(5:42 pm)*** : The dog entered a shrubland thicket and disappeared from my view. ***(5:48 pm)*** : The male wolf suddenly got up and rushed in the direction the dog was travelling. The alpha female got up and followed the male wolf within seconds. Loud growls, barks and yips were heard from the direction (hidden from my view by *Prosopis* shrubs). The encounter was taking place in the saline region where the dog must have reemerged from the shrubs in direct view of the wolves. The commotion lasted for about 2 minutes. ***(5:58 pm)*** : The alpha female was seen returning to the den.

From the above account it is apparent that wolves and dogs interact quite frequently. Dogs may act as serious competitors for wolves due to their habit of preying on fawns and blackbuck and the consequent predation pressure due to their sheer numbers. Dog numbers are unlikely to vary

with prey abundance as they subsist off human settlements. In periods when prey is low, dogs may pose a serious threat to wolves and blackbuck. Dogs and wolves are known to hybridize in the wild especially when wolf densities approach low levels (Bibikov 1982, Boitani 1982, Mech 1970:28, Mendelssohn 1982, Young and Goldman 1944). At present it is not known if such matings occur with Indian wolves in the wild. In several areas of the wolf's range, wolf density is quite low (Jhala and Giles 1991). Because of the abundance of pariah dogs, likelihood of hybridization does exist. A subadult male wolf that died during the course of the study was suspected to have distemper. Dogs can act as carriers of canine diseases like rabies, distemper, canine parvovirus, lyme disease, and canine hepatitis to which wolves would be susceptible (Goyal et al. 1986, Mech 1970:311-314, Peterson pers. comm.). It seems essential to eliminate all dogs whenever they are encountered within the park for the benefit of both wolves and blackbuck. It is not possible to solve the dog problem at its roots since villagers would object to dog eradication within the villages. A poisoning campaign attempt by the park authorities failed due to local opposition (Majethia pers. comm.).

Wolf Interaction with People

The Bhal region, like the rest of India (and the world), has several local stories and myths about wolves. The wolf is considered a cunning vicious creature, dangerous to livestock and human lives. The most common stories were about wolves having killed and eaten an old shepherd, and another of a pregnant woman that was attacked by a lone wolf. Almost all the locals were aware of these 2 incidences which allegedly occurred within the last 40 years. The stories varied in details from person to person but the location and context were the same. Another incident the villagers believed occurred about 35 years ago had a supernatural element. According to the story at that time wolves were rampantly killing cattle. The cattlemen prayed to their Goddess and the wolves were cursed. The locals believe that since then, wolves do not molest cattle in this region of the Bhal.

There have been no authenticated reports of wolves killing children or adults in regions of Gujarat like the ones reported by Shahi (1982). On only 2 occasions during the course of this study did the wolves react aggressively towards me. On one occasion I was hiding in tall grass observing pups at a rendezvous site, when an adult male wolf accidentally approached me from the side without my knowledge. It was within 5 m from me when it got my odor but could not see me. It gave a loud growl and a bark which surprised me into a jerky movement. At the instant the wolf confirmed my presence it bounded away. On another occasion I was photographing the pups of 1990 at their first rendezvous site. The alpha male was sleeping under a *Prosopis* bush about 25 m from me with a channel of the Utavali rivulet between us. The camera clicks awakened the wolf, and on detecting me, he growled and barked with hackles raised. He circled to a shallow area of the rivulet about 50 m away and crossed over to my side, continually growling and barking. He approached me within 30 m with a few *Prosopis* bushes intervening while I slowly backed away. The wolf moved away into the shrubs but continued to bark for about 7 minutes. Both instances involved pups and I was intruding into a rendezvous site. On all other occasions when wolves detected my presence they have shyed away or ignored me as long I kept my distance.

In the Velavadar area, local people were rarely aware of wolf activity. Most of the local people out of fear would avoid going to areas used by wolves on foot. Six wolves were shot during the 1960's in the Velavadar area by police as a measure to protect blackbuck (Ranjitsinh 1982:26). Wolves, when located were chased by people on tractors and motorcycles. Even the local staff of the park would chase wolves from a kill during the initial year of the study. With the support from the park officers and patient efforts on my part the attitudes changed by the second year. In other regions of the Bhal, wolves are persecuted, pups dug out of dens, and adults killed (Jhala and Giles 1991). The somewhat tolerant attitude towards wolves in Velavadar is due to: (1) lack of predation on livestock, and (2) legal protection and enforcement within the park. A drastic change in people's attitudes and values is essential if the wolf is to continue to survive (Naess and Mysterud 1987). A national conservation strategy for the wolf incorporating probable reductions in human-wolf conflicts was proposed by Jhala and Giles (1991).

Optimization Modeling

Models are an abstraction, a simplification of a process or reality rather than a replication of the process (Starfield and Beloch 1986:3). Optimization models are ideal from the management point of view, where decisions have to be made despite the lack of data and understanding. However, it is important to recognize that results obtained from studying models require interpretation in light of the degree to which the models are abstractions from reality (Dykstra 1984:5).

The optimization model developed here addresses the habitat needs of only the blackbuck and wolves. The haubara bustard and lesser florican have habitat preferences similar to blackbuck and thus the model would tend to maximize their habitats simultaneously. Management options for other fauna like shorebirds, nilgai, raptors, etc. are not formally incorporated into the model. Most species inhabiting Valavadar National Park would tend to benefit or be unaffected under the current formulation of the model.

The model has 3 critical assumptions, which were essential due to lack of data on these parameters. I shall discuss each of these in view of the sensitivity analysis of the model and the implications these assumptions have on model results.

(1) Regression analysis could not be done with the peak-above-ground biomass (PAGB) production and rainfall in shrubland and saline regions due to a limited sample size of only 3 years. An assumption was made that PAGB production in shrublands was similar to PAGB production in grasslands, but due to *Prosopis* cover only 50% of it would be available to blackbuck. The average ratio of PAGB production in saline regions to PAGB production in grassland for the 3 years data was used to estimate AGB production of saline regions from predicted PAGB of grasslands.

These estimates of AGB in saline regions and shrublands were used as coefficients of decision making variables in the objective function of the model and would affect the value of the optimal solution of the objective function. However, the numerical value of the optimal solution of the

objective function had little meaning in the context of the model formulation and solution. The objective function, in this case, merely served to drive the model to solve for a maximum value possible within the limits specified by the constraints. The real interest was to obtain insights into what management actions to take in the field. These were obtained from the optimal values allocated by the linear programming model to the various areas under each management activity (i.e., the optimal values for each habitat type, the decision making variables). Sensitivity of the model solution to change in the coefficients of mean PAGB production in saline regions and shrublands was low. Thus the optimal model solution would remain unaltered (the basis would not change) even if these coefficients were increased or decreased by 55% of the current values (see Appendix 7).

The coefficients of PAGB production in saline region and shrublands would also be critical in the constraint specifying the forage requirements of a minimum (desirable) blackbuck population (see Appendix 7). With the current land area under different habitats, this constraint was not binding. The grassland habitat alone met all of the blackbuck's forage needs. In the future, grasslands are likely to increase unless the park budget is drastically reduced and the current grasslands are allowed to be colonized by *Prosopis*. Thus, errors in these estimates (PAGB) would not affect the model's solution. The model is thus quite robust regarding PAGB estimates of shrublands and saline region.

(2) The second assumption which would likely affect the models solution is the assumption about the proportion of the peak above-ground biomass (PAGB) available for consumption to blackbuck. Thirty percent of the PAGB is assumed to be available to blackbuck for the model's solution. Blackbuck were responsible for a reduction of 40% of AGB by summer during this study (see Exclosure Studies under Results). A bias could have been introduced with the exclosure study since 3 of the 6 exclosures constructed were in areas of the grassland where blackbuck preferred to graze. During drought years, almost all the AGB was utilized. A 30% utilization would ensure a model solution that would allocate habitat areas in a way that would produce PAGB to more than meet the minimum needs of the blackbuck population.

(3) Though locations of critical wolf-used sites were recorded accurately, it was not possible to ascertain objectively the minimum areas essential for a shrubland to be used by wolves. Wolf use of shrubland would depend on several confounding factors besides its area. These may include human disturbance, shade, availability of water, prior experience, cover, season etc. The smallest shrubland areas used by wolves during the course of this study were considered the minimum essentials. The criteria of 50 m, 150 m and 200 m radii around locations of lying up sites, rendezvous sites and denning sites were considered a minimum requirement in the model.

This constraint was not binding and the model is not sensitive to a 2-fold increase in this parameter. However if the budget of the park is increased 10 times, the constraint will change the solution (becomes binding) and errors in the estimate would affect the optimal solution. However, as recommended in the results, if the saline region is simultaneously developed, then the wolf habitat would never approach the minimum essential area. Thus it seems that by long-term planning and by solving the model with land area values probable in the future, a better "optimal" management strategy is suggested than an annual optimal for which the model was designed.

Initially, I was attempting to design an optimization model which would have a spatial resolution. This was to be achieved by generating a 1 ha cell grid for the park area. Each cell of the grid would be a decision-making variable. Thus, a shrubland cell would have an option of being cut or maintained as wolf habitat, subject to constraints used in the current model. Two major problems were subsequently envisioned: (1) classification of cells with more then one habitat type, and (2) the model being too specific, and than having to be updated once a management activity was performed. The updating would require altering coefficients of hundreds of variables and regenerating "new" habitats on the computer map. This would make the model "person specific" and unsuitable for wider understanding and application. The solutions recommended by both models, the one planned and the one implemented, would have been the same.

The model in its current framework is relatively easy to update and the solution can be implemented by referring to the habitat map of Velavadar with critical wolf areas marked on it (Fig. 13). The manager can decide on where to implement the habitat alterations depending on other

factors not incorporated into the model, for example avoiding cutting near saline regions, or a new wolf use area, or for economics.

The model is not cumbersome and can be solved manually with the simplex algorithm (Dantzig 1963) if computers and software are not available. Thus, high spatial resolution and specificity were sacrificed to achieve ease of solution, and simplicity in understanding and updating the model. Simplicity and easy understanding are critical for application since "No manager with real responsibilities should base important decisions on the outcome of a process which he himself does not adequately understand" (Edelman 1972).

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Appendix 1. Plant species found growing in Velavadar National Park during 1988 to 1990.

Scientific Name	Habit	Palatibility	Local Name
Dichanthium annulatum	p. grass	edible	Jingvo
Sporobolus virginicus	p. grass	edible	Dharant
Sporobolus madraspetansis	p. grass	edible	Moti Dharant
Sporobolus coromandelianus	a. grass	edible	Chakimaki
Chloris virgata	a. grass	edible	Mindado
Aeluropis lagopoides	a. grass	edible	Dale
Panicum trypheron	a. grass	edible	
Setaria glauca	a. grass	edible	Kang
Eragrostis pilosa	a. grass	edible	
Eragrostis japonica	a. grass	edible	Dhundh
Themeda triendra	a. grass	edible	Sameru
Ischaemum rugosum	a. grass	edible	Ghavli
Dinebra retroflexa	a. grass	edible	
Apluda mutica	a. grass	edible	
Dactyloctenium aegypticum	a. grass	edible	Padu
Echinochloa colonum	a. grass	edible	
Iseilema anthephoroides	a. grass	edible	Vardi
Paspalum sp.	a. grass	edible	
Digitaria ciliaris	a. grass	edible	
Digitaria stricta	a. grass	edible	
Paspaladium flavidum	a. grass	edible	
Tragus roxburghii	a. grass	edible	
Hackelochloa granularis	a. grass	not eaten	
Heteropogon ritchie	a. grass	edible	

Appendix 1 continued. Plant species found growing in Velavadar National Park during 1988 to 1990.

Scientific Name	Habit	Palatibility	Local Name
Aristida stocksii	a. grass	edible	Garol
Aristida adscenscionis	a. grass	edible	Garol
Eriochloa proscera	a. grass	edible	Mansu
Brachiraria eruciformis	a. grass	edible	
Brachiraria ramosa	a. grass	edible	
Eremopogon foveolatus	a. grass	edible	
Urochloa panicoides	p. grass	edible	
Cyperus nutans	sedge	edible	
Cyperus rotundus	sedge	edible	
Fimbristylis ferruginea	sedge	edible	Chhaiya
Fimbristylis miliacea	sedge	edible	Chhaiya
Digera arvensis	a. forb	nonedible	Kanejero
Heliotropium paniculatum	a. forb	nonedible	
Sida grewioides	a. forb	nonedible	
Phaseolus trilobus	a. forb	edible	Magamathi
Striga anjustifolia	a. forb	edible	
Hibiscus tetraphyllus	a. forb	nonedible	Jungli Bhindo
Indigofera tinctoria	forb	edible	
Gonogyna hirta	a. forb	nonedible	
Polygala eryocarpa	a. forb	nonedible	
Prosopis juliflora/chinensis	shrub/tree	nonedible	Gando Baval
Salvadora perscia	shrub/tree	edible	Piludi
Suaeda nudiflora	p. forb	edible	Morad
Rungia repens	a. forb	nonedible	

Appendix 1 continued. Plant species found growing in Velavadar National Park during 1988 to 1990.

Scientific Name	Habit	Palatibility	Local Name
Leucas aspera	a. forb	nonedible	
Triantheme monogyna	a. forb	nonedible	
Portulaca quadrifida	a. forb	nonedible	Kharu
Portulaca oleracea	a. forb	nonedible	Kharu
Justicia procumbens	a. forb	nonedible	
Corchorus olitorius	a. forb	nonedible	
Vernonia cinerea	a. forb	nonedible	Kalar
Euphorbia lanciolata	a. forb	nonedible	Dudhali
Euphorbia hirta	a. forb	nonedible	Dudhali
Phyllanthus maderaspatensis	a. forb	nonedible	Hajar Dana
Phyllanthus niruri	a. forb	nonedible	Hajar Dana
Justacia procumbens	a. forb	nonedible	
Tamarix sp.	shrub	not eaten	
Corchorus olitorius	a. forb	nonedible	
Enicostema littorale	a. forb	nonedible	Mamejo
Heylandia latebrosa	a. forb	nonedible	
Pulicaria angustifolia	a. forb	nonedible	
Convolvulus sp.	a. twiner	nonedible	Undardi
Cressa cretica	a. forb	edible	
Sesbania grandifolia	a. shrub	edible	Eekad
Acacia nilotica	tree	edible	Baval

a - annual, p - perinniel

Appendix 2 a. Percent lignin content of forage species in Velavadar National Park.

Species	Monsoon88	Winter88	Summer89	Monsoon89	Winter89	Summer90
DBM		18.9 (0.15)	23 (2.1)		18.9 (1.5)	21 (1.21)
Dichanthium	5.36 (1.1)	9.87 (0.55)	6.5 (1.51)	8.5 (1.25)	13.3 (1.01)	13.8 (1.5)
Sporobolus virginicus	5.57 (1.5)	27.3 (2.5)	28.2 (2.1)	12.4 (1.9)	9.4 (3.2)	22.5 (4.1)
S. maderaspetansis	3.6 (0.11)	4.2 (0.01)	21 (2.1)	11.8 (1.2)	8.6 (1.1)	18 (2)
Chloris	5.7 (1.5)	6.1 (1.9)	6.5 (1.8)	5.8 (2.1)	6.6 (2.01)	8.25 (2.1)
Cyperus sp.	3.1 (0.81)			3.25 (1.2)		
Fimbristylis		10.2 (0.25)		15.7 (2.2)		
Striga	6.8 (0.51)			8.3 (1.6)		
Iseilema	4.5 (1.1)			5.1 (1.25)		
Paspalum	3.8 (0.51)			8.3 (1.2)		
Dinebra	4 (1.1)			6.4 (1.98)		
Phaseolus	5 (0.25)			10.3 (2.2)		
S. coromandelianus	5.2 (1.25)		4.1 (2.1)	4.85 (2.1)	7.61 (1.5)	
Dactyloctenium	3.3 (0.25)			3.57 (1.01)		
Suaeda	10 (2.1)	11 (2.5)	11.95 (1.98)	10 (2.1)	11.2 (2.5)	11.98 1.87

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Appendix 2 a continued. Percent lignin content of forage species in Velavadar National Park.

Species	Monsoon88	Winter88	Summer89	Monsoon89	Winter89	Summer90
Eriochloa	3.1 (0.253)			3.65 (1.15)		
Aeluropis		5.3 (0.89)		11 (2.24)	17 (3.11)	
Themeda	4.5 (1.1)			5.1 (1.7)		
Prosopis pods	2.85 (0.51)	3.95 (1.98)	3.78 (2.5)	3.97 (1.7)(2.1)	8.2 (2.7)	7.25

DBM - dead biomass Values in parentheses are standard errors.

Appendix 2 b. Gross energy content of forage species (kcal/gm) in Velavadar National Park.

Species	Monsoon88	Winter88	Summer89	Monsoon89	Winter89	Summer90
DBM		3.71 (0.27)	3.7 (0.25)		3.8 (0.3)	3.67 (0.27)
Dichanthium	4.2 (0.32)	3.83 (0.125)	3.91 (0.15)	4 (0.18)	(0.35)	3.95 3.89 (0.31)
Sporobolus virginicus	3.95 (0.41)	3.85 (0.051)	4.2 (0.51)	3.91 (0.25)	3.85 (0.42)	3.95 (0.44)
S. maderaspetansis	3.9 (0.25)	3.75 (0.25)	3.95 (0.29)	3.9 (0.3)	3.8 (0.2)	3.79 (0.23)
Chloris	3.75 (0.12)	3.7 (0.31)	3.5 (0.71)	3.8 (0.51)	3.65 (0.11)	3.64 (0.57)
Cyperus sp.	3.92 (0.41)			4.1 (0.35)		
Fimbristylis		3.8 (0.75)		3.82 (0.81)		
Striga	4.12 (0.25)			3.91 (0.41)		
Iseilema	3.81 (0.11)			3.95 (0.42)		
Paspalum	3.8 (0.41)			4.2 (0.33)		
Dinebra				3.8 (0.12)		
Phaseolus	4.12 (0.31)			4.2 (0.25)		
S. coromandelianus	4.3 (0.29)	4.25 (0.31)	3.98 (0.34)	4.11 (0.29)	3.89 (0.45)	3.88 (0.32)
Dactyloctenium	3.8 (0.51)					

Appendix 2 b continued. Gross energy content of forage species (kcal/gm) in Velavadar National Park.

Species	Monsoon88	Winter88	Summer89	Monsoon89	Winter89	Summer90
Suaeda	3.8 (0.25)	3.51 (0.31)	3.78 (0.51)	3.89 (0.12)	3.73 (0.56)	3.81 (0.25)
Eriochloa	4.1 (0.31)			3.91 (0.41)		
Aeluropis		5.61 (0.81)		4.1 (0.51)		
Themeda	4.12 (0.35)			4 (0.51)		
Prosopis pods	4.92 (0.35)	5.1 (0.25)	4.85 (0.71)	4.82 (0.51)(0.44)	4.95 (0.71)	4.67

DBM- dead biomass
Values in parentheses are standard errors.

Appendix 2 c. Percent acid detergent fiber (ADF) content of forage species in Velavadar National Park.

Species	Monsoon88	Winter88	Summer89	Monsoon89	Winter89	Summer90
DBM		58 (2.1)	63 (2.58)		61 (3.2)	64 (2.1)
Dichanthium	38 (3.2)	47.5 (1.5)	48.5 (1.2)	57 (1.5)	64 (1.8)	65.5 (2.1)
Sporobolus virginicus	30 (4.2)	39 (4.8)	39.9 (4.95)	65.5 (5.1)	52.1 (3.4)	53.9 (3.45)
S. madraspetansis	30 (2.3)	33 (2)	28 (2.9)	50.3 (3.01)	51.4 (3)	50 (2.45)
Chloris	38 (2.1)	47 (1.9)	45 (3.1)	45 (4.1)	52 (4.8)	57 56 (4.5)
Cyperus sp.	26 (2.1)			28 (3.1)		
Fimbristylis		49.1 (3.1)		55.5 (3.25)		
Striga	30.6 (2.5)			40.5 (3)		
Iseilema	41 (2.3)			40.5 (5.1)		
Paspalum	30 (1.25)			46.5 (3.1)	43 (1.25)	
Dinebra	39 (1.29)			52 (2.5)		
Phaseolus	17 (2.25)			43 (3.1)		
S. coromandilianus	31 (1.98)		39 (2.1)	43 (1.91)	48 (4.1)	
Dactyloctenium	24 (2.1)			25 (1.15)		

Appendix 2 c continued. Percent acid detergent fiber (ADF) content of forage species in Velavadar National Park.

Species	Monsoon88	Winter88	Summer89	Monsoon89	Winter89	Summer90
Suaeda	31 (1.9)	34 (2.5)	36 (1.79)	31 (2.1)	35 (4.1)	33 (4.21)
Eriochloa	25 (2.1)			26 (3.15)		
Aeluropis		37 (2.12)		53 (2.79)	62 (3.4)	
Themeda	38 (2.4)			41 (3.3)		
Prosopis pods	12 (1.9)	13 (1.56)	12.5 (2.12)	13.5 (4.5)(4.9)	11.9 (4.12)	14

DBM - dead biomass
Values in parentheses are standard errors.

Appendix 2 d. Percent acid insoluble ash (AIA) content of forage species in Velavadar National Park.

Species	Monsoon88	Winter88	Summer89	Monsoon89	Winter89	Summer90
DBM		8.9 (0.15)	9.4 (0.11)		9.2 (1.01)	10.5 (0.11)
Dichanthium	1.65 (0.2)	3.8 (0.51)	9.1 (1.1)	8.3 (1.1)	10.4 (0.81)	10.9 (1.01)
Sporobolus virginicus	5 (0.11)	6.3 (1.11)	6.75 (0.98)	8.1 (0.77)	8.7 (0.01)	(1.1)
S. maderaspetansis	0.3 (0.05)	5.5 (0.11)	3.7 (0.51)	6.1 (0.5)	5.5 (0.3)	5.7 (0.31)
Chloris	0.7 (0.02)	5 (0.71)	4.5 (1.01)	3.71 (1.1)	8.1 (1.25)	8.51 (1.5)
Cyperus sp.	0.5 (0.11)			1.79 (0.25)		
Fimbristylis		6.6 (1.01)		17.5 (1.1)		
Striga	1.37 (0.2)			7.8 (0.89)		
Iseilema	0.2 (0.05)			6.1 (0.51)		
Paspalum	0.8 (0.05)			2.8 (0.11)	6.3 (0.22)	
Dinebra	1 (0.2)			3 (0.22)		
Phaseolus	0.4 (0.01)			2 (0.05)		
S. coromandelianus	0.2 (0.06)		0.3 (0.3)		1 (0.11)	
Dactyloctenium	0.3 (0.1)			1.34 (0.34)		

Appendix 2 d continued. Percent acid insoluble ash (AIA) content of forage species in Velavadar National Park.

Species	Monsoon88	Winter88	Summer89	Monsoon89	Winter89	Summer90
Suaeda	3.1 (1.1)	3.24 (0.89)	2.79 (0.78)	3.2 (0.58)	3.45 (1.01)	4.5 (0.65)
Eriochloa	0.8 (0.02)			1.2 (0.12)		
Aeluropus		8.5 (1.01)		2 (0.3)	5.5 (0.13)	
Themeda	3.7 (0.52)			461 (0.58)		
*Prosopis*pods	0.2 (0.01)	0.5 (0.1)	0.4 (0.1)	0.8 (0.21)(0.12)	0.5 (0.22)	0.9

DBM - dead biomass Values in parentheses are standard errors.

Appendix 3 a. Body weight in $kg^{0.75}$ of captive blackbuck.

	Male 1	Male 2	Female 1	Female 2
Monsoon 88	12.82	9.63	8.92	1.99
Winter 88	14.7	11.51	9.81	4.76
Summer 89	11.68	11.35	10.16	6.45
Monsoon 89	13.45	12.69	10.16	8.37
Winter 89	14.7	14.7	11.51	9.81
Summer 90	12.5	13.2	9.81	9.46

Appendix 3 b. Total fecal output (gms/day) of captive blackbuck as estimated by Cr_2O_3

	Male 1	Male 2	Female 1	Female 2
Monsoon 88	218 (20.7)	248 (21.4)	224.1 (23.6)	
Winter 88	334 (25.4)	342 (20.1)	338 (20.1)	
Summer 89	190.5 (10.45)	159 (8.54)	136 (7.7)	83.3 (5.4)
Monsoon 89	387 (25.1)	445 (27)	430 (25)	330 (20.1)
Winter 89	358 (25)	352 (21.0)	510 (18.9)	351 (17.8)
Summer 90	205.1 (8.9)	187 (10.2)	133 (7.9)	129.5 (6.89)

Values in parentheses are standard errors.

Appendix 3 c. Total dry matter intake (gms/day) of captive blackbuck as estimated by AIA as internal indicater.

	Male 1	Male 2	Female 1	Female 2
Monsoon 88	1237.5 (117.51)	1407.8 (212.48)	1272.16 (133.97)	
Winter 88	1327.2 (100.93)	1359 (79.87)	1343 (79.87)	
Summer 89	261.38 (14.34)	218.16 (11.72)	186.6 (10.56)	114.29 (7.41)
Monsoon 89	1315.8 (85.34)	1513 (91.8)	1122 (85)	1462 (68.34)
Winter 89	1196.2 (83.53)	1176.1 (70.17)	1704.6 (63.15)	1172.8 (59.47)
Summer 90	324.93 (14.1)	296.25 (16.16)	210.7 (12.52)	205.16 (10.92)

Values in parentheses are standard errors.

Appendix 4 a. Blackbuck population from seasonal total counts at Velavadar National Park.

	Fawns	Adolesent Males	Adolescent Females	Subadult Males	Subadult Females	Adult Males	Adult Females	Outside	Total
Summer 88	12 (3.2)	18 (2)	17 (6)	42 (2)	105 (11.7)	250 (4.1)	377 (11)	74 (6)	895 (11)
Monsoon 88	58 (4.2)	24 (2.6)	38 (3.4)	38 (1.5)	86 (7.6)	190 (3.3)	187 (9.2)	281 (6)	902 (7)
Winter 88	253 (4.7)	33 (1.2)	23 (2.3)	23 (1.07)	57 (3.6)	156 (2.3)	339 (6.11)	184 (4.2)	1068 (5.77)
Summer 89	90 (5.2)	53 (1.31)	135 (3.6)	35 (1.2)	151 (4.6)	220 (3.11)	392 (6.8)	70 (3.1)	1146 (13.1)
Monsoon 89									
Winter 89	91 (4.2)	101 (1.5)	68 (4.1)	20 (2)	72 (1.41)	191 (3.2)	286 (7.11)	230 (5.2)	1059 (10.51)
Summer 90	14 (2.1)	175 (1.85)	212 (6.7)	27 (3.2)	164 (8.9)	196 (4.1)	350 (10.2)	206 (6.1)	1344 (12.61)

Values in parenthesis are standard errors.

Appendix 4 b. Blackbuck population at Velavadar National Park from 1966 to 1990.

Year	Population	Source
1947	> 8,000	Ranjitsinh 1989
1966	200	Mungall et al. 1981
1969	400	Ranjitsinh 1989
1973	1,840	Ranjitsinh 1989
1974	2,000	Mungall et al. 1981
1976	2,400	Dharmakumarsinhji 1978
1977	1,554	Prak Management Records
1980	2,006	Mungall et al. 1981
1981	2,307	Ranjitsinh 1989
1983	1,218	Park Management Records
1984	2,000	Satyanarayan 1985 and Shivaprasad 1985
1987	2,200	Ranjitsinh 1989
1988	895	This Study
1989	1,146	This Study
1990	1,344	This Study

Appendix 5. Life table analysis for the female blackbuck population at Velavadar National Park from age at death (1988 to 1990).

Years	f'_x		$f'_x e^{rx}$	F'_x	d_x	$\sum d_x$	l_x	q_x	p_x	m_x	$l_x m_x$	$l_x m_x x$
0	32	395.062	1438	390.35	0.39	0.39	1	0.39	0.61	0	0	0
1	1	12.346	14.78	4.012	0.004	0.394	0.6096	0.0066	0.993	0.125	0.0762	0.0762
2	1	12.346	17.695	4.804	0.0048	0.399	0.6056	0.008	0.992	0.75	0.454	0.908
3	2	24.69	42.37	11.5	0.0115	0.41	0.601	0.0191	0.98	0.75	0.45	1.352
4	6	74.074	152.181	41.31	0.0413	0.452	0.589	0.07	0.93	0.75	0.442	1.768
5	6	74.074	182.194	49.457	0.049	0.501	0.548	0.09	0.91	0.75	0.411	2.055
6	7	86.4198	254.48	69.08	0.069	0.57	0.499	0.138	0.862	0.75	0.374	2.244
7	7	86.4198	304.669	82.704	0.0827	0.653	0.43	0.192	0.808	0.75	0.322	2.255
8	8	98.765	416.863	113.159	0.113	0.766	0.3469	0.326	0.674	0.75	0.26	2.081
9	5	61.7284	311.923	84.673	0.0846	0.851	0.234	0.362	0.638	0.75	0.175	1.578
10	3	37.037	224.064	60.823	0.061	0.912	0.149	0.408	0.592	0.75	0.112	1.12
11	1	12.3457	89.418	24.273	0.024	0.936	0.0883	0.275	0.725	0.75	0.066	0.729
12	1	12.3457	107.053	29.06	0.029	0.965	0.064	0.453	0.547	0.75	0.048	0.577
13	1	12.3457	128.165	34.79	0.0348	1	0.035	0.992	0.008	0.75	0.026	0.342
Total	81	1000	3683.855	1000							$R_o = 3.218$	17.084

r = 0.18 , '0' age mortality = 0.39 obtained from census data.

Appendix 5 continued. Life table analysis for the male blackbuck population at Velavadar National Park from age at death (1988-1990).

Age in years	f'_x		$f'_x e^{rx}$	F'_x	d_x	$\sum d_x$	l_x	q_x	p_x
0	34	390.8045	1190	390.137	0.39137	0.390137	1	0.39	0.61
1	2	22.989	27.522	7.747	0.0077	0.398	0.61	0.0127	0.987
2	2	22.989	32.95	9.275	0.009	0.407	0.602	0.0154	0.985
3	5	57.471	98.621	27.76	0.028	0.435	0.593	0.047	0.953
4	3	34.483	70.843	19.94	0.02	0.455	0.565	0.035	0.965
5	3	34.483	84.814	23.874	0.024	0.479	0.545	0.044	0.956
6	11	126.437	372.318	104.8	0.105	0.583	0.521	0.2	0.799
7	11	126.437	445.747	125.469	0.125	0.709	0.417	0.301	0.699
8	8	91.954	388.114	109.247	0.109	0.818	0.291	0.375	0.625
9	3	34.483	174.246	49.047	0.049	0.867	0.182	0.269	0.73
10	1	11.494	69.537	19.57	0.0196	0.887	0.133	0.147	0.853
11	1	11.494	83.251	23.434	0.023	0.91	0.113	0.207	0.793
12	2	22.989	199.339	56.11	0.056	0.966	0.09	0.624	0.376
13	1	11.494	119.326	33.588	0.034	1	0.034	0.992	0.008
Total	87	1000		1000.000					

r = 0.18 , '0' age mortality = 0.39 obtained from census data.

Appendix 5 continued: Life table analysis for the total sample of dead blackbuck of both sexes collected at Velavadar National Park (1988-1990).

Age in years	f'_x		$f'_x e^{rx}$	F'_x	d_x	$\sum d_x$	l_x	q_x	p_x
0	73	390.374	1352	390.215	0.39	0.3891	1	0.39	0.61
1	5	26.73796	32.011	9.239	0.009	0.3995	0.6	0.015	0.985
2	6	32.086	45.989	13.27	0.013	0.434	0.587	0.022	0.978
3	8	42.781	73.412	21.188	0.021	0.434	0.587	0.036	0.964
4	10	53.476	109.863	31.709	0.032	0.466	0.566	0.056	0.944
5	12	64.17112	157.836	45.555	0.046	0.511	0.534	0.085	0.915
6	19	101.604	299.194	86.354	0.086	0.597	0.489	0.177	0.823
7	19	101.604	358.201	103.384	0.103	0.701	0.402	0.257	0.743
8	17	90.909	383.703	110.745	0.111	0.811	0.299	0.37	0.63
9	7	37.433	189.155	54.594	0.055	0.866	0.189	0.289	0.711
10	3	16.043	97.054	28.012	0.028	0.894	0.134	0.209	0.791
11	3	16.043	116.195	33.536	0.033	0.928	0.106	0.316	0.684
12	3	16.043	139.111	40.15	0.04	0.968	0.072	0.554	0.446
13	2	10.695	111.031	32.046	0.032	1	0.032	0.992	0.008
Total	187	1000	2976.413	1000					

r = 0.18 , '0' age mortality = 0.39 obtained from census data, all aged jaws pooled for lifetable analysis.

Appendix 6. **Population Model:**

General Information :
Species name: *Antelope cervicapra*
Maximum age : 13 years
Time to run : 50 years
Comments : The female population of blackbuck at the Velavadar National Park is modeled. Information on survival and fecundity schedules is obtained from the life-table analysis. Fawn mortality was obtained from the field census data (39%).

The initial matrix with demographic variables was as follows :

Age in years	Initial population	Fecundity	Survival
0	200.00	0.00	0.610
1	100.00	0.12	0.992
2	80.00	0.75	0.991
3	76.00	0.75	0.979
4	50.00	0.75	0.924
5	40.00	0.75	0.903
6	36.00	0.75	0.853
7	30.00	0.75	0.799
8	26.00	0.75	0.663
9	16.00	0.75	0.627
10	8.00	0.75	0.582
11	6.00	0.75	0.719
12	4.00	0.50	0.542
13	2.00	0.50	0.008

Density dependence in the model was incorporated using a Beverton-Holt function. The function parameters rho and k estimated to fit the past population data of the Velavadar blackbuck population were :
$Z = 1/(\text{rho} + K/E)$
Z = recruitment to the population.
E = the number of young produced
1/rho is the maximum number of "0" age individuals produced, rho was empirically estimated as 0.0013.
K is a scalar that determines the steepness of the functions ascent, K was given the value of 1.

The number of replications of the simulation were 250.

Coefficients of variation used in the model (computed from field data and obtained from literature, see Methods and Results) were : Survival for age 0 = 0.30000
Survival for ages 1+ = 0.07000
Fecundity = 0.33300

Probability distributions used in Ramas/age simulation for the various variables were as follows :
Survival for age zero was considered a lognormal distribution with mean 0.61 and a standard deviation of 0.175.
Survival for age 1 and older was considered a lognormal distribution with means as given in the initial matrix.
Fecundity was considered to be normally distributed.

The correlations between variables were given the following values :
Fawn survival and adult survival = 0.85

Fawn survival and fecundity = 0.95
Adult survival and fecundity = 0.85

Appendix 6 continued **Simulation Results**

Years	Minimum number	Minus sd	Mean	Plus sd	Maximum number
1	414	490	544	598	660
2	4.3975E + 02	5.6903E + 02	6.5128E + 02	7.3353E + 02	8.7492E + 02
3	4.5276E + 02	6.5020E + 02	7.5059E + 02	8.5099E + 02	1.0486E + 03
4	5.0541E + 02	7.3016E + 02	8.5404E + 02	9.7792E + 02	1.2344E + 03
5	5.8848E + 02	8.0223E + 02	9.4161E + 02	1.0810E + 03	1.4112E + 03
6	5.9973E + 02	8.4279E + 02	9.9733E + 02	1.1519E + 03	1.4035E + 03
7	7.0322E + 02	8.8933E + 02	1.0494E + 03	1.2094E + 03	1.5106E + 03
8	6.8797E + 02	9.2403E + 02	1.0990E + 03	1.2739E + 03	1.6493E + 03
9	7.2087E + 02	9.4954E + 02	1.1312E + 03	1.3128E + 03	1.5707E + 03
10	7.1606E + 02	9.6070E + 02	1.1540E + 03	1.3473E + 03	1.6987E + 03
11	7.2214E + 02	9.9337E + 02	1.1753E + 03	1.3572E + 03	1.7538E + 03
12	8.0125E + 02	1.0099E + 03	1.1874E + 03	1.3648E + 03	1.8061E + 03
13	7.3697E + 02	1.0280E + 03	1.2011E + 03	1.3742E + 03	1.7343E + 03
14	7.8053E + 02	1.0248E + 03	1.2002E + 03	1.3756E + 03	1.7318E + 03
15	6.0571E + 02	1.0005E + 03	1.1898E + 03	1.3791E + 03	1.8359E + 03
16	8.0799E + 02	1.0110E + 03	1.2028E + 03	1.3946E + 03	1.8747E + 03
17	7.7540E + 02	1.0164E + 03	1.2123E + 03	1.4081E + 03	1.8483E + 03
18	7.8333E + 02	1.0215E + 03	1.2140E + 03	1.4064E + 03	1.7465E + 03
19	7.6105E + 02	1.0189E + 03	1.2178E + 03	1.4166E + 03	1.7092E + 03
20	7.8087E + 02	1.0310E + 03	1.2229E + 03	1.4149E + 03	1.7649E + 03
21	7.6505E + 02	1.0262E + 03	1.2302E + 03	1.4342E + 03	1.7503E + 03
22	8.1321E + 02	1.0183E + 03	1.2199E + 03	1.4216E + 03	1.8291E + 03
23	7.8333E + 02	1.0186E + 03	1.2199E + 03	1.4213E + 03	1.7751E + 03
24	7.2144E + 02	1.0238E + 03	1.2206E + 03	1.4175E + 03	1.7934E + 03
25	7.1743E + 02	1.0178E + 03	1.2113E + 03	1.4049E + 03	1.7578E + 03
26	8.0670E + 02	1.0158E + 03	1.2071E + 03	1.3984E + 03	1.8239E + 03
27	7.4786E + 02	1.0229E + 03	1.2140E + 03	1.4051E + 03	1.8515E + 03
28	7.7721E + 02	1.0219E + 03	1.2201E + 03	1.4182E + 03	1.8185E + 03
29	6.9658E + 02	1.0083E + 03	1.2119E + 03	1.4155E + 03	1.7799E + 03
30	7.2087E + 02	1.0175E + 03	1.2144E + 03	1.4113E + 03	1.7612E + 03
31	7.3805E + 02	1.0167E + 03	1.2054E + 03	1.3941E + 03	1.6565E + 03
32	6.9511E + 02	1.0229E + 03	1.2090E + 03	1.3950E + 03	1.7174E + 03
33	6.9382E + 02	1.0349E + 03	1.2210E + 03	1.4072E + 03	1.6721E + 03
34	7.3708E + 02	1.0344E + 03	1.2173E + 03	1.4001E + 03	1.7826E + 03
35	7.3509E + 02	1.0250E + 03	1.2164E + 03	1.4078E + 03	1.8453E + 03
36	7.8832E + 02	1.0171E + 03	1.2175E + 03	1.4180E + 03	1.8095E + 03
37	7.8853E + 02	1.0267E + 03	1.2251E + 03	1.4235E + 03	1.7964E + 03
38	7.5109E + 02	1.0181E + 03	1.2196E + 03	1.4211E + 03	1.8881E + 03
39	7.6780E + 02	1.0094E + 03	1.2106E + 03	1.4118E + 03	1.8041E + 03
40	8.0009E + 02	1.0101E + 03	1.1993E + 03	1.3885E + 03	1.7936E + 03
41	7.1716E + 02	1.0027E + 03	1.2026E + 03	1.4025E + 03	1.7137E + 03
42	7.7442E + 02	1.0047E + 03	1.1982E + 03	1.3917E + 03	1.7766E + 03
43	7.4455E + 02	9.9716E + 02	1.1941E + 03	1.3911E + 03	1.8121E + 03
44	7.1844E + 02	9.9681E + 02	1.2057E + 03	1.4146E + 03	1.7924E + 03
45	7.5210E + 02	1.0100E + 03	1.2091E + 03	1.4083E + 03	1.7446E + 03
46	7.3914E + 02	9.9824E + 02	1.2023E + 03	1.4064E + 03	1.7393E + 03
47	6.7115E + 02	9.8644E + 02	1.1984E + 03	1.4104E + 03	1.7732E + 03
48	7.0206E + 02	9.9920E + 02	1.2009E + 03	1.4027E + 03	1.7625E + 03
49	7.3241E + 02	1.0037E + 03	1.2023E + 03	1.4009E + 03	1.7677E + 03
50	7.2434E + 02	1.0122E + 03	1.2096E + 03	1.4070E + 03	1.7256E + 03

APPENDIX 7. **Linear programming model 1** : "Normal" years and 1990 coefficients.

Objective function:

MAX 5463 GC + 4917 G + 5463 PC + 2732 P + 2459 SD + 1311 S + 5463 H - DAC - DA

Subject to the following constraints :

Area constraints (see Methods constraint 1):

1) GC + G + PC + P + SD + S $\leq$ 2525 ha (total area that can be managed)

2) GC + G $\leq$ 805 ha (current area under grasslands)

3) PC + P $\leq$ 935 ha (current area under shrubland)

4) SD + S $\leq$ 785 ha (current area under saline region)

Production with 99% lower bound on the peak biomass production coefficients to suffice the forage needs of 1900 blackbuck (see Methods constraint 2):

5) 3659 GC + 3293 G + 3659 PC + 1830 P + 1650 SD + 880 S + DA $\geq$ 2513857 kg

If deficit occurs in the above production, it should be of a magnitude that can be provided for by the stored fodder in the godown.

6) DA $\leq$ 300000 kg (godown capacity for storage of fodder)

The production of PAGB in the current year should suffice the forage needs of the current blackbuck population (2300 blackbuck) (see Methods constraint 3).

7) 5463 GC + 4917 G + 5463 PC + 2732 P + 2459 SD + 1311 S + DAC - SP = 3041788 kg (PAGB to suffice forage needs of 2300 blackbuck).

If there is a deficit (DAC) in the forage production it would be provided for from the godown storage, if the deficit exceeds the storage then the appropriate amount of fodder would be bought (D).

8) DAC - D $\leq$ 300000

In case of surplus production of forage during the current year (SP) appropriate area would be harvested depending on the surplus, storage space and budget constraint.

9) - 5463 H + SP $\geq$ 0

The harvested amount should not exceed the storage space.

10) 5463 H $\leq$ 300000 kg

The area to be harvested should not exceed the current area under grasslands.

11) $H \leq 805$ ha

The minimum wolf shrubland needs (see Methods constraint 4).

12) $P \geq 280$ ha

The total costs of management activities is met by the available budget (see Methods constraint 5).

13) $50\ GC + 5000\ PC + 5500\ SD + 300\ H + 0.2\ D \leq 500000$ Rs.

END

LP OPTIMUM FOUND AT STEP 11

OBJECTIVE FUNCTION VALUE

1) 8523387.00

VARIABLE	VALUE	REDUCED COST
GC	805	0.0
G	0.0	518.6899
PC	88.65511	0.0
P	846.3449	0.0
SD	0.0	1856.1
S	785	0.0
H	54.91488	0.0
DAC	0.0	1
DA	0.0	1
SP	5181599	0.0
D	0.0	0.10924

ROW	SLACK OR SURPLUS	DUAL PRICES
1)	0.0	0.0
2)	0.0	5435.69
3)	0.0	2732
4)	0.0	1311
5)	2995638	0.0
6)	300000	0.0
7)	0.0	0.0
8)	300000	0.0
9)	4881599	0.0
10)	0.0	0.970006
11)	750.0851	0.0
12)	566.3449	0.0
13)	0.0	0.5462

NO. ITERATIONS = 11

SENSITIVITY ANALYSIS

RANGES IN WHICH THE BASIS IS UNCHANGED:

OBJ COEFFICIENT RANGES

VARIABLE	CURRENT COEF	ALLOWABLE INCREASE	ALLOWABLE DECREASE
GC	5463	INFINITY	518.6899
G	4917	518.6899	INFINITY
PC	5463	51869	1687.364
P	2732	1687.364	2732
SD	2459	1856.1	INFINITY
S	1311	INFINITY	1311
H	5463	INFINITY	5299.14
DAC	-1	1	INFINITY
DA	-1	1	INFINITY
SP	0.0	1	1
D	0.0	0.10924	INFINITY

RIGHTHAND SIDE RANGES

ROW	CURRENT RHS	ALLOWABLE INCREASE	ALLOWABLE DECREASE
1	2525	INFINITY	0.0
2	805	0.0	805
3	935	0.0	566.3449
4	785	0.0	785
5	2513857	2995638	INFINITY
6	300000	INFINITY	300000
7	3041788	4881599	INFINITY
8	300000	INFINITY	300000
9	0.0	4881599	INFINITY
10	300000	4097715	300000
11	805	INFINITY	750.0851
12	280	566.3449	INFINITY
13	500000	2831725	443275.5

APPENDIX 7 continued. **Linear programming model 2**: Increased budget from Rs. 500,000 to Rs. 5,000,000.

Objective function:

MAX 5463 GC + 4917 G + 5463 PC +
2732 P + 2459 SD + 1311 S + 5463 H - DAC - DA

Subject to the following constraints :

1) GC + G + PC + P + SD + S ≤ 2525

2) GC + G < = 805

3) PC + P < = 935

4) SD + S < = 785

5) 3659 GC + 3293 G + 3659 PC + 1830 P + 1650 SD + 880 S + DA > = 2513857

6) DA < = 300000

7) 5463 GC + 4917 G + 5463 PC + 2732 P + 2459 SD + 1311 S + DAC - SP = 3041788

8) DAC - D < = 300000

9) - 5463 H + SP > = 0

10) 5463 H < = 300000

11) H < = 805

12) P > = 280

13) 50 GC + 5000 PC + 5500 SD + 300 H + 0.2 D ≤ 5000000 (ten times the current budget)

END

LP OPTIMUM FOUND AT STEP 13

OBJECTIVE FUNCTION VALUE = 10418290.0

VARIABLE	VALUE	REDUCED COST
GC	805	0.0
G	0.0	535.5635
PC	655	0.0
P	280	0.0
SD	303.3228	0.0
S	481.6772	0.0
H	54.91488	0.0
DAC	0.0	1
DA	0.0	1
SP	7076502	0.0
D	0.0	0.041745

ROW	SLACK OR SURPLUS	DUAL PRICES
1)	0.0	1311
2)	0.0	4141.563
3)	0.0	3108.364
4)	0.0	0.0
5)	4265042	0.0
6)	300000	0.0
7)	0.0	0.0
8)	300000	0.0
9)	6776502	0.0
10)	0.0	0.988538
11)	750.0851	0.0
12)	0.0	-1687.364
13)	0.0	0.208727

NO. ITERATIONS = 13

RANGES IN WHICH THE BASIS IS UNCHANGED:

OBJ COEFFICIENT RANGES

VARIABLE	CURRENT COEF	ALLOWABLE INCREASE	ALLOWABLE DECREASE
GC	5463	INFINITY	535.5635
G	4917	535.5635	INFINITY
PC	5463	INFINITY	1687.364
P	2732	1687.364	INFINITY
SD	2459	1856.1	1148
S	1311	1148	1311
H	5463	INFINITY	5400.382
DAC	-1	1	INFINITY
DA	-1	1	INFINITY
SP	0.0	1	1
D	0.0	0.041745	INFINITY

RIGHTHAND SIDE RANGES

ROW	CURRENT RHS	ALLOWABLE INCREASE	ALLOWABLE DECREASE
1	2525	0.0	481.6772
2	805	486.0963	0.0
3	935	333.6551	0.0
4	785	INFINITY	0.0
5	2513857	4265042	INFINITY
6	300000	INFINITY	300000
7	3041788	6776502	INFINITY
8	300000	INFINITY	300000
9	0.0	6776502	INFINITY
10	300000	4097715	300000
11	805	INFINITY	750.0851
12	280	529.8449	280
13	5000000	2649225	1668276

APPENDIX 7 continued.: **Linear programming model 3** Worst case senario, extreme drought year coefficients for PAGB production.

Objective function:

MAX 5463 GC + 4917 G + 5463 PC + 2732 P + 2459 SD + 1311 S + 5463 H - DAC - DA

Subject to the following constraints :

1) GC + G + PC + P + SD + S ≤ 2525

2) GC + G ≤ 805

3) PC + P ≤ 935

4) SD + S ≤ 785

5) 3659 GC + 3293 G + 3659 PC + 1830 P + 1650 SD + 880 S + DA ≥ 2513857

6) DA ≤ 300000

7) 308 GC + 277.2 G + 308 PC + 154 P + 154 SD + 73 S + DAC - SP = 3041788

8) DAC - D ≤ 300000

9) - 5463 H + SP ≥ 0

10) 5463 H ≤ 300000

11) H ≤ 805

12) P ≥ 280

13) 50 GC + 5000 PC + 5500 SD + 300 H + 0.2 D ≤ 5000000

END

LP OPTIMUM FOUND AT STEP 12

OBJECTIVE FUNCTION VALUE = 5389442.00

VARIABLE	VALUE	REDUCED COST
GC	805	0.0
G	0.0	551.3477
PC	0.249429	0.0
P	934.7505	0.0
SD	0.0	1954.773
S	785	0.0
H	0.0	0.0
DA	0.0	1
DAC	2592514	0.0
SP	0.0	0.681613
D	2292514	0.0

ROW	SLACK OR SURPLUS	DUAL PRICES
1)	0.0	1392.476
2)	0.0	4385.258
3)	0.0	1511.398
4)	0.0	0.0
5)	3193936	0.0
6)	300000	0.0
7)	0.0	-1.116116
8)	0.0	0.116116
9)	0.0	-0.434502
10)	300000	0.0
11)	805	0.0
12)	654.7505	0.0
13)	0.0	0.580578

NO. ITERATIONS = 12

RANGES IN WHICH THE BASIS IS UNCHANGED:

OBJ COEFFICIENT RANGES

VARIABLE	CURRENT COEF	ALLOWABLE INCREASE	ALLOWABLE DECREASE
GC	5463	INFINITY	551.3477
G	4917	551.3477	INFINITY
PC	5463	2216.705	1771.337
P	2732	1771.337	1516.342
SD	2459	1954.773	INFINITY
S	1311	1511.398	1392.476
H	308	209.9369	133.8266
DA	-1	1	INFINITY
DAC	-1	0.657684	14.39422
SP	0.0	0.681613	INFINITY
D	0.0	0.1154	14.39422

RIGHTHAND SIDE RANGES

ROW	CURRENT RHS	ALLOWABLE INCREASE	ALLOWABLE DECREASE
1	2525	0.0	84.89456
2	805	413.1535	0.0
3	935	785	0.0
4	785	INFINITY	0.0
5	2153857	3193936	INFINITY
6	300000	INFINITY	300000
7	3041788	6197.303	2278393
8	300000	2278393	6197.303
9	0.0	0.0	1272.513
10	300000	INFINITY	300000
13	805	INFINITY	805
12	280	654.7505	INFINITY
13	500000	3253587	1239.461

Vita

Yadvendradev V. Jhala, son of Iladevi and Vikramsinhji J. Jhala was born on February 27, 1962. He is a native of Wadhwan in the state of Gujarat, India. He obtained his Bachelorof Science and Master of Science degrees from the University of Bombay in 1983 and 1985 in Zoology. Mr. Jhala has been awarded the National Merit Scholarship, Daxina Fellowship, University Grants Commission Junior Research Fellowship, Pratt Fellowship at VPI & SU, and a Post Doctoral Fellowship at the Smithsonian Institution.

Mr. Jhala served as a lecturer at St. Xavier's College affiliated with the University of Bombay from 1985 to 1987. He was a graduate teaching assistant in the Department of Fisheries and Wildlife Sciences at Virginia Polytechnic Institute and State University in 1987. Mr. Jhala took leave of absence from VPI & SU from January 1988 to May 1990 during which time he was the co-principal investigator for the research project "Habitat and Population of Wolves and Blackbuck in Velavadar National Park, Gujarat, India". The project was funded by the U.S. Fish and Wildlife Service and sponsored by the Bombay Natural History Society.