Investigating the impacts of donkeys on a communal range in Namaqualand:

How much does a donkey "cost" in goat units?

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Susanne Vetter

Supervisors:
Prof. W. J. Bond
Dr. M. T. Hoffman

Abstract

Donkeys are used extensively in Namaqualand and other rural areas in South Africa for pulling carts, carrying loads, ploughing and threshing grain. There is, however, an ongoing debate among farmers, agriculturalists and the wider population about the implications of keeping donkeys, particularly on communal lands. Donkeys are reported to cause more damage to the veld than other animals, and it is commonly said that one donkey eats as much as seven goats. This project was initiated as a case study to investigate the impacts of donkeys in a communal area in the succulent shrublands of Namaqualand, and to generate suggestions for the management of donkey populations. The degree of competition between goats and donkeys was investigated by predicting daily food intake using a model based on ruminant and non-ruminant digestion, which takes into account the animal's body weight and digestibility characteristics of its diet. The ratio predicted food intakes is discussed in the light of the degree of dietary and habitat overlap, which were obtained from field observations. Habitat use was scored using dung frequency transects, and feeding was directly observed. It was found that in the wet season, one donkey eats as much as 5 / 7.6 goats (donkey weight set at 200 and 250 kg respectively). In the dry summer, this ratio increases to 7.6 / 8.6 because in ruminants, the passage of food through the gut slows down as the digestibility of the diet decreases. Habitat overlap is concentrated in the riverine areas and sandy pediments, which make up 15 % of the landscape and are strongly favoured by donkeys. No significant differences were found to exist between the intensities of goat use of the different habitats. The botanical composition of the diets of donkeys and goats were found to be similar, but there is a great difference in the quality of the diet consumed by each species as goats are able to select plant parts of a higher quality. The implications of this are that whereas a donkey takes in as much dry matter as 5 - 8.6 goats, the diet of this food is not high enough to satisfy the dietary requirements of goats, and hence fewer goats than predicted can be supported for every donkey that is eliminated. Donkeys are

commonly reported to have destructive feeding habits; little of this was directly observed, but donkeys were found to bite deeper into the wood of shrubs, which may damage the plants in the long term. There are two main management measures that should be applied. The feral donkey population in Paulshoek, estimated at 50-100 animals, must be eliminated - even at a conservative estimate, these animals could be replaced with 250 goats. However, one must look beyond the number to the processes taking place to make management effective. Even if one donkey can be replaced with fewer than 5 goats, the vegetation is relieved of the indirect effects donkeys have through their feeding habits. Control of working donkeys should focus on the riverine and flat, sandy areas, as they are potentially of high nutritional importance (especially the riverine areas which support grass throughout the year), and which are also the most susceptible to erosion due to their sparse vegetation cover. These areas are small and valuable, and plans should be made to protect some areas through the growing season.

Contents

Introduction

Donkeys are used extensively in Namaqualand and other rural areas of South Africa for pulling carts, carrying loads, ploughing and threshing grain. There is, however, an ongoing and unresolved debate among farmers, agriculturalists and the wider population about the implications of keeping donkeys, particularly on communal lands. Donkeys are said to cause disproportionate damage to the land and vegetation, and to compete with other livestock for scarce food resources. People in many parts of the country also claim that there is an increasing element of feral donkeys, which is said to exacerbate the problem.

Such allegations need to be taken seriously and investigated in communal areas in the arid parts of South Africa, which already experience severe grazing pressure. While arid ecosystems have evolved to tolerate nutrient-poor soils, drought, temperature extremes and sometimes saline soils, the greatest stress factor affecting the productivity of these ecosystems is the grazing impact of livestock which may consume up to 75% of the primary productivity (Noy-Meir 1974). The effects of overgrazing are particularly severe in arid ecosystems because of the suite of environmental stress factors which limit vegetative and reproductive growth (van der Heyden, 1992). The plants of semi-arid and arid shrublands can be permanently damaged if they are overutilized during droughts (Richardson, inaugural lecture and references therein), when livestock are forced to feed on plants which have not fully recovered from prior grazing. This often leads to irreversible damage (Noy-Meir 1974). Desertification of arid and semi-arid areas has become a world-wide threat, and overgrazing as a result of high animal densities is commonly considered to be the most important cause for the desertification of the Karoo (e.g. Acocks 1988).

Paulshoek, the communal area where this study was carried out, supports livestock at about twice the recommended carrying capacity for farming in the Karoo (M. T. Hoffman, unpublished data). People living in Paulshoek describe the veld as deteriorated when compared to past years. It is therefore important to identify and avoid any additional pressure on the range if permanent damage is to be prevented.

Donkeys world-wide

The donkey is a descendant of the African wild ass of Ethiopia and Somalia (Seegmiller and Ohmart 1981). Donkeys are well adapted to arid environments, and have spread throughout the world since their first domestication approximately 4000 B.C. (Protsch and Berger 1973, cited in Seegmiller and Ohmart 1981). There are now over 40 million donkeys world-wide (Mueller et. al. 1994), used mainly in the arid and semi-arid rural areas of Asia, Africa and Latin America (Starkey 1995).

In the second half of this century, feral donkey populations have proliferated in the south-western United States, Australia and some other arid areas of the world, where domestic donkeys became redundant and were set free. In these countries, donkeys are perceived as nuisance animals, and there is concern that donkeys may compete with indigenous animals and damage the vegetation. This negative view of donkeys is widespread in most developed countries where donkeys are seldom used. South Africa faces the more unusual situation where both working and feral of donkeys exist, although little is known about the sizes and distributions of such feral populations.

There are few, if any, reports of the long-standing use of donkeys by indigenous South African peoples, and there is little information available on the origin of donkeys in South Africa. The first reports of donkeys in South Africa date from 1656, when they were imported by European settlers

(Starkey 1995). During the nineteenth century, donkeys became important in agriculture, mining and transport. An estimate of the donkey population in South Africa at the beginning of this century is about one million animals (Abstract of Agricultural Statistics 1994, in Starkey 1995), but reliable data is not available. With the increasing mechanisation of agriculture and mining, donkeys rapidly decreased in importance, and their populations declined from the 1950s onward. Donkeys and other draught animals are, however, still used extensively in the less affluent rural areas where machine power is beyond the reach of most people. Today's donkey population in South Africa is estimated at about 150 000 (Starkey et al 1995).

The Donkey Problem in Paulshoek

Complaints about the damaging impacts of donkeys are widespread in South Africa. It was therefore decided to perform a case study to investigate the effects donkeys have on the land and livestock in a communal area. The study comprises two parts. Firstly, the perceptions of the people in the area were assessed by conducting informal interviews and conversations with about twenty people in Paulshoek. Long and formal interviews were beyond the scope of this study. People questioned included men and women, donkey owners, livestock farmers and people who live in the village and do not farm or keep donkeys to include a variety of people who might be expected to see donkeys in different lights. Their opinions and descriptions formed the basis of the hypotheses which were tested in the second component of this study.

Paulshoek is one of nine wards that comprise the Leliefontein communal area, a former "Coloured Reserve", in Namaqualand (Fig. 1). The study covers the southern third of the ward, which has an area of about 8 000 ha, and includes the village of Paulshoek.

In Paulshoek, as in large areas in Namaqualand and elsewhere in South Africa, donkeys are used for pulling carts, carrying water and firewood (since

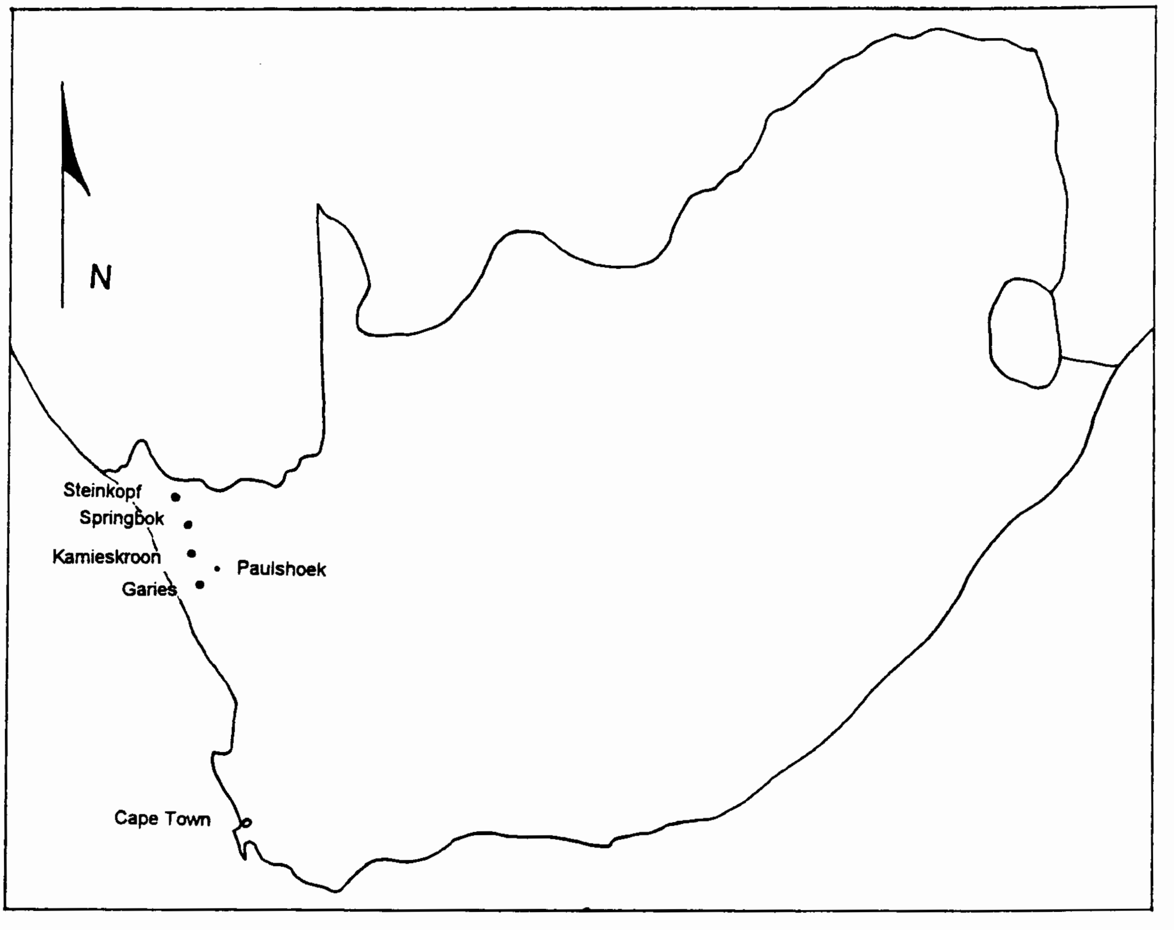


Figure 1: Map showing the position of Paulshoek in South Africa.

there is no running water and electricity), ploughing fields and threshing grain. Although anyone in Paulshoek who was asked would prefer the more modern alternatives, mechanisation and the necessary wealth are not within close reach for the majority of Paulshoek's inhabitants. However, the management of donkeys is said to have changed, to the detriment of the environment and livestock farming. Everybody in Paulshoek seems to agree that donkeys are not controlled adequately and that there is an increasing element of stray, ownerless donkeys in the area. People in Paulshoek describe how in the past, every donkey owner looked after their own donkeys, herded them with their livestock, kraaled them at night in special stone kraals ("klipkraale"), and breeding was controlled by castrating most male donkeys. Now, donkeys roam freely in the veld most of the year, and are tracked and caught by their owners (who recognise their own and other people's donkeys) when they are needed. They reproduce freely, and being polyoestrous can produce foals throughout the year (Perryman and Muchlinsky 1987). Some people also say that because donkeys reproduce without interference from human breeding efforts, the quality (particularly the size) of the donkeys is decreasing every generation. It appears that wild donkeys are not domesticated and trained because of the difficulty of such a task. In addition to more and more wild donkeys being born, some people also say that stray donkeys are a "bad influence" on working donkeys when they roam around in the veld together, making them more difficult to handle.

The size of the feral donkey population in Paulshoek is not known; The farmers in the area estimate it at between 50 and 100 animals, but the accuracy of these estimates is unknown. Donkey numbers for Paulshoek obtained from Mr Gert Fredericks, the veterinarian in the nearby town of Steinkopf, who treats and inoculates farmers' livestock at certain collection points along the road, fluctuated between 50 and 80 animals between 1971 and 1995 (Fig. 2). These numbers do not include stray donkeys since they would not be rounded up for veterinary attention. If these estimates are

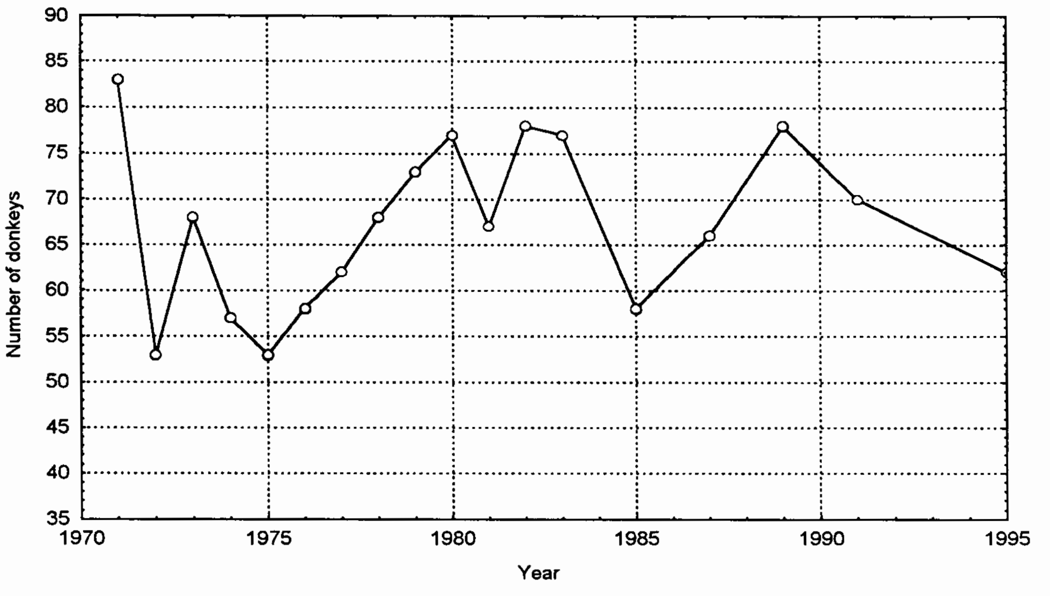


Figure 2: Donkey numbers in Paulshoek between 1971 and 1995.

correct, the total donkey population in Paulshoek is therefore between 100 and 180 individuals, of which up to half are wild.

While most people's complaints concern the existence and behaviour of stray donkeys, all donkeys are charged with destructive eating habits, trampling of the veld, causing other forms of damage and eating voraciously. In Paulshoek, the people who were asked expressed these opinions unanimously whether they were farmers or not, and regardless of whether they owned donkeys themselves. This contrasts with the outcome of a countrywide animal traction survey carried out in 1994 by the South African Network of Animal Traction (SANAT) where farmers, agricultural officials and other relevant people were interviewed about animal traction issues (Starkey 1995). According to the SANAT survey, officials and misinformed people in urban areas in general are to be blamed for the negative image donkeys have today, mostly because these people associate donkeys with poverty and consider them backward and contradictory to modernisation and progress. Inhabitants of the poorer rural areas (mostly former "homelands" or "reserves") are said to unanimously defend donkeys against the negative comments that are commonly made about them.

Apparently there is a feeling among these rural people that there are not enough donkeys, and that all donkeys, even those roaming around freely, have owners and even names. The survey found no evidence of feral donkey populations. According to Starkey (1995), the allegations that donkeys cause damage and that they compete with livestock to the latter's detriment are myths and misconceptions, propagated by mostly office-bound officials and agriculturalists, which are aimed at discouraging donkey use.

In Paulshoek, everybody who was asked acknowledged that donkeys are important work animals and that it would be impossible to live without them at this stage; however, informants also agreed that there is an urgent need for managing donkey populations so that their sizes are controlled and their impacts on the livestock, vegetation and soils of the area can be minimised. What follows is a summary of the allegations made by the people of Paulshoek and some counter-arguments in order to outline the present debate (and confusion) about donkeys in communal areas. The arguments made by people in Paulshoek formed the basic hypotheses on which this study is based.

1. Donkeys feed destructively and cause overgrazing

It is a widely held view that donkeys have destructive feeding habits and are responsible for overgrazing in many areas. In Paulshoek, donkeys were generally seen as a major cause of veld degradation in some areas. Many informants said that donkeys pull up plants while they feed, particularly shallow-rooted mesembs which are important palatable forage plants. In the field, uprooted plants were pointed out by farmers, and donkeys were said to be the culprits. Donkeys are also reported to rip or chew branches off plants, kick plants with their hooves until they are uprooted and feed wastefully because plant parts are often found scattered around the plant. Wasteful and destructive feeding habits were observed in various studies of feral donkey populations in the south-western United States (e.g. McKnight 1958; Seegmiller and Ohmart 1981 and references therein). These findings will be discussed more fully with the observations of this study.

Donkeys are also charged with "brandbek" ("fire mouth") or a "poisonous breath" by farmers in Paulshoek. It is often said that after a donkey has grazed a plant, regrowth is suppressed, or the plant may even die.

Starkey (1995) reports that officials complain about donkeys destroying pastures, but his reaction is that these allegations are unsubstantiated and arose out of prejudice. He argues that the association of donkeys with overgrazing is a result of donkeys being able to survive dry and degraded conditions and that they are unjustly blamed as the cause of degradation, although he presented no data or observations to support his views.

2. Donkeys cause erosion.

People in Paulshoek say that trampling by donkeys causes erosion because they break up the soil surface with their hooves, especially when they gallop during their mating behaviour. Goats were not blamed for erosion. Starkey (1995) argues, as in the case of overgrazing, that because donkeys survive well under degraded conditions, they are unjustly blamed as the cause of such conditions, largely due to the prejudice of extension officers and other officials.

3. One donkey eats as much as seven goats

Farmers and officials alike repeatedly quoted this figure to explain why donkeys had such a big impact on livestock farming. Some farmers simply said that donkeys eat much more than goats, but "seven times as much as a goat" was the generally accepted figure. Where this estimate originates, and how accurate it is, is not known. Farmers explain the proportionally larger intake by the fact that whereas goats are kraaled at night (and spend part of the day ruminating), donkeys eat continuously, day and night. According to the SANAT survey, officials claim that donkeys eat 24 hours a day, whereas farmers did not say this. Starkey (1995) did not, however, report whether farmers said the statement was untrue. Although studies have not been done in South Africa, research with feral burros in the Virgin Islands suggested that they grazed for 54 percent of the time during daylight hours (Rudman 1990, cited by Starkey 1995). Other reports (Starkey 1995, no references given) suggest that horses may graze up to 16 hours a day. No data is available for donkey behaviour over 24 hours.

4. Donkeys compete with goats for water

In addition to competing for food resources, donkeys are also said to compete with livestock for drinking water. Water is a scarce and thinly scattered resource in the semi-arid area of Paulshoek, which is said to limit the feeding range of livestock and donkeys. Donkeys allegedly drink more than goats and tend to congregate around water points in the dry season. Seegmiller and Ohmart (1981) observed that donkeys drank water every 24 hours in the dry season, which limited the range of their daily movement. Watering took place in the evening or at night. Woodward and Ohmart (1976) on the other hand found that feral burros in California only went to drink every three days during the dry season, but that their range of movement was nevertheless restricted to about 1.5 km from the river.

McKnight (1958) describes how donkeys commonly cause deterioration of the quality of water holes because their protracted stays frequently result in the destruction of the surrounding vegetation, packing of the soil and pollution of the water by defecation. Seegmiller and Ohmart (1981) cite several studies where donkeys have been found to foul, usurp and monopolise water holes in the dry season, but found no evidence for this in their own study, and a number of other studies they cited did not report pollution of water sources either. People in Paulshoek did not mention this problem. The only form of water contamination that was described is the transmission of a disease locally known as "snotsiekte". This is a potentially fatal disease which is characterised by the release of large amounts of mucus from the nostrils. This contaminates drinking water, particularly in the dry season. Both donkeys and small stock are affected by this sickness, but small stock can be treated against it whereas donkeys seldom receive veterinary attention.

These are the main problems people describe in Paulshoek. The following main questions emerged which were addressed in this study:

1: Do donkeys reduce the forage available for goats, and to what degree?

It is a generally held view that one donkey eats as much as seven goats. This implies that for every donkey removed from the veld, there would be extra forage to support seven additional goats or sheep. If this is indeed the case, it would provide a strong incentive for eliminating feral donkeys and controlling the numbers and behaviour of working donkeys. All stock farmers in Paulshoek are required to pay taxes per head of livestock. A scientifically based donkey - goat equivalence figure would aid in decisions regarding the taxing of donkeys.

The prediction of the "cost" of a donkey in goat units on a biological basis takes into account three main components: their relative daily intakes in the dry and wet seasons, the degree to which the same food is used, and habitat overlap. These three factors are all important when trying to investigate the claim that one donkey eats as much as seven goats. Intake values give a figure for identical diets and use of the same habitats; however, the degree of competition decreases as the differences between the habitats and diets utilised by each species increases. If no overlap existed between donkey and goat diets, donkeys and goats would not actually compete for the same resources, and decreasing donkey numbers would have no effect on goat numbers unless other factors such as interference competition came into play. Daily intake of the animals was predicted using a model based on diet characteristics and animal weights. Diet choice and habitat use were determined through field observations.

2: Do donkeys cause disproportionate damage to the veld?

People in Paulshoek say that donkeys cause more damage to the vegetation than other livestock. This impression seems to prevail among officials and extension staff as well (Starkey 1995). Any grazing animals, especially in high concentrations, have some impact on the vegetation, as well as possible impacts on soils. Observations of feeding goats and donkeys were compared and evidence in the veld was compiled. These are discussed in the light of the allegations by farmers and findings of other studies about the impacts of donkeys.

The aim of this investigation was to investigate the habits and impacts of donkeys in the succulent shrublands of Namaqualand, so that their negative impacts can be minimised. It is also important to clear up the debate which is sometimes heated and emotionally or even politically charged, and to provide an objective framework for sound and effective management strategies.

Study Area

Paulshoek (30°20'S, 18°15'E) lies at the southern end of the Kamiesberg. Elevations range between 900 and 1250 m. a. s. l., increasing towards the more mountainous North. The landscape is characterised by mountain ridges, often with large granite boulders and domes, which are intersected by semi-perennial rivers. The rocky pediments at the base of the steeper mountain slopes give way to sandy pediments with deeper soils in some valleys. Most of the latter areas have been ploughed in the past, and while some are still used for cropping today, most have been abandoned.

Climate.

Paulshoek experiences an arid to semi-arid climate characterised by hot, dry summers and mild winters. Temperatures range from 10-12°C in July to 20-22°C in January. Paulshoek receives an annual rainfall of 230 mm (CCWR, unpublished data), mostly frontal rain which is concentrated in the winter months (May to August). As in arid areas in general, biological processes are controlled primarily by the infrequent, discrete and largely unpredictable nature of rainfall events (Noy-Meir 1973). Frost commonly occurs during the night in winter.

Vegetation

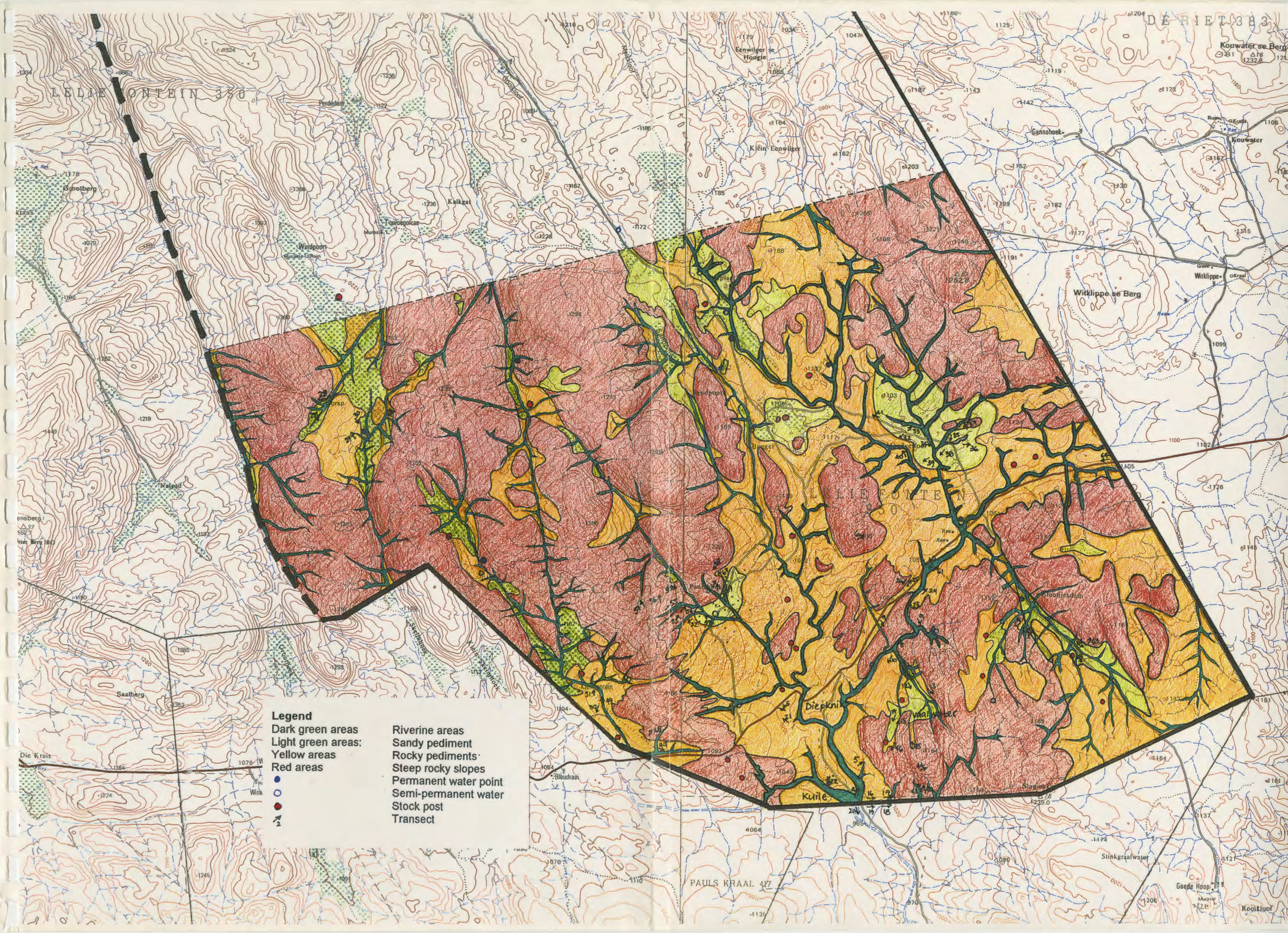
The vegetation in the area has been described as Namaqualand Broken Veld (Acocks 1988) and is dominated by asteraceous shrubs and mesembs. *Pentzia incana* and *Eriocephalus africanus* are common in most parts of the study area. A low annual herbaceous cover appears after the winter rains, but compared to many similar (often disturbed) areas in Namaqualand, this is relatively sparse, possibly as a result of heavy grazing pressure in the flatter areas where these annuals are most commonly found. Perennial grasses are scarce and are almost entirely confined to river banks, where there is subsurface water available throughout the year. Some grass is also found under shrubs which afford the tussocks some protection from grazing.

Old cropping areas are recognisable by their level and rock-free appearance, relatively deep soils and the fact that even after twenty or more years, little but *Galenia africana* has re-established in these areas. According to farmers in the area, many of the flat or gently sloping areas of Paulshoek were covered in a palatable leaf succulent *Ruschia* species (known as !naroevy), which has largely been replaced in ex-croplands and overgrazed areas by *G. africana*. This latter species is unpalatable to livestock and causes a serious, often fatal, disease known as "waterpens". Apart from *G. africana*, the flat, sandy areas support *Lycium* spp. and *Zygophyllum microphyllum*, but in much lower densities.

The rocky pediments are characterised by shallower soils and ubiquitous small to medium-sized rocks. Slopes are flat or gentle. These areas support a larger variety of plants, particularly mesembs (e.g. *Ruschia* and *Cheirodopsis* spp.) and asteraceous shrubs.

The steeper slopes arise quite abruptly from the gentler pediments, and are generally covered by fairly large rocks and boulders of granite. Apart from asteraceous shrubs and mesembs, *Hermannia amoena* and a variety of species in the family Crassulaceae are commonly found on these slopes. There are also a few *Aloe dichotoma* individuals, a species which is considered a characteristic part of the vegetation of these regions (Acocks 1988).

Figure 3 (overleaf): Map of the study area in Paulshoek showing the different habitat types and the positions of stock posts, water points and the transects sampled in this study. Scale: 1 : 50 000



Legend
Dark green areas
Light green areas:
Yellow areas
Red areas
Riverine areas
Sandy pediment
Rocky pediments
Steep rocky slopes
Permanent water point
Semi-permanent water
Stock post
Transect
LELIEFONTEIN 350
DE RIET 383
Kouwater se Berg
Kouwater
Gannahoek
Witklippe se Berg
Witklippe
Klein-Eenwilger
Eenwilger se Hoogte
Perdedam
Kalkgat
Windpoort
Grootberg
Malpad
Saalberg
Die Kruis
Bloudraai
Kuile
Walwater
PAULS KRAAL 417
Stinkgraafwater
Goede Hoop

The riverine areas which consist of the banks and sandy beds of semi-perennial rivers, are fringed and partly covered by small areas of grass, sedges, renosterbos (*Elytropappus* sp.), due to the year-long availability of sub-surface water. The grass has the appearance of a lawn due to grazing by livestock and donkeys. These riverine areas are narrow, usually not more than 10 or 20 m in width. A variety of mesembs, *Lycium* spp. and *Galenia africana* are commonly found next to the banks.

Water

Permanent water sources in the form of boreholes with windmills are few and scattered, as seen on Figure 3. There are a number of non-perennial water sources, mostly in the form of wells which are frequently found in or near rivers, and the rivers themselves which flow for a short time during winter and spring. After the rain, water also collects temporarily in some places. Stock farmers reported that this enables them to utilise larger stretches of grazing land during the wet season, whereas their livestock's foraging range is limited in the dry season by the scarcity of water points. In some of the bigger rivers, subsurface water can be made available for stock by digging holes. Donkeys are able to dig holes into the sand of river beds using their strong hooves (McKnight 1958; Seegmiller and Ohmart 1981). Such a hole (of uncertain origin) was observed in early May in one of the bigger rivers, by which time the area had become very dry.

The community

The communal area of Paulshoek is home to ca. 800 people in 138 households. The majority of the population is concentrated in Paulshoek village. There are 30 stock posts in Paulshoek (see Fig. 3 for the locations of the ones in the study area), where herds of goats and sheep are kraaled. These herds are between 15 and over 200 animals in size, and sometimes herds of different owners are kept together in the same stock post. A substantial proportion of these stock posts are clustered in the near vicinity of the village, partly because of the availability of water and basic supplies, partly because the farmers' homes and families are based in the village. Very few of the stock farmers have vehicles, and existence in a stock post 10 or 20 km from the village is thus quite an isolated one. Although the stock posts are traditionally part of a nomadic or semi-nomadic herding system, many of the stock farmers have become established in a particular place for a long time.

Materials and Methods

Habitat selection

Transect data

To determine how heavily and frequently different areas and habitats are utilised by donkeys and goats, 66 transects of 100 by 10 metres were sampled (their positions in the study area are marked in Fig. 3). A transect was walked 10 metres at a time, noting in each segment the presence or absence of goat and donkey dung within five metres on either side of the line walked. The frequency of dung was used to obtain a score reflecting the intensity with which an area is used by animals of either species. Goat and sheep dung were not differentiated, and the dung frequency data for goats therefore includes sheep as well. Goats were chosen for this study because they are the most important species of livestock in the area. Sheep and goats may have different habitat choices; since the two species are herded together, the values should be accurate for goats and reflect the habitat use by small stock herds.

The more commonly employed method to assess habitat choice is direct observation, from which the percentage of the time animals spent in different habitats is calculated. To obtain reliable data this way, a large set of thorough observations is needed, and not enough time for this was available during this study. It also often proved difficult to find donkeys, and a group of donkeys was often found to occupy the same general area. Transport difficulties and time limits also made spending several hours tracking donkeys an impossibility. Using donkey and goat dung as an indicator of habitat use was therefore a way to cover a wider variety of areas and habitats, which would not have been possible using direct observations.

In order to differentiate between recent (and presumably frequent) and past (and presumably infrequent) presence, dung was classified according to age. The assumption that recent presence implies frequent use of that habitat was made *ad hoc* and may not always hold if habitat use is very different between seasons.

A score out of three was awarded to any dung found along the transect. The age of the dung was scored as 1 (old): dung grey and crumbly; 2 (intermediate): dung grey but in its original firm shape in the case of donkey dung, or black and dry in the case of goat dung; 3 (recent): dung fresh or at least still black and not dried out. If dung of different classes was found in a 10 metre section, the highest score was noted. Zero was given in the absence of dung. Scores were then added up over the whole transect, giving a value between zero and 30 which was used as an index of goat / donkey use of the habitat. The occupancy scores are not directly comparable between the two species because of the much larger numbers of goats present in Paulshoek, differences in herd size, different dung quantities produced by individuals of the different species, and other factors. The scores are therefore compared within each species to determine habitat preferences.

The occupancy scores reflect intensity and frequency of use per area; they do not show where a donkey or goat spends the greatest proportion of its time, since the areas are of vastly different sizes. In this respect, the methods of this study differ from those used in most studies of habitat preference (e.g. McKnight 1958; Woodward and Ohmart 1976; Seegmiller and Ohmart 1981), where direct observation of the animals was used to determine habitat preferences. However, the percentage spent in each habitat does not necessarily indicate preference, as it may to some degree be a function of availability. For example, 30 % of the day spent on a habitat which makes up 70 % of the total available area does not indicate the same degree of preference nor the same animal densities experienced by that habitat as the same percentage of time spent in a habitat which constitutes only 10 % of the total area. The impact of donkeys, as well as the intensity of competition is better measured by estimating the intensity of use.

The degree of rockiness along a transect was given a rating between 1 (no or very little rock cover) and 5 (many and large rocks covering all or most of the ground).

Each transect was classified into one of four broadly defined habitat categories, which are largely based on topography and other physical characteristics.

- Category 1 contains the riverine areas, which are characterised by sandy soils. Transects were walked in or immediately next to the river.
- Category 2 comprises flat areas with deep, sandy soils and little or no rock cover. These were generally former crop lands, because these areas are the only ones suitable for cropping; some may have been modified to their present rock-free, level state through ploughing.
- Category 3 encompasses all flat and gently sloping areas with some rock cover, which generally constitute foothills between the river valleys and the steeper mountain slopes.
- Category 4 includes all steep, rocky slopes which are covered by large rocks.

The most abundant plant species were noted in each transect with the aim of obtaining vegetation categories by means of cluster analysis (DCA and correspondence analysis).

The positions of permanent and non-perennial water sources and stock posts were plotted on the map (M. T. Hoffman, unpublished data). For each transect, the distances from the nearest perennial and non-perennial water source and from the nearest stock post were measured on the map (Fig. 3) and converted to metres.

The locations of the transects were chosen on the map to evenly represent a variety of habitats, but randomly with respect to potential donkey or goat presence.

Donkey occupancy scores were plotted against habitat type, rockiness score, distance from nearest perennial water source, distance from nearest non-perennial water source and distance from nearest stock post. Average donkey and goat scores and their standard deviations were plotted for each of the habitat categories and for the different degrees of rockiness. Kruskal-Wallis (non-parametric) ANOVAs were performed to test for significant differences within each species in the use of different habitat types, with the null hypothesis that habitat use is random and occupancy scores are therefore the same in each habitat type. Spearman rank coefficients were calculated for the correlation between rockiness and donkey and goat scores. Correlation coefficients (Pearson's product moment) were calculated for the relationships of distances from water points and stock posts with animal occupancy scores. All tests were performed using the statistical package STATISTICA.

Mapping habitats

The areas falling under the four abovementioned habitat categories were superimposed on a 1:50 000 map (Fig. 3), using field observation during transect sampling as well as stereo pairs of aerial photographs. The topography in the study area is very heterogeneous, with many small enclaves of one habitat type within the other (especially in the case with steep and gentle rocky slopes), and some of this small scale variation is not resolved on the map. This should not affect the estimation of the overall locations and proportions of the different habitat types in the landscape.

The total area occupied by each habitat type within the study area was determined by photocopying the map, cutting out each area with fine scissors and weighing all the pieces belonging to each category to determine the percentage each occupies on the map. The size of the whole mapped area was determined by running the section of the map through an area meter (usually used to measure leaf area) and converting the result to hectares.

Diet selection

Feeding groups of animals were observed using binoculars. Goats could be approached to within ten metres without disturbing their feeding activities, but donkeys were more wary and would often turn around, walk away or stare intently when they were approached to within a distance of about 30 m or less. A feeding group of animals was observed for as long as possible before they became shy, moved away, or started ruminating (in the case of goats). Every five minutes, note was taken of which plant species each animal in sight was busy eating. If an animal spent longer than five minutes eating a particular plant, two (or more) observations for that plant were noted. When the herd moved on, plants were investigated for evidence of herbivory to confirm the correctness of the observations. At the same time, note was taken of the characteristics of goat- and donkey- browsed plants (depth of bite, maximum diameter of branches bitten off and whether plants were uprooted or otherwise damaged). This information was used to assess differences in damage caused by the two species.

Modelling daily food intake

Daily food intake is most commonly measured using oesophageal fistulas, which require a surgical procedure and were not a viable option for this study. In some other studies (e.g. Owen-Smith and Cooper 1987; Dumont *et al.* 1995), intake was determined by observing bite rate and size and collecting plant matter by clipping plants in such a way as to simulate biting. This method was also unsuitable for this study, firstly because of time constraints, and secondly because donkeys could not be approached closely enough to obtain a good impression of bite size. It was therefore decided to use a mathematical model to predict daily intake of ruminants and non-ruminants.

Model structure

The daily dry matter intake of donkeys and goats was predicted on the basis of the animal's body weight and the digestibility characteristics of the diet consumed. The model was originally developed for ruminants (Illius and Gordon 1991) and a version for non-ruminants was later developed, based on their different digestive systems (Illius and Gordon 1992). The model was prepared for use and modified to include the effect of night kraaling in goats by Dr. David Richardson (Applied Mathematics Department, U.C.T.).

The model assumes that intake is not limited by the availability of forage, but by clearance of digesta and residues from the gut. Components of the digesta, such as the cell contents, particles of cell wall and microbial matter, are depicted as a number of compartments with unidirectional flow between them in the rumen (goats) or stomach and large intestines (donkeys). The primary site of fermentation (either rumen or large intestine) is taken to be the site of physical intake control. When, due to digestion and passage, the digesta load falls below a certain threshold, more food is ingested to refill the guts and maintain a specified average daytime digesta load (Illius and Gordon 1992).

A sensitivity analysis was performed to investigate the effect of varying input variables on intake predictions and to identify the parameters which influence the result most strongly. Predictions for animals in Paulshoek were made using data obtained in this study, data from literature and approximations where no data was available.

Input variables

1. Animal weights. These were not measured directly in the study area due to time, practical and financial constraints. A wide variety of goat and donkey weights appears in the literature (Table 1). The estimate of a donkey weight of 91 kg (Kazirer-Izraely, pers. comm. in Illius and Gordon 1992) seems to be an extremely small value. For the sensitivity analysis, weight ranges of 150 to 300 kg for donkeys and 20 to 50 kg for goats were used.

Table 1: Goat and donkey weights reported in various studies.

Weight (kg)	Study area	Breed	Source
Goats			
14 kg	India	Zalawadi	Solanki 1994
18 kg	Brazil	no specific race	Pfister and Malenchek 1986)
18 - 26 kg	Zimbabwe	indigenous breed	Nyamangara and Ndlovu 1995
23 - 47 kg	Northern Kenya	Small East African; Galla	Rutagwenda et al 1990
33 kg	Southern Italy	Maltese; Rossa Mediterranea	Fedele et al 1993
40 kg	Angora (yearling)	Texas, USA	Ekblad et al 1993
52 kg	Southern France	local Rove breed	Dumont et al 1995
Donkeys			
130 - 300 kg	Northern Kenya		Rutagwenda et al 1990
91 kg	?		Kazirer-Izraely, in Illius and Gordon 1992
183±19.7 kg	U. S. A.		Mueller et al. 1994
250 kg	France		Tisserand et al. 1991

2. <u>Diet characteristics</u>. The digestibility characteristics required to run the model are the fractions of cell contents (CC), digestible cell wall (DCW) and indigestible fibre (INDF) of the plants eaten. The sum of these parameters is 1. For a few plant species (e.g. certain grasses, Richardson pers. comm.), these parameters are available in the literature; where such data is unavailable, their values can be approximated using digestibility data.

The values of CC, DCW and INDF can be calculated if the in vitro digestible organic matter content (IVDOM) of the diet and some additional information on digestibility data is known. For example, the percentage of neutral detergent fibre (NDF), the percentages of dry matter (DM), in vitro digestible organic matter (IVDOM) and ash can be used to calculate CC, DCW and INDF:

CC = DM - NDF - Ash

INDF = DM - IVDOM - ASH

DCW = (DM + Ash) - CC - INDF

All three values are then divided by (1 - DM - Ash) to convert to fractions of 1.

The fraction of NDF of Karoo plants or diets consumed by herbivores in the Karoo are not available. In arid Mexican shrublands, goat diets were found to have an NDF content of 0.6-0.7 (Ramirez et al. 1990) and 0.6-0.8 in a semi-arid area in Zimbabwe (Nyamangara and Ndlovu 1990). these values were used as a guideline.

IVDOM (in vitro digestibility of organic matter) and DOM values have been experimentally determined for a variety of feed plants including Karoo shrubs (Brand 1992) as well as diets of oesophageal fistulated animals. IVDOM can be calculated by multiplying total digestibility D by 1.1 (Richardson, pers.

comm.). Digestibility values have been determined for a variety of plant species and herbivore diets, including a variety of Karoo plants (Brand 1992) and goat and cattle diets on Karoo pastures (Zeeman et al 1983).

It is possible to determine digestibility of the diet from faecal nitrogen content, using the following regression (Holmes and Curran 1967):

$$D = 0.4433 + 0.00913\ Fn$$

where D is digestibility as a decimal fraction and Fn is faecal nitrogen in $g.kg^{-1}$.

This regression was determined using sheep and has been used to determine the quality of cattle diets (Holmes and Curran 1967). In animals where substantial microbial fermentation of the food occurs, the faecal nitrogen concentration increases with digestibility. In diets with a higher digestibility, more microbial nitrogen is produced per unit of food since the substrate supports greater microbial growth, and the proportion of faeces relative to microbial nitrogen is smaller (Richardson, pers. comm.).

Strictly speaking, a regression derived for ruminants cannot be applied to donkeys which are hindgut fermenters, as the parameters are somewhat different. No regression for determining diet quality of non-ruminants from faecal nitrogen has been published. It is therefore not possible to obtain an exact figure for the quality of the diet consumed by donkeys from the faecal nitrogen data. However, the concept remains valid and faecal nitrogen is useful for obtaining a reasonable estimate of digestibility (Richardson, pers. comm.).

In September, 15 samples of goat dung and 16 samples of donkey dung were collected. Only fresh dung in the vicinity of the study animals was taken. Samples were air dried, oven dried at 70°C and ground in a Wiley mill to pass through a 0.4 mm mesh. Each sample was thoroughly mixed, and 0.05 g were used to determine the nitrogen content using the Kjieldahl digestion method followed by colorimetric analysis. The digestibility values thus determined were used to predict daily intakes in spring; values for summer are estimated using data from the literature.

3. k_2. This is defined as the fractional degradation rate (per hour) of the food in the foregut and is a property of the diet. For goats, the variable k_2 is calculated as follows:

$$k_2 = -\frac{D_{ru} * k_3}{D_{ru} - IVDOM}$$

where D_{ru} is rumen digestibility (about 85% of total digestibility) and k_3 is the passage rate of small particles in the foregut, which is related to animal weight.

4. Ash. This is a measure of mineral content of the diet. Values for Karoo shrubs range between about 0.05 to 0.15, and most are close to 0.1 (Brand 1992).

5. Feeding time. The goat model allows for night kraaling, and the times when the animals start and stop feeding can be changed. For the prediction of intakes of goats in Paulshoek, there variables were set at 6 a.m. and 6 p.m.; For comparison, a feeding period of 24 h was included in the sensitivity analysis. the model simulates feeding cycles each lasting three hours. During each cycle the goat starts eating, stops when the rumen is filled and then ruminates. The model is set so that feeding cycles start at 3 am.; 6 am.; and every three hours until midnight.

Damage

The number of uprooted plants or plants that appeared to have been damaged by livestock or donkeys was noted for each transect. Uprooted plants were only counted when their bark was intact to avoid including rodent and termite damage (evidence of which was observed in the study area) in the data set. The aim was to correlate the number of damaged plants to donkey or goat scores to indicate which species caused high levels of damage.

It proved difficult to determine conclusively which damage (e.g. broken branches) was due to livestock. Plants which have been uprooted may also be consumed entirely if they are not too woody, leaving no evidence. Uprooted plants may not necessarily be a result of animal feeding: humans are also known to uproot plants for their own use. For example, some mesembs (particularly *Polymita albiflora*, an unpalatable species known locally as "muisoor") are pulled up and packed tightly together around the cooking shelters that form part of the stock posts. Individuals of this species were sometimes seen lying around.

Results

Habitat selection and overlap

Influence of habitat category

Donkey and goat dung was found in all areas covered by transects. The four habitat categories were classified largely according to their topography and physical characteristics. DCA and correspondence analyses (Figure 4) of the vegetation show no discrete groupings, but there is some agreement between habitat categories and vegetation. Riverine areas are characterised by grass,

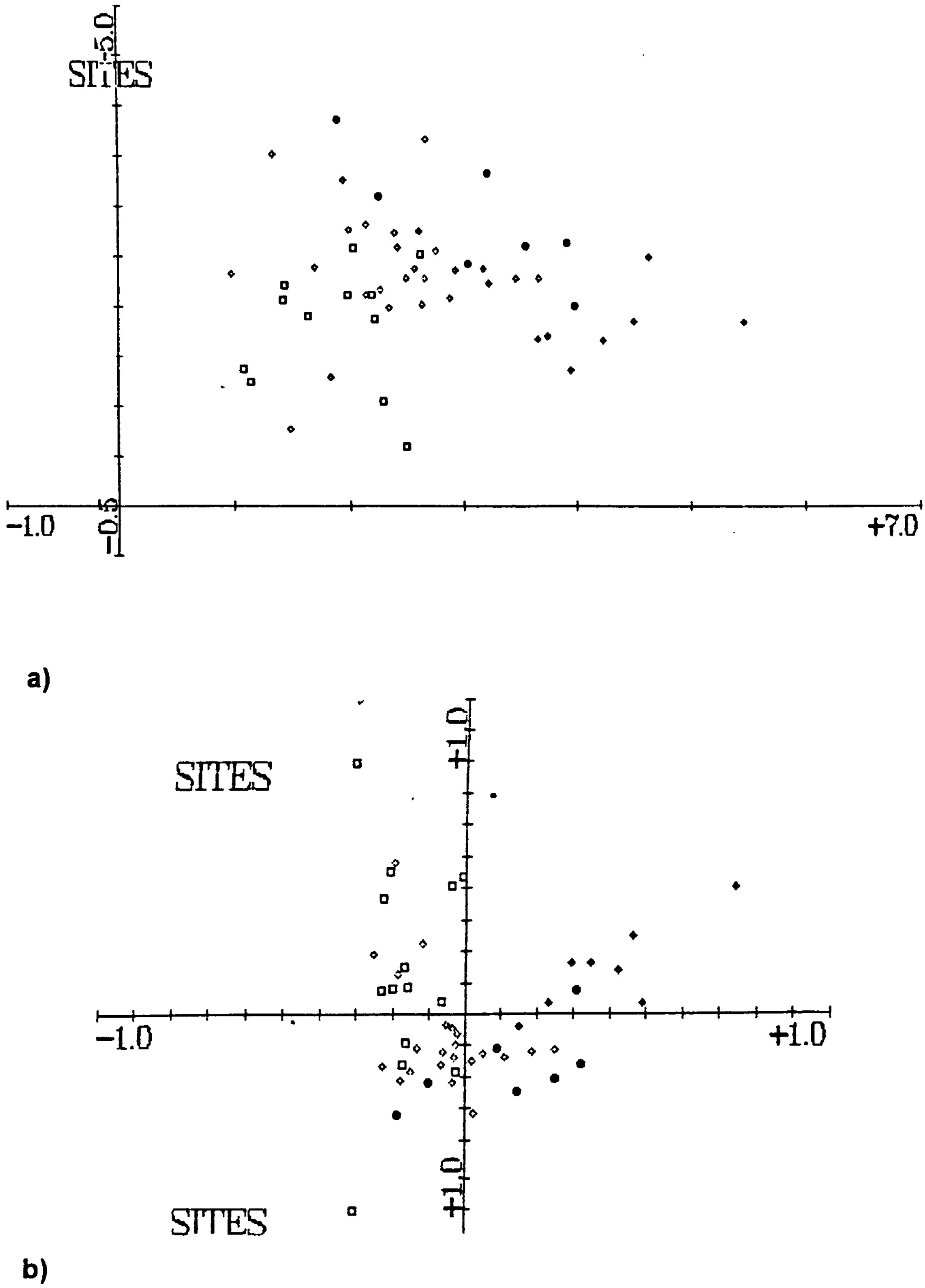


Figure 5: DCA (a) and correspondence analysis (b) of transects in the four habitat types (♦ - riverine; ● - sandy pediment; ✧ - rocky pediment; □ - steep rocky slope) according to the common plant species found.

sedges and renosterbos (*Elytropappus* sp.) which were seldom found anywhere else. *Galenia africana* and *Lycium* spp. are also frequently found in riverine areas. The sandy pediments are generally covered in *Galenia africana* (found on all but one of the transects in this habitat type). These areas have the lowest diversity of common plants. Habitats 3 and 4 are quite similar in their vegetation; Crassulaceae are mostly confined to the steeper rocky slopes. The latter areas are also seldom home to *G. africana*, which is common in all the other habitats. "Muisoor" (*Polymita albiflora*) is found exclusively on the rocky pediments and slopes.

Kruskal-Wallis tests were used to determine whether different habitats were used significantly more intensively than others, the null hypothesis being that all areas are used randomly and occupancy scores are therefore the same in each habitat. A highly significant relationship was found to exist between donkey scores and habitat type ($H = 20.4$; $n = 66$; $df = 4$; $p = 0.0001$). The relationship between goat scores and habitat type is not significant at the 5 % level ($H = 5.6$; $n = 66$; $df = 4$; $p = 0.23$).

Figure 5 shows average donkey and goat scores, their standard errors and their standard deviations in the different habitats. Donkey scores were highest in riverine areas, followed by sandy pediments, and extremely low in the steep rocky areas. Goat scores were not significantly influenced by habitat type.

Influence of rockiness

Spearman Rank Order correlations of goat and donkey scores against different degrees of rockiness show that both relationships are significant at the 5 % level. Donkey scores against rockiness had a higher R value ($R = -0.64$; $n = 66$; $p < 0.001$) than goat scores ($R = -0.29$; $n = 66$; $p = 0.018$), indicating that donkeys avoid rocky areas more than goats. Figure 6 shows the average scores and their standard deviations at different degrees of rockiness.

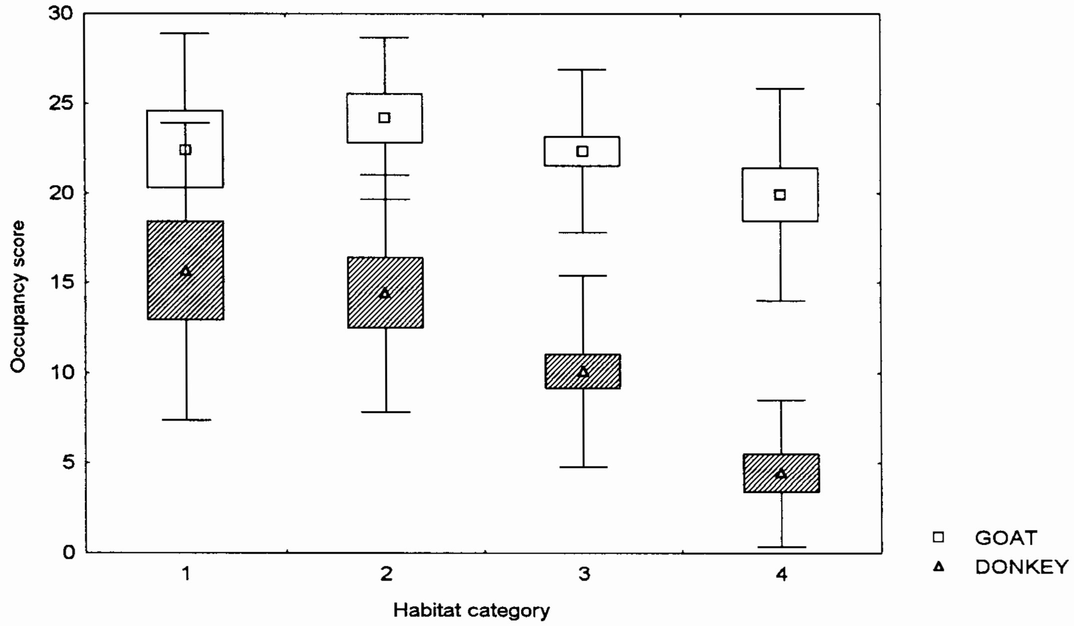


Figure: Goat and donkey occupancy scores in the four different habitat types. (1: Riverine areas; 2: Sandy pediment; 3: Rocky pediment; 4: Steep rocky slope). Graph shows means, standard errors and standard deviations.

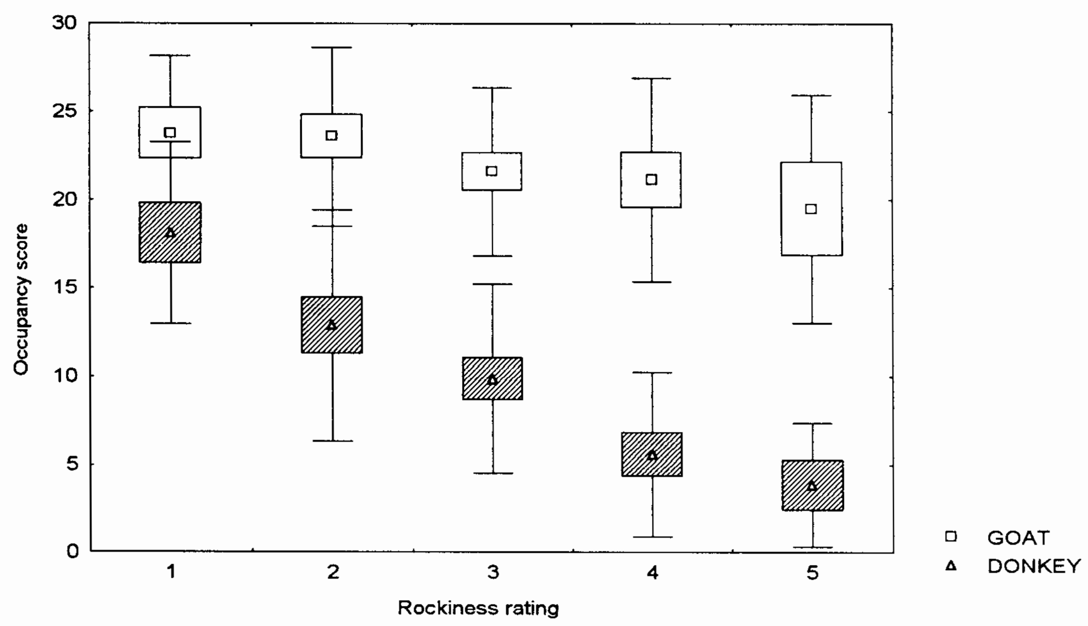


Figure 6: Goat and donkey occupancy scores at different degrees of rockiness, increasing from 1 (little or no rock) to 5 (extremely rocky with large rocks). Graph shows means, standard errors and standard deviations.

Distance from water points

Distances of transects from the nearest permanent water point ranged from 0 to 2550 m; distances from the nearest non-perennial water source were between 0 and 2350 m. Neither donkey nor goat scores showed any significant correlation with distance from permanent water points (goats: $r2 = 0.016$; $n = 66$; $p = 0.31$; donkeys: $r2 = 0.0015$; $n = 66$; $p = 0.76$). Donkey occupancy scores declined with distance from non-permanent water points ($r2 = 0.063$; $n = 66$; $p = 0.043$), but not goat scores ($r2 = 0.0007$; $n = 66$; $p = 0.84$). Correlation analysis of donkey and goat scores against the distance from permanent and non-permanent water using only the transects done in the dry season showed no significant relationships.

Distance from stock posts

Neither donkey nor goat scores were significantly correlated with distance from the nearest stock post (goats: $r2 = 0.0001$; $n = 66$; $p = 0.93$; donkeys: $r2 = 0.0008$; $n = 66$; $p = 0.82$). These distances ranged between 150 and 2250 m.

Mapping the habitats

The total size of the study area is 2780 ha. The proportions of each habitat type in the study area are shown in Table 2.

Table 2: The percentages of the total area occupied by each habitat type, and some of the characteristic plants found in each.

Habitat type	% of total area	Characteristics and common plants
1: Riverine	6	Sandy; inundated annually. Grass, sedge, *Elytropappus* sp.
2: Sandy pediment	9	Little rock cover, deep soils, slopes flat or gentle. *G. africana*; some *Lycium* and *Z. microphyllum*
3: Rocky pediment	33	Soils shallower, slopes flat or gentle. Variety of asteraceous shrubs and mesembs
4: Steep rocky slope	52	Slopes steep with high rock cover. Variety of asteraceous shrubs and mesembs; Crassulaceae

Diet selection and overlap

Since the vegetation was different in each of the areas where feeding observations were done, the results are difficult to compare directly. What is eaten in each observation is influenced by what is available. For example, a score of zero percent of a certain species in a feeding observation may indicate avoidance by a herbivore, or simply that the species does not grow in the observation site. Therefore, abundance rankings of all the species in the observation site are included in Table 2 (0 = absent; 1 = rare; 2 = common and 3 = abundant), in which the percentages of plants ingested by donkeys and goats area shown. The botanical compositions of donkey and goat diets were observed to be very similar.

Asteraceous shrubs with ericoid leaves (e.g. *Pentzia incana*, *Eriocephalus africanus*) made up a large proportion of the plants eaten wherever these plants were available. Mesembs were commonly eaten as well, but seemed to be more prominent in goat than in donkey diets. Both animal species displayed a strong liking for the two *Lycium* species present in the study area, and *Lycium* bushes (especially in the heavily grazed flat areas), show obvious evidence of grazing. Soft-leafed asteraceous shrubs such as *Osteospermum* spp. were also heavily grazed by donkeys and goats, but these plants are relatively scarce and therefore did not make up a large proportion of the animals' diets. The grass found in the riverine areas was commonly eaten by both species, but since goats were not observed in riverine areas during formal observation sessions, the data does not reflect this. Both donkeys and goats were observed to eat the grass on other occasions. Donkeys commonly eat the sedge found in riverine areas; whether goats eat this plant is not known, as they were not observed in areas where it grew. *Lebeckia multiflora* is a palatable plant eaten by goats when it is available. In many areas, this species is not found and donkeys were not observed near it. People in Paulshoek say that donkeys eat *L. multiflora* as well. Herbaceous annuals (mostly Asteraceae) form a large proportion of the

Table 2: Diets of goats and donkeys based on feeding observations. Each figure represents the percentage of the total (N) feeding observations made up by each plant group. The figures in bold to the right of each column indicate availability where 0 = absent; 1 = rare; 3 = common and 4 = abundant.

Goats

Location	**Witbank**		**outside Paulshoek**		**outside Paulshoek**		**Diepknik**	
Habitat type	**3**		**3**		**3**		**3**	
date	**30/4/96**		**2/8/96**		**2/8/96**		**12/9/96**	
Ast shrub (ericoid)	19.4	2	31.3	2	25.6	2	35.3	**2**
Ast shrub (soft)	0	0	0.5	1	8.4	1	8.6	**1**
Mesemb (exc M. c.)	67.7	2	13.5	2	55	3	0.7	**2**
M. crystallinum	0	1	0	1	0	1	0	**1**
Lycium spp	0	1	41.8	2	8.9	1	22.8	**2**
Grass	3.2	1	0	0	0	0	0.7	**1**
Sedge	0	0	0	0	0	0	0	**0**
Hermannia	0	0	0	1	0	1	0	**0**
Zygophyllum micro.	0	0	0	0	0	0	0	**0**
Lebeckia multiflora	6.5	0	12.9	1	2.1	2	0	**0**
Herbaceous annuals	0	0	0	0	0	1	34.5	**2**
Galenia africana	3.2	3	0	1	0	2	0.7	**2**
Euphorbia spp.	0	2	0	2	0	2	0	**1**
Total	**100**		**100**	2	**100**		**100**	
N	**31**		**201**		**191**		**136**	

Donkeys

Location	**Vaalwater**		**Paulshoek village**		**Diepknik**	
Habitat type	**1**		**2**		**3**	
date	**27/4/96**		**1/8/96**		**12/9/96**	
Ast shrub (ericoid)	50	**2**	0.7	**1**	38.8	**2**
Ast shrub (soft)	0	**0**	0	**0**	0	**0**
Mesemb (exc M. c.)	0	**2**	1.4	**1**	0	**2**
M. crystallinum	0	**0**	63.3	**3**	0	**0**
Lycium spp	8.3	**1**	1.4	**1**	27.2	**2**
Grass	28.4	**2**	0	**0**	0	**1**
Sedge	0	**1**	0.7	**1**	0	**1**
Hermannia	0	**0**	18.1	**2**	0	**0**
Zygophyllum micro.	8.3	**3**	0	**0**	10.7	**3**
Lebeckia multiflora	0	**0**	0	**0**	0	**0**
Herbaceous annuals	0	**0**	3.4	**2**	22.3	**2**
Galenia africana	5	**3**	11	**1**	1	**2**
Euphorbia spp.	0	**2**	0	**0**	0	**2**
Total	100		100		100	
N	60		144		103	

diet when they are available. The asteraceous annuals commonly found in large, dense expanses in Namaqualand (the Namaqualand daisies) are not very abundant in Paulshoek, possibly as a result of the heavy grazing pressure.

The *Ruschia* species known as "!naroevy", which is considered by stock farmers to be one of the most palatable and valuable browse plants was not present in any of the sites where feeding observations were made.

There are some differences between donkey and goat diets. *Mesembryanthemum crystallinum* (known locally as "soutslaai") is a fleshy, fast growing plant which has a relatively high salinity. Neither animal ate this species in the dry season when the salinity of the plant tissue was very high. While donkeys ate large amounts of *M. crystallinum* after the rains when large new creeping shoots were rapidly produced, goats still avoided this species. It appears, however, that this plant makes up a significant proportion of the diet only for only a short time of the year, and only in the disturbed areas (the sandy pediments which have been ploughed) where it proliferates.

Another species which donkeys like to eat but which does not seem to be important to goats is *Hermannia amoena*, known as "jeukbos". This plant is described as unpalatable (le Roux *et al.* 1988), although some people report that goats sometimes eat this plant.

Zygophyllum microphyllum was observed to be eaten by donkeys in the areas where it is abundant, although it does not appear to be one of the strongly preferred species. Goats were not observed to eat *Z. microphyllum*, but they were not observed in areas where it was common.

Galenia africana is unpalatable to livestock and causes "waterpens", a serious sickness which often kills animals. Donkeys are known to eat and tolerate moderate amounts of it. It does not appear, however, that *G. africana* is an important part of donkeys' diets. Also, while donkeys were sometimes observed to rip several branches off *G. africana* shrubs, closer inspection afterwards often revealed that most or all the branches lay scattered around the bush, and little if anything was eaten.

There are two common *Euphorbia* species in Paulshoek: *E. mauritanica* ("bittermelkbos") which is toxic and is never eaten by donkeys or livestock, and *E. decussata* ("soetmelkbos"), which is grazed by both, but only at certain times of the year according to people in Paulshoek. No direct feeding observations were made where animals ate *E. decussata* , but most individuals of this plant species showed evidence of grazing. No species which were eaten by goats but avoided by donkeys were identified.

Daily food intake

Sensitivity analysis

The model was run using a standard set of variable values, changing only one variable at a time (except for DCW, CC and INDF, which change interdependently). Figures 7-9 show the effect of changes in different variables on the model output.

Animal weight has a strong influence on the model output; within the ranges of goat and donkey weights reported in the literature for each species, the variation in daily intake is considerable. A donkey weighing 250 kg eats 50% more than one weighing 150 kg. Donkeys have a higher intake per unit of body mass. The relationship between animal weight (W) and predicted daily food intake is linear; usually, intake is scaled linearly with $W^{0.75}$ (e.g. Dumont et al. 1995). Illius and Gordon found, using the same model, that the allometric coefficient which scales energy intake to body mass is 0.88 in ruminants and 0.82 in hindgut fermenters. The reason the model predicted a linear relationship may be that another parameter which changes with weight was kept constant; k_3 (the passage rate of small particles in the foregut / large intestine) is directly related to weight, but the model did not appear to adjust the k_3 value at different weights. For the final output, however, the k_3 values for 35 kg (goats) and 250 kg (donkeys) were available in the reference file, and the intake predictions for donkeys and goats should be correct.

The k_2 value (fractional degradation rate of cell wall in the foregut/large intestine) influences daily intake more strongly in donkeys than in goats. For goats, k_2 values commonly range between 0.02 and 0.1 (Richardson, pers. comm.); over this range, differences in the predicted daily food intake are relatively small. Donkey k_2 values are generally smaller than for goats, because donkeys tend to eat diets of a lower quality.

Compared to other variables, the ash content of the diet has a negligible influence on predicted intakes of both species. Figure 7 shows the response of intake predictions to changes in weight, k_2 and ash content of the diet.

Intake increases with increasing fractions of DCW and CC, while a high proportion of INDF leads to lower intake (Figure 8). Intake increases more sharply with increasing CC than with increasing DCW. These trends are the same in donkeys and goats. At any given DCW, variations in CC (or INDF) lead to considerable variation in the predicted intake.

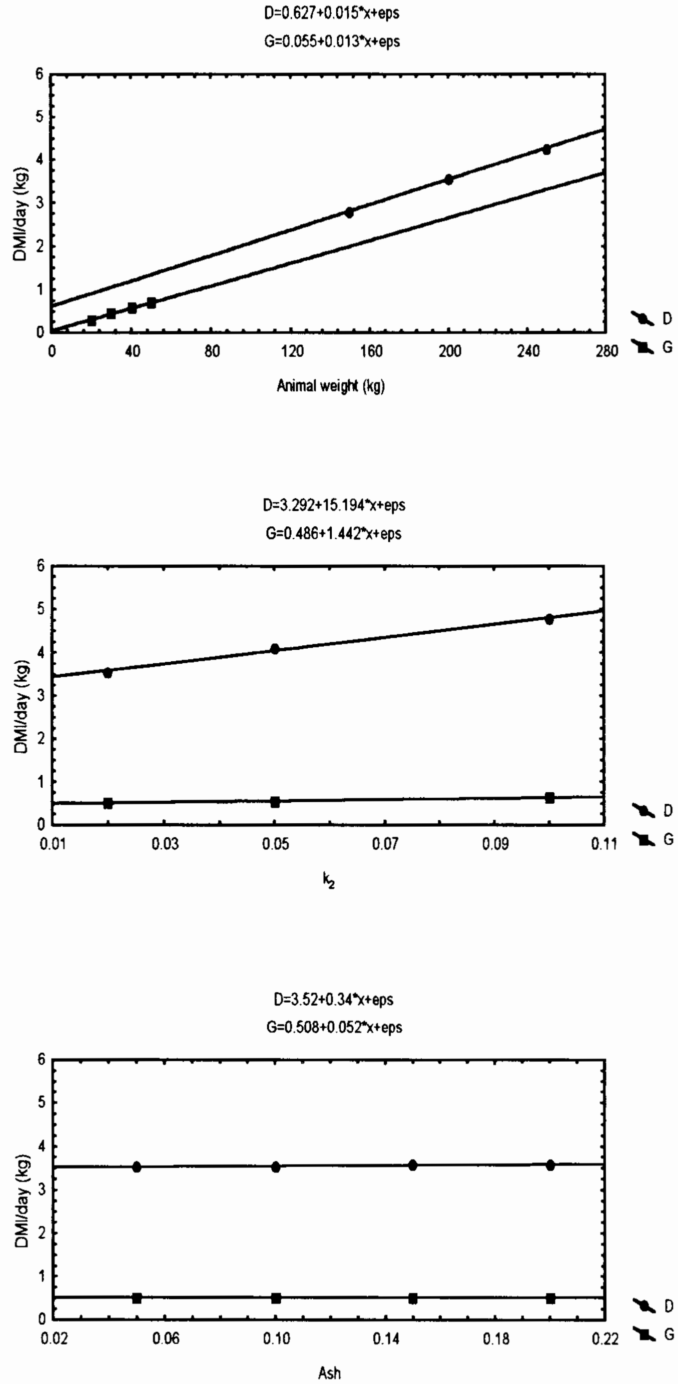
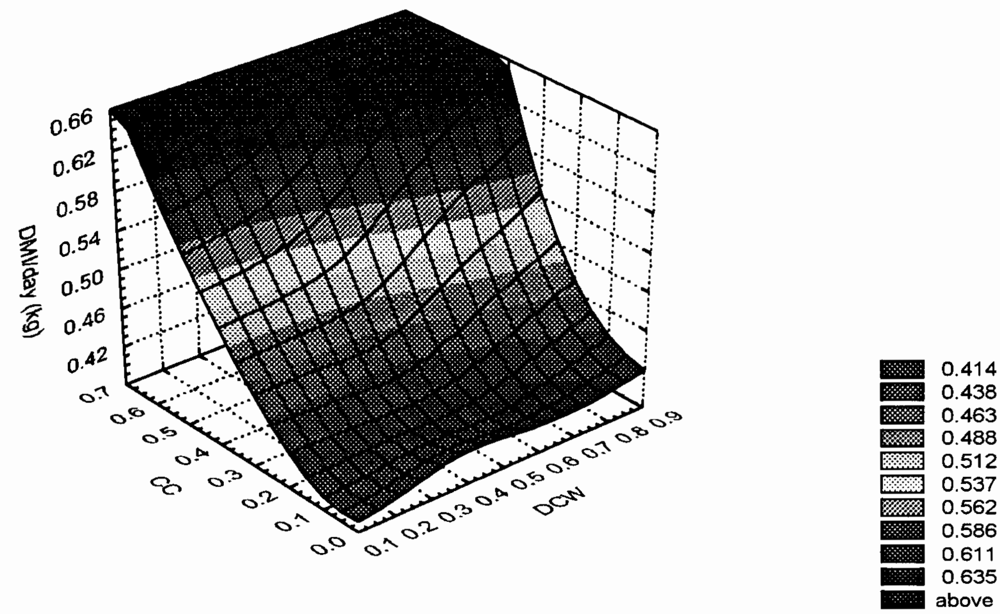
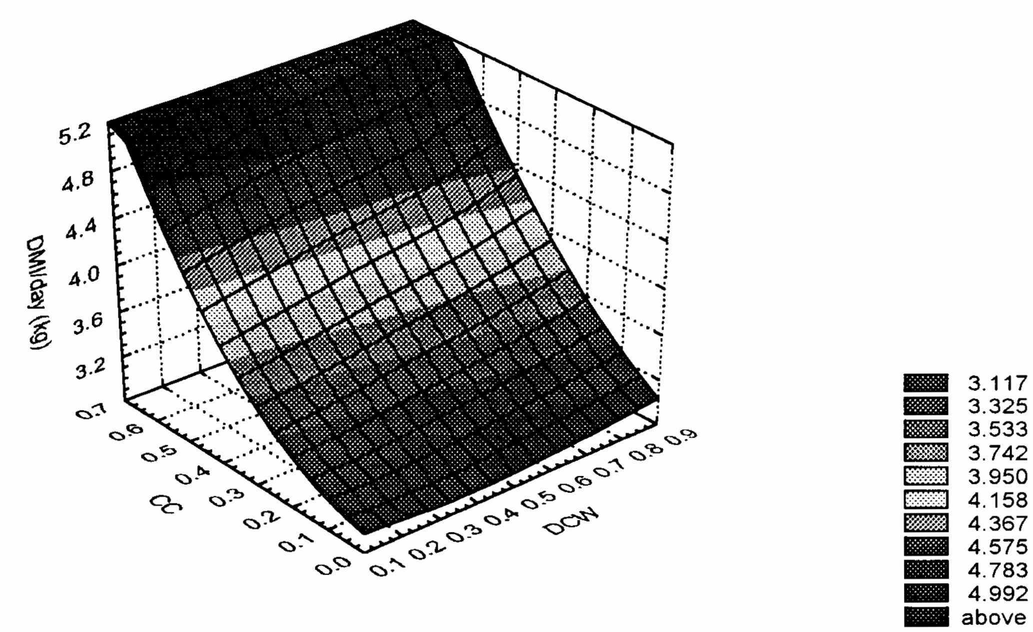


Figure 7: Predicted daily dry matter intake (DMI/day) at different weights, k_2 and ash content of the diet



Goats



Donkeys

Figure 8: Daily dry matter intakes (DMI/day) of (a) goats and (b) donkeys at different proportions of DCW and CC.

Effect of kraaling

Intake increases with longer feeding time in goats, where night-time kraaling was simulated. Intake over 24 h was not, however, twice as much as intake for 12 h starting 6 am (see Figure 9). The reason for this is that goats have to ruminate and hence they are unable to feed continuously. No simulation model for donkey kraaling is available. As in the case of goats, however, donkeys are unable to feed continuously because of the limits imposed by digestion (Illius and Gordon 1992; Richardson, pers. comm).

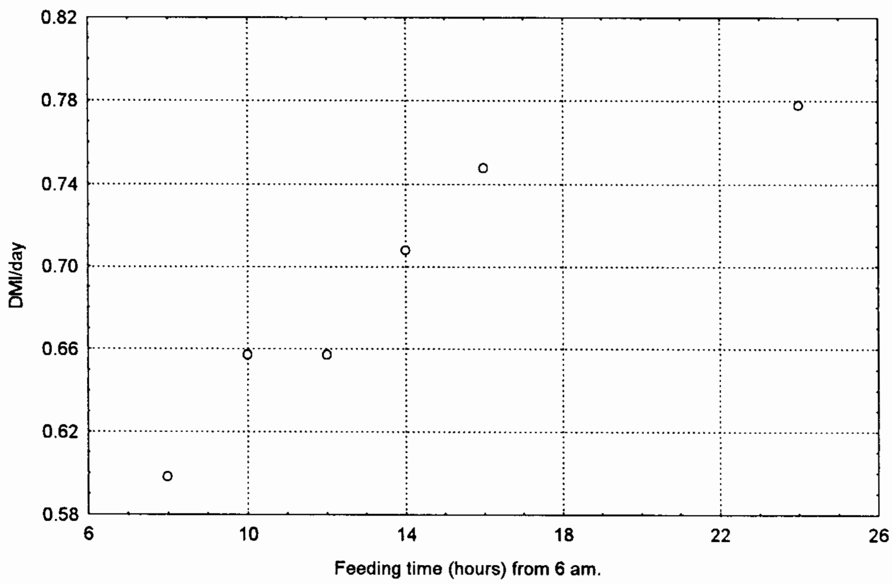


Figure 9: Daily food intake (DMI/day) at feeding times of different length. All feeding periods start at 6 am. except for the 24 h period which starts and ends at midnight.

Table 4 shows the values of the variables used for the final output. Digestibilities of the spring diets were determined from the faecal nitrogen analysis. The digestibility of goat diets in September in Paulshoek was calculated to be 74.2±5.3 %. Donkey diets have a digestibility of around 50% (49.3±1.9 % according to the regression). Other digestibility values were taken from a study of the diet qualities of goats, cattle and sheep in the Karoo (Zeeman et al. 1983). Their goat diet digestibility values for the dry season were used for predicting intake by goats in summer, and in the absence of donkey diet data for the Karoo, cattle diet values were used from the above source. Cattle and donkey diets were found to be very similar in quality in a study of goats, sheep, camels, cattle and donkey diets in the arid North of Kenya (Rutagwenda et. al. 1990).

Table 4: Variable values and predicted daily food intakes (DMI/day) of goats and donkeys in spring and summer

Variable	**Goats Spring**	**Goats Summer**	**Donkeys Spring**	**Donkeys Summer**
Weight (kg)	35	35	250 / 200	250 / 200
DCW	0.71	0.5	0.57	0.36
CC	0.25	0.12	0.12	0.12
INDF	0.04	0.38	0.31	0.52
k2	0.119	0.116	0.1	0.05
Ash	0.1	0.1	0.1	0.1
DMI/day (kg)	**0.75**	**0.54**	**5.7 / 4.8**	**4.7 / 3.9**

Daily food intakes of goats are 0.75 kg dry matter per day in the wet season and 0.54 kg per day in the dry season. Food consumption decreases in summer as the digestibility of the diet declines. The daily dry matter intake of donkeys ranges between 4.8 and 5.7 kg in spring and 3.9 and 4.7 kg in summer. The ratio in food intake of donkeys and goats is thus 7.2 in summer and 5.0 in spring (donkey and goat weights 200 and 35 kg respectively), and 8.6 in summer and 7.6 in spring when donkey weight is set at 250 kg. Food intake of donkeys varies considerably with weight: the 50 kg difference in body mass results in a 1 kg difference in daily dry matter intake, and hence in a shift in the donkey - goat intake ratio of more than 1. Contrary to predictions based on the digestive physiology of equines, food intake of donkeys does decrease as diet quality declines, but at a lesser rate than that of ruminants. The ratio of donkey and goat feed intakes thus widens considerably in summer when diet quality is low.

Damage

During transect observations, a total of 42 uprooted plants that were almost certainly pulled up by grazing herbivores were observed. The total area of the 66 transects is 132 000 m^2 (13.2 ha), which gives a rate of one plant uprooted in every 3.2 ha if we extrapolate.

Other damage, such as plants with many broken branches, was observed in some of the transects but recording this was discontinued when it became apparent that it was generally very difficult to identify what the damage was caused by. Overall, the impression gained was that the effects of heavy grazing *per se* in many areas, such as severely reduced plant size and reduced vegetation cover, are much more prominent and have a greater influence on animal production.

Three "rolplekke" (places where donkeys roll on their backs) were found during the study period; these consist of sandy patches of about 2-3 m in diameter and are caused by repeated rolling of several donkeys in the same place. These rolling places are also given as an example of damage done by donkeys, as nothing grows on them. I observed several donkeys rolling in the same place after each other, and according to a farmer in Paulshoek, these places are used repeatedly, which explains why plant life is unable to re-establish there. Again, however, the total plant production lost as a result of these rolling places is very small compared to the effects of overgrazing.

When feeding, donkeys were observed to bite far more deeply into the wood of shrubs than goats do. While goats feed very nimbly, stripping the leaves off the branches without consuming or breaking off the latter, donkeys are less selective. In addition, donkeys have an upper and a lower set of incisors, which enables them to bite off fairly thick branches. After one feeding observation, the maximum diameters of *Pentzia incana* branches that had been bitten off by donkeys were measured. The average maximum diameter was 3.4±0.3 mm. This corresponds to a main axis in this species, which does not have thick branches. Pieces of branches this thick were also frequently found in the faeces of donkeys. The depth of the bite was up to about 10 cm (measured inwards from the tips of uneaten branches). Whereas goats ate leaves in localised places on the plant, donkeys tended to systematically bite off all the plant matter in a section of the plant. Both species were observed to pull at plants; no instances where plants were uprooted were observed. Donkeys were sometimes seen to pull off whole branches of plants (especially *Galenia africana*), of which they would eat very little (if anything) before dropping them on the ground. When *Mesembryanthemum crystallinum* shoots grew rapidly after the rains, donkeys ate large amounts of that species. In the vicinity of feeding donkeys, one could often find large plants that were trampled and that had long pieces of their fleshy branches scattered around them.

Discussion

Habitat overlap

The movement of donkeys is much more strongly influenced by habitat type than that of goats. Donkeys show a strong preference for the riverine and sandy areas, which they may prefer for a variety of reasons. Goat occupancy scores, on the other hand, are not significantly different in the different habitats. Part of the reason why goats appear to be less selective may be the fact that they are herded and therefore do not always determine themselves where they graze. Sheep are also present in the area, and the observed effect includes habitat selection by mixed herds.

Donkeys may select the riverine and flat areas because their preferred forage grows there. Riverine areas represent a food reservoir in the dry season, when plants elsewhere are generally dry and grazing pressure has taken its toll. However, when the vegetation in the other areas starts to regrow after the rains, the riverine areas may no longer be nutritionally superior since they are more sparsely vegetated. It is however possible that donkeys have a preference for grass all year round, and this is not commonly found outside the riverine areas. Turner (1984), for instance, found that habitat use by donkeys (scored by counting the number of scat piles and donkey tracks leading off transects) was positively correlated to grass abundance. Goats, which are generally viewed as browsers, were also found to have a strong preference for grasses in the arid piedmont of Argentina (Grünwald *et al.* 1994), selecting a greater proportion of grasses in their diet than were available in the range. Grasses were found to have higher digestibility values than shrubs in a study of livestock diets in Karoo vegetation (Zeeman et al. 1983).

The flat, sandy pediments are nutritionally the poorest areas. The vegetation cover is lower than that of the rocky areas (except in those where rock cover is very great), and what few palatable plants grow between the *Galenia africana* are severely grazed. It seems unlikely that donkeys would prefer the sandy pediments for the superior forage that grows there, although nutrient accumulation in these areas may result in higher nutritional quality of individual shrubs.

Since riverine areas and sandy pediments are characterised by low rock cover and donkey occupancy scores have a strong negative correlation with rockiness ratings, this factor obviously plays an important role in determining habitat preferences. Goats are also influenced in their habitat choice by the degree of rockiness, but less strongly than donkeys. Goats are adapted to living in mountainous areas, and can climb over rocks and boulders with great ease; donkeys on the other hand have more difficulty moving in rugged terrain. On the steep slopes, donkey dung was usually found on paths, in small river beds, or in other patches that were easily accessible to a walking human. In their study of bighorn sheep and feral donkeys, Seegmiller and Ohmart (1981) found that while sheep were found predominantly in the rugged, mountainous areas, donkeys were seldom seen in these and preferred the gentler slopes and river washes. It seems that riverine areas, in addition to providing forage, serve as paths for donkeys. Donkeys were found to walk primarily on paths in tall vegetation in the Virgin Islands National Park (Turner 1984) and in dry river washes on their way to drink from the Colorado River (Woodward and Ohmart 1976).

Donkeys have their greatest impact in the riverine and flat sandy areas. These areas make up only 15% of the total area of Paulshoek. The steep rocky slopes, where donkey impacts are minimal, constitute 52% of the total area. Thus, half of the study area (and possibly more in the more mountainous northern areas of Paulshoek) probably experiences negligible impacts from donkeys. In terms of total feeding time spent, donkeys are probably most commonly found on the gentler rocky pediments, but their impact would be more "diluted" over the large area (33% of the total area).

Although donkeys are allegedly very dependent on water points, particularly in the dry season, there was no correlation between donkey occupancy scores and distances from the nearest perennial water point. Donkeys are able to dig holes into river beds and are able to utilise subsurface water that way (McKnight 1958; Seegmiller and Ohmart 1981), which might make them less dependent on permanent water points at any time of the year. Only a weak correlation exists between donkey occupancy scores and distances from the nearest semi-permanent water points. This correlation may be a result of the donkeys' preference for riverine areas, even when they are dry (in fact, riverine areas have a particularly great nutritional importance in the dry season).

The lack of correlation of donkey and goat occupancy scores with water sources may be due to the fact that distances between the transects and water points were never more than 2.5 km, an easy distance for a donkey or a goat to travel in a day. In California, donkeys were found to stay closer to the Colorado River, the only permanent source of water in the dry season; donkeys were reported to be "often only 1.5 km from the water source" (Woodward and Seegmiller 1976). Norment and Douglas (1977; cited in Seegmiller and Ohmart 1981) reported average distances of 2 km from water during the dry season.

Distances of transects from stock posts were equally short, and within a goat's daily range of movement. Donkeys are independent of stock posts, since they are not kraaled; wild donkeys might even stay away from them since they are reported as being shy of humans.

This study did not explore seasonal variation in habitat use because of time constraints. Other studies of habitat use by donkeys (McKnight 1958; Woodward and Ohmart 1976; Seegmiller and Ohmart 1981) have found significant differences in habitat use between seasons which were mostly driven by the need for water sources in the dry season, shade-seeking in riverine areas in summer and exploitation of annual herbs after the rains (Woodward and Ohmart 1976). People in Paulshoek say that donkeys cover long distances in a day, but that they prefer to keep closer to sources of water in the dry season. If the generally observed pattern that donkeys spread widely during the wet season and concentrate around water in the dry season applies in Paulshoek, this would further increase the impact of donkeys on the riverine and adjacent areas.

Diet choice and daily intake

The botanical composition of donkey and goat diets shows a large degree of overlap, as all the most important plant groups (asteraceous shrubs, mesembs, *Lycium* spp., herbaceous annuals and grass) are eaten by both animal species. All the plant groups eaten by goats appeared to be palatable to donkeys as well, and donkeys are able to eat plants which are unpalatable or even toxic to goats (e.g. *Galenia africana* and *Mesembryanthemum crystallinum*). From a veld management point of view, this is a good thing, since very selective grazing (as done by goats or sheep) can lead to the proliferation of unpalatable plant species at the expense of the more palatable ones. Feral donkeys in the United States are also known to eat unpalatable plant species, including Ocotillo (*Fouquieria splendens*), which is not known to be eaten by any other mammals (McKnight 1958; Seegmiller and Ohmart 1981).

It appears that donkeys are able to eat and digest a larger variety of plants than goats. On the other hand, Rutagwenda *et al.* (1990) found that donkey diets contained a much smaller number of different plant species, which was attributed to the very flexible, opportunistic feeding habits of goats which enable them to maintain diets of relatively high quality throughout much of the year. It is possible that the goats in Paulshoek use a wider variety of plant species than donkeys - the feeding observations were not comprehensive enough to detect the use of rare plants, for instance.

Both donkeys and goats appear to be very adaptable with respect to diet choice, and both are repeatedly described as opportunistic feeders which adapt to the vegetation available and cannot generally be categorised as grazers or browsers (e.g. for donkeys: Woodward and Ohmart 1976; Seegmiller and Ohmart 1981; Fowler de Neira and Johnson 1985 and references therein; for goats: Pfister and Malechek 1986; Rutagwenda et al. 1990).

As with habitat selection, seasonal differences in diet choice were not addressed in this study. In other studies on diet selection and feeding behaviour of goats, diet choice varied seasonally (e.g. Zeeman et. al 1983; Fedele et al. 1993), but interannual (Zeeman et al. 1983) and even diurnal (Solanki 1994) changes in diet composition and quality were found to exist.

Although the botanical compositions of goat and donkey diets seem to be very similar, donkeys eat food which has a much lower digestibility. Goats are better able to select the more digestible leaves and young shoots of shrubs, while donkeys ingest much more fibre and lignin along with the digestible parts.

In the numerous studies on goat diet selection performed in various countries, goats were generally reported to select diets with a higher digestibility than would have been estimated from the plant material available (e.g. Zeeman et al. 1983; Fedele et al. 1993) and to be able to select high quality diets even when range condition declined (Grünwaldt et al 1994). Goats were also found to select diets with a high crude protein content (e.g. Ramirez et al 1990 and Lopez-Trujillo and Garcia-Elizondo 1995 in Mexico; Rutagwenda et al. 1995 in Kenya; Nyamangara and Ndlovu 1995 in Zimbabwe). Donkeys, on the other hand, were found to be less selective, and to ingest diets with a low digestibility comparable to that of cattle (Rutagwenda et al. 1990).

Donkeys, like other large hindgut fermenters, can survive on diets of considerably lower qualities than ruminants. In ruminants, passage rate through the gut is limited by particle size, as food particles must attain a minimum size before they can pass through the small reticulo-omasal orifice. When the diet consumed is more fibrous, retention time increases in ruminants because it takes longer for plant particles to break down into small enough fragments (Janis 1976). Below a certain level of digestibility, the ruminant is unable to cover its energy requirements with the amount of food that can be digested in a day. Since energy requirement per unit body mass is greater in smaller animals, (Illius and Gordon 1992 and references therein) smaller ruminants suffer more from low quality diets than larger ones. In contrast to these theories, the food intake of donkeys was found decrease in summer when digestibility of the diet decreased, but food intake in goats decreased at a greater rate, and the ratio of daily food intakes of the two species widened at lower diet quality as predicted.

Hindgut fermenters, on the other hand, can compensate by eating more, as passage rate stays the same or is even able to increase with decreasing digestibility (Janis 1976; Richardson, pers. comm). One implication of this is that equines can survive on diets of a lower quality than can ruminants of the same or smaller body size. According to Janis (1976), it seems that the strategy of equines is to maintain the same absorption per unit time as a ruminant by having a greater intake and a shorter passage time at the expense of a reduced efficiency of cellulose digestion. Because passage decreases with decreasing diet quality in ruminants while it remains constant and allows increased food intake, the ratio of intakes per body mass of goats and donkeys widens as diet quality decreases (Richardson, pers. comm.).

An important implication of the differences in digestive systems and the quality of the diets selected by donkeys and goats is that although one donkey eats as much dry matter as five goats, some proportion of the food is too fibrous to satisfy the maintenance requirements of goats and is thus of no use to them. The faecal nitrogen content of donkeys in Paulshoek was as low as that determined for feral donkey populations at carrying capacity in Australia, where population growth was found to be limited by juvenile mortality as a result of nutrient stress in the mother (Freeland and Choquenot 1990), indicating that donkeys in Paulshoek eat a diet with a very low digestibility. It follows that for every donkey removed from the veld, fewer than five goats can be supported. For example:

Blaxter (1960, cited in Zeeman et al 1983) inferred that goats need to consume a diet with a minimum of 50% digestibility to satisfy their maintenance requirements. If donkeys eat a diet with a digestibility of 30% due to their inability to select the more digestible plant parts, a kilogram of the donkey's diet will only yield 300g digestible matter. If goats manage to maintain the overall digestibility of the plant matter eaten above 50% by feeding selectively, a maximum of 600g plant matter is yielded. It is for this reason that carrying capacities in terms of animal body mass per hectare are higher for large unselective feeders, especially hindgut fermenters, than for smaller, more selective herbivores (Mentis 1977). In order to assess the "costs" of a donkey in goat units from a nutritional point of view, intake *per se* can thus be a deceptive indicator if the diet quality is not known.

Other attempts to quantify herbivore competition have also found that diet selection and intake were not necessarily sufficient to estimate to what degree the nutrient supply of a species is threatened by the other. For example, Ekblad et al. (1993), in a study of goats and white-tailed deer, found that both species were able to acquire nutrients at the same rate as without competition, despite a dietary overlap index of 75-88 % over the year. This was explained by the fact that both species shifted their dietary habits and biting strategies in response to competition. Such complexities make the task of quantifying the impact of one species on another difficult. In Australia, for example, reducing the size of a feral donkey population at carrying capacity to 45 % of its original size had no detectable effect on population sizes of feral horses and cattle, the study area's other two major herbivores (Freeland and Choquenot 1990).

<u>Damage</u>

Both McKnight (1958) and Seegmiller and Ohmart (1981) report that donkeys have wasteful feeding habits. A common observation was that only part of the plant parts removed are actually consumed, for instance: "In general, burros are wasteful feeders, frequently pulling up entire plants by the roots, eating only one or two mouthfuls, and dropping the remains on the ground" (Lou Hallock, pers. comm., quoted from McKnight 1958). During their observations of diet selection of feral burros on Galapagos, Fowler de Neira and Johnson

(1985) frequently observed feeding donkeys raising their heads with whole plants dangling from their mouths. Seegmiller and Ohmart (1981) describe how burros, unlike bighorn sheep with whom they share their range, feed destructively on palo verde (*Cercidium microphyllum*) trees by chewing and breaking off branches of up to 200 cm in length and 4 cm in diameter. They were then reported to shred and consume a small portion of the foliage before discarding the rest. Palo verde was reported to be an important part of burro diets in the area and browse lines, torn branches and in extreme cases, entire small trees from which all branches had been ripped off were found frequently. This browsing behaviour was also described by Farrel (unpublished thesis, cited in Seegmiller and Ohmart 1981).

It was pointed out earlier in this report that damage of the kind described above seems to account for a relatively small fraction of the overall grazing damage done by livestock and donkeys. It is difficult, however, to infer the process of rangeland degradation from "snapshot" observations such as the ones obtained during the transects in this study, and hence to estimate the amount of damage donkeys have done to the veld over the years. It is even more difficult to distinguish between the damage done by donkeys and that done by goats, which are also frequently blamed for veld degradation in many parts of the world. It is important to investigate the damage done by livestock and donkeys more carefully, as the findings have important implications for management of the grazing resources.

Apart from the damage caused by uprooting and kicking plants and similar actions supposedly typical of donkeys, this animal can also damage plants by biting more deeply into the wood of shrubs, which was found during feeding observations and is reflected in the considerably lower diet quality. This can lead to reduced regrowth of the plants, and may lead to permanent damage if the plant's carbon resources are depleted to a high degree. Clipping experiments showed that defoliation at moderate levels adversely affected both vegetative growth and reproductive output of Karoo shrubs for periods of up to 26 weeks following defoliation. Perennial shrubs were most strongly affected, and *Ruschia spinosa* suffered most severely (van der Heyden 1992). This may, at least partially, explain the demise of !naroevy (*Ruschia* sp.) in Paulshoek. The phenomenon termed "brandbek" by people in Paulshoek, where plants are said to be poisoned by the donkey's bite, may also be a manifestation of excessive defoliation and removal of woody tissue.

While a donkey may only "cost" five or fewer goat units in terms of the quality and quantity of the food consumed, the additional destruction donkeys cause to the veld (which has yet to be quantified anywhere) may reduce the food resources available to goats in a more indirect, but possibly more permanent manner than direct competition.

Implications for the management of donkey populations

It emerged from conversations with people in Paulshoek that there are two main components to the management of donkey populations in Paulshoek and other areas faced with a similar situation. One of these is dealing with feral donkey populations, and managing donkeys used by their owners is the second one.

Feral populations

In contrast to the findings of the SANAT survey (Starkey 1995), all people in Paulshoek who were questioned reported that numbers of feral donkeys were on the increase in the area. If there are feral donkey populations unchecked by human efforts to control them, their populations could increase fairly rapidly if one considers examples of donkey populations elsewhere.

Feral donkey populations in Australia and the United States have displayed high rates of increase due to the donkey's high natural fecundity and the lack of predators and parasites which are able to kill or significantly weaken a donkey (Freeland and Choquenot 1990; Seegmiller and Ohmart 1981). The biggest predators present in Paulshoek are jackals which can kill young sheep and goats, but do not affect donkeys. According to farmers in Paulshoek, diseases seldom kill donkeys. Feral donkeys in Northern Australia exist at a density of at least 30 times that recorded among natural populations of wild asses (Freeland and Choquenot 1990). Donkey populations in that area increased at a rate of 28 percent per annum following experimental reduction of stable donkey populations at carrying capacity (Freeland and Choquenot *op. cit.*). In a study of feral donkeys in the south-western United States, Seegmiller and Ohmart (1981) found annual natality to be 20 percent with no juvenile mortality, and they conclude that the burro population in their study area increased by as much as 19 to 22 percent in one year. In Death Valley, an annual increase of nearly 22 percent was calculated for a feral burro population over a 4.5 year study period (Norment and Douglas 1977, cited in Seegmiller and Ohmart 1981), and in the Chemhuevi Mountains of California, Woodward and Ohmart (1976) reported a 20 - 25 percent recruitment rate in the burro population every 13 - 18 months. Perryman and Muchlinsky (1987) modelled population growth using Leslie matrix models and predicted increase rates of around 10 percent annually. According to their predictions, a population of donkeys with a large proportion of young, high survival rates and a pregnancy rate of 70 percent or greater is capable of doubling in 10 years or less.

In the light of these examples, the large estimates of the feral donkey population in Paulshoek could be realistic, and the need to control donkey populations is highlighted. Since feral donkeys are not domesticated and there is no other use for them, an effort, possibly aided by extension staff, should be made to eliminate them from the land. Once the feral population is removed, domestic donkeys and their offspring must be prevented from giving rise to new feral populations.

Populations of working donkeys

Solving the problems caused by working donkeys is a more difficult task, since these are needed and cannot simply be removed from the veld. It is for this purpose that the areas that suffer the greatest impact from donkeys were identified. Riverine and flat, sandy areas, which constitute only 15 % of the total study area, are most intensively used by donkeys. Being the most sparsely vegetated areas with the highest percentage of open soil, heavy grazing is more likely to lead to increased erosion in these areas; reduced plant cover was found to be one of the primary factors determining the susceptibility to erosion in grasslands (Venter et al. 1989).

Riverine areas represent a food reservoir in the dry season. The importance of such "key resource areas" is highlighted by Scoones (1995) who explained the sustained presence of cattle on a communal range in Zimbabwe at twice the predicted carrying capacity by the fact that the animals were able to use certain small areas which had a relatively high nutritional value. These areas play a disproportionately great role in determining carrying capacities of grazing land. It appears that the 6 % made up by riverine areas in Paulshoek, if properly protected from excessive overgrazing and damage by donkeys (and goats?) and allowed to recover during the growing season, may contribute greatly to the survival and good nutrition of goats. One suggestion would be to select a large stretch of river, such as the one flowing from Kuile to the eastern boundary of Paulshoek parallel to the main road, and to fence it off during the growing season, when food is abundant in all the other areas.

The flat areas with deeper soils, which are nowadays associated with little more than the unpalatable *Galenia africana*, were nutritionally valuable areas covered in !naroevy in the past, according to reports of people who were interviewed in Paulshoek. There are no signs that these areas are recovering from the ploughing that took place on them as much as 20 years ago. This may be a result of the reproductive physiology and ecology of *G. africana*, *Ruschia* sp. (!naroevy) and other plants which naturally occupied these areas, but the situation is sure to be exacerbated by heavy grazing. Since donkey impact in these areas is relatively high (even annuals are rare in these areas in Paulshoek, while annuals elsewhere in Namaqualand favour this kind of habitat), these areas should also be targeted in management programmes. The small size of the areas in question, and their potentially high nutritional value should be additional motivation for protecting them from excessive damage.

Conclusion

Given the complexity of all the interactions between vegetation, feeding, digestion and human strategies of livestock keeping among several factors, it is a difficult task to quantify the impact one herbivore species has on another. In this report, a figure of between 5 and 8.6 goats for every donkey emerged, depending on the season and on animal weight. The commonly cited figure that one donkey eats as much as seven goats is therefore a reasonable estimate on which to base taxation. This figure should also raise attention to the need to eliminate feral donkeys: if there are 50-100 feral donkeys in the area, and if every one only ate as much as 5-8 goats, this translates into between 250 and 800 goats.

It did, however, emerge that while a figure such as this is a useful guideline for devising taxation and drawing attention to the need for action, that a figure by itself is insufficient to lay bare the complexities which are important to understand in order to target management efficiently. Habitat overlap, diet choice and quality, damaging feeding habits, herding and kraaling all make a difference to the outcome. In this particular case, the problem is probably best investigated experimentally using exclosures. This is costly and takes time, and the approach used in this study generated some useful approximations and highlighted problems and threats which are in particular need of attention, such as the protection and management of riverine and flat, sandy areas. It also emerged that management efforts need to be primarily confined to a small proportion of the area, which is important for directing the flow of resources for management.

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