

Herbivore dynamics in an arid environment

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PhD
The University of Edinburgh
2010

This thesis was typeset using KOMA-Script and L^AT_EX 2_ε.

To Mum, Dad, Tessa and Mel

Declaration

I have composed this thesis myself. The work contained herein is my own, except where collaboration is explicitly stated. I have not submitted this work for any other degree or professional qualification. Gareth Hempson, August 2010.

Funding

The financial assistance of the National Research Foundation (NRF) towards this research is hereby acknowledged. Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to the NRF.

Acknowledgements

The kindness and generosity of Ernest Pieterse has given me the world of opportunity. One does not know how life might have turned out otherwise, but I truly believe that his support has enabled me to experience and achieve more than I could otherwise have dared hope for. Thank you, you have made an immeasurable difference in my life.

It has been an absolute privilege to have Prof. Andrew Illius as my principal PhD supervisor. I have learnt from you far beyond the bounds of the classroom, and hope to follow your example through life. Dr. Susi Vetter has given me valuable guidance in this PhD and has been a good friend. Prof. Josphine Pemberton has also helped give me direction, particularly in the early phases of this degree. Prof. William Bond hosted me in the Botany Department at the University of Cape Town. You too are a man I look up to, thank you for generosity and support over the years. Dr. Howie Hendricks provided an absolute wealth of insight into the Richtersveld, not to mention census data, which greatly enhanced this study. Prof. Timm Hoffman was also very kind in sharing his thoughts, and his Paulshoek dataset. Martha Konje, Glynis Humphreys, Andrew Booth - my fellow RNP teammates - thanks for the good times and discussions in the long hours in the field and on the road.

Jarrod Hadfield dragged me out of various statistical quagmires, thank you. I would also like to thank Dan Nussey and Katie Stopher for assistance with my analyses. Thomas Slingsby and Nick Lindenberg got me up and running with ArcGIS, thank you. Sven Kaehler kindly assisted with vehicle provision for much of the duration of the study. Prof. Norbert Jurgens kindly allowed me to make use of the BIOTA research station, thank you - I came to think of that as home.

The Richtersveld was just one of those faraway places you'd heard about. When I arrived, Oom Piet Domrogh was upset that they'd sent a 'rooitaal'. My Afrikaans has improved Oom Piet, thank you for the encouragement. The people of the Richtersveld gave me a chance to experience their lives. It has been an absolute privilege to live

in their homes and experience their culture and perspectives. I would in particular like to thank the following farmers for allowing me to work with their animals: Oom Piet and Tant Sanna Domrogh; Oom Koos Diergaardt, Tannie Mietjie Diergaardt and Mr Dumpies Diergaardt; Oom Joseph Domrogh; Oom Willem Slander; Oom Dawid (Oompie Dap) and Oom Willem Hans; Oom Gert Joseph and Oom Johannes Joseph; Auntie Rosie Obies and Mr Patrick Obies; Mr. Paul Cloete and Mr. David Cloete; and Mr. Koos Jossob. There are so many stories I'd like to share about experiences with each family, but perhaps the best place for that would be with a cup of tea in the Richtersveld.

Johannes 'Dood' Cloete and Elias 'Jahman' Links worked with me during almost every fieldtrip over the course of three years. Reliable and entertaining - what more could I ask for? I could not have done it without them. Seth Domrogh and Aubrey de Wet were also pivotal in getting the job done. Seth got me up and running when I arrived, I wish you all the best with your dreams for the Richtersveld. Eddie Moos, Hendrick 'Ziggas', Stephan Basson and many other men assisted me with the task of getting the ladies on the scale, and provided outstanding company over the three years. Thank you.

Koos Jossob, as head ranger in the Richtersveld National Park, provided me with total support throughout my time in the Richtersveld. In particular, keeping track of the herd positions for over three years has added much value to this study.

The Richtersveld is an isolated place, and people need to rely on each other. The RNP park staff members were always willing to help. I could still be stuck out there, waiting for someone to tow me home. Johannes Domrogh, Oom Freddie, Nico and Kobus all bailed me out in one way or another at some point in time, as well as many others I fail to recall right now - your help is nevertheless appreciated. Mechanically speaking, Oom Willie Mostert kept the show on the road, asking nothing in return. Thank you. Leana and Wilma, thank you for your assistance over the years. Kyle, Mexico, Tshabalala, Touks, Liesel - it was great having a few fellow students around. Good memories. Likewise, watching the rugby with the guys from the mine; thanks for letting me join you!

I made a fourth home in Edinburgh, and have been privileged to spend time in the company of the many fellow students and friends I have met over the years. The good people of Howe Street - Juan-Carlos, Adel and Jarrod - thank you for finding a way to

fit me into the house every few months. Your friendship made me feel at home; I look forward to having you all come and visit me in South Africa. It's unfair to mention names, but Adin, Gethin, Laura and Ellie have all been great fun over the years. Alex and Daniela, you have been true friends to me - I am really looking forward to you coming to visit me in South Africa.

The clock is running down, but I must mention the folks at Leo's Beanery: Joe, Mary, Ally and Cat and all the other folks there. I couldn't have asked for a better office, thank you for the friendship and smiling faces in busy times.

In Cape Town, I am blessed with a rare group of friends. Matt, Jasper, Ben, Julia, Richard and Thomas, again I am unfairly mentioning names to my later detriment, but you guys (and the many I'll blame the coffee for forgetting) are first class. Thank you for everything. Too much to mention, no need to mention.

Yoh! Team Nature. Sean Earle and Melinda McCann (and Merlin, Gandalf, Luka, Trigger, Ayla and Purdy of course) have given me a home in Grahamstown. One of the finer things to come out of this PhD: the opportunity to meet you folks. Thank you for the key to Hotel River Street, your bakkie and your fishing rods. James Puttick, you can *gooi* my bru.

To all those I've failed to mention: I can explain. I look forward to catching up with you to get the chance to do so.

To my family: thank you one and all for your love, support, fun and guidance in tough times. You really do make it all worthwhile. Mum, Dad and Tessa - the four of us are always together. So, so blessed. Mel, babe, I'm sorry I've been away so much. You've been there for me all along, and have been with me every step of the way. I can't imagine life without you.

31 August 2010

Abstract

This study investigated the effects of a seasonally variable forage resource on herbivore population dynamics. This involved estimating the relative importance of environmental conditions, and the accessible and used forage resources, at different stages of the seasonal cycle to herbivores in different life-stages and at different points in the reproductive cycle. This study was carried out in the Richtersveld region in South Africa, using goats kept by semi-nomadic Nama pastoralists. In the main study site, the Richtersveld National Park (RNP), herd movements follow a general seasonal migratory pattern: herds are based in the riparian zone of the Orange River during the dry season, and on plains away from the river in the wet season. Over 800 uniquely marked female goats in three life-stages (adults, yearlings and kids) were monitored over a three year period (2007 to 2009). These goats were weighed at 2 - 3 month intervals to provide an estimate of body condition. Browse availability in the riparian zone was estimated using measurements at an individual branch-level and a whole tree-level. FPAR satellite imagery was used to estimate forage abundance outside the riparian zone. Goat density was mapped for each week of the study using census data and the herd positions. Goat body condition, survival rates and fecundity rates for each life-stage were modelled as a response to forage availability, density and climatic conditions. The riparian zone in the RNP was found to function as the key resource of the RNP goat population. Forage depletion by goat browsing resulted in a negative feedback on goat body condition. This decline in body condition was directly related to lower adult survival over the dry season. Fecundity was also most influenced by dry season conditions through the negative effect of poor body condition on pregnancy rates and birth rates. Asymmetric competition between life-stages, resulting from the riparian browse profile being depleted from the bottom-up, was predicted to have a strong effect on goat demography by contributing to differences in body condition and survival rates between life-stages. Wet season conditions appeared to have little effect on goat population dynamics, either through increased neonate survival or through a mass carry-over effect influencing dry season survival. Goat body condition and

vital rates were compared between the RNP and the neighbouring Kuboes rangeland, which does not have access to the Orange River, to assess the impact of differences in their dry season forage resource. The long-term size and variability of the livestock population in the RNP was also compared with livestock dynamics in Paulshoek, a rangeland 250 km south east of the RNP. The *a priori* predictions of relative population dynamics in each region, based on perceived differences in the nature of the key resource in each region, were largely supported.

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1 Introduction

Much of our understanding of herbivore population dynamics comes from temperate northern hemisphere studies, but the greatest diversity of herbivores is found in tropical African ecosystems. In African studies, mortality during the dry season has frequently been found to be a crucial factor shaping herbivore population dynamics (Sinclair 1985, Fryxell 1987, Mduma *et al.* 1999, Gaidet & Gaillard 2008). All dry seasons are not equal though, and higher mortality across all age classes during extended dry periods - or droughts - is widely perceived as being the main driver of herbivore populations in semiarid systems. The significance attached to droughts has been taken a step further, with the suggestion that if droughts occurred frequently enough, they could totally uncouple herbivore population dynamics from their forage resources (Ellis & Swift 1988, Behnke & Scoones 1993).

A long standing view is that herbivore populations are limited from the bottom-up by food shortages at certain times of the year (Sinclair 1975), as opposed to being limited by top-down processes e.g. predation (Hairston *et al.* 1960). There is considerable evidence that food limitation is the critical factor limiting herbivore populations in temperate systems without large predators (e.g. Clutton-Brock *et al.* 1997), but also from African systems despite the presence of large predators (e.g. Sinclair 1985, Mduma *et al.* 1999, Owen-Smith *et al.* 2005). One current view is that top-down predation interacts with bottom-up forage limitation, with body size affecting both an individual's nutritional requirements and vulnerability to predation (Hopcraft *et al.* 2010). Seasonal variation in forage quality and abundance plays an important role in this framework, shaping the distribution patterns of herbivores and their susceptibility to predation.

If plant growth is largely limited to the wet season, then food limitation during the dry season would appear to be a particularly important process limiting herbivore populations. Illius & O'Connor (1999) argue that the marked seasonality in the strength of plant-herbivore coupling will result in the herbivore population tending towards a long-term equilibrium with the forage resources available in the plant

dormancy season. The abundance of forage resources then would thus be of critical importance in determining herbivore population dynamics. These forage resources are referred to as 'key resources' (Scoones 1991, 1995, Illius & O'Connor 1999). Herbivore populations in climatically variable and spatially heterogeneous landscapes are thus predicted to be regulated via density-dependent coupling with their key resource (Illius & O'Connor 1999). The key resource is defined as the component of the resource base that determines the size of the 'key factor' (*sensu* Varley & Gradwell 1960) that shapes herbivore population dynamics (Illius & O'Connor 2000). In a semiarid African landscape, this is predicted to be the forage resource that determines the adult survival rate over the dry season (Illius & O'Connor 1999).

There are important consequences of a herbivore population being coupled to a spatio-temporally restricted subset of its forage resources (Illius & O'Connor 1999, 2000: P1 - P4). If coupling is limited to only a part of the system (P1), then the herbivore population could potentially be uncoupled, in the dynamical sense, from resources elsewhere in the system (P2). This suggests that the strength of coupling would vary with proximity to the key resource, and be weakest during the wet season. These predictions were tested using a modelling approach, which showed that even partial separation of the foraging area used in each season (i.e. the only constraint was to limit herbivores to a dry season range during the dry season) was sufficient for the size of the dry season range to have a strong impact on the herbivore population, but the size of the wet season range had almost none (for wet season range > dry season range, Illius & O'Connor 2000). Notably, the size and variability of conditions in the dry season range was detectable in the herbivore population trajectory. If population size is determined by only a subset of resources, then more animals are supported in the whole system than would be if those resources were absent or smaller. It was thus predicted that the potential for degradation across the whole system was linked to the key resource (P3). In addition, increased variability of the key resource would result in more frequent disparities in resource availability and animal demand, increasing the potential for probably short but severe episodes of defoliation (P4). Both P3 and P4 were supported by the key resource model (Illius & O'Connor 2000).

The key resource model was initially developed in response to a vigorous debate in the rangeland scientist community, and which to date has not been universally concluded (Ellis & Swift 1988, Behnke *et al.* 1993, Scoones 1994, Illius & O'Connor 1999, Briske *et al.* 2003, Vetter 2005, Gillson & Hoffman 2007, Derry & Boone 2010).

The main point of contention is that environmental variability can at times be so great as to ‘uncouple’ herbivore populations from their forage resource. The relative importance of abiotic and biotic factors in driving plant community composition in rangelands has thus been questioned, and has particular bearing on the possibility for rangeland degradation as a consequence of grazing impacts. The debate originated with the contention that equilibrium processes were irrelevant in rangelands, because prescribing one fixed stocking rate was clearly inappropriate in a seasonally variable environment (Ellis & Swift 1988). Livestock numbers over the whole system were shown to not be correlated with environmental parameters, and were thus assumed to have negligible feedback on the vegetation. High drought induced mortality was thus perceived to be the main driver of the system, and focus shifted to developing strategies to mitigate their effects. Tracking (e.g. through supplementary feeding or well timed stock sales) and buffering strategies (e.g. loan schemes, central livestock banks and marketing schemes) were pursued as means to stabilise the effect of drought on the livelihoods of pastoralist communities (Scoones 1995, Illius *et al.* 1998, Campbell *et al.* 2000, 2006). There would appear to be some merit in these approaches, but there is as yet no solution to dealing with the destabilising effect of high environmental variability on pastoral livelihoods in semiarid systems. As such, Illius & O’Connor (1999, 2000) sought to address these dynamics by re-examining the role of plant herbivore-coupling in these highly variable systems, with particular emphasis on the effects of key resources on system dynamics.

Our understanding of what determines herbivore population sizes in highly variable environments has improved considerably over the last few decades, particularly due to insights from long term studies of large mammal populations. General patterns have been identified, which emphasise the importance of taking the demographic structure of a population into account. Amongst these is the apparent trade-off between adult survival and recruitment parameters (Gaillard *et al.* 1998, 2000). Adult survival rates typically have low variability, but variation in this parameter has a large impact on the population trajectory. In contrast, temporal variation in recruitment parameters tends to be high, but the relative impact on the population is low compared to a similar change in adult survival rates. Gaillard *et al.* (2000) suggest that the degree of temporal variability in most environments should be sufficient for recruitment parameters to dominate the population growth signal. The generally low variability in adult survival in large herbivore populations has been considered to be a bet-hedging

strategy, with adult survival being canalised against temporal variation (Gaillard & Yoccoz 2003). Adult females thus tend to avoid the risk of investing in reproduction under unfavourable conditions, and rather opt for the conservative strategy of having a long reproductive life. Populations are also expected to show a distinct series of responses as resource availability starts to become limiting. Eberhardt (2002) summarises this sequence of responses as 1) increased juvenile mortality rates, 2) increased age at first reproduction, 3) reduced fecundity of adults and 4) increased adult mortality rates. This series of events occurs with decreasing frequency (Gaillard *et al.* 2000), which emphasises the degree to which adult survival is preserved. The demographic structure of a population is thus critical to understanding its dynamics, but the age and sex of individuals also needs to be taken into account (Loison *et al.* 1999, Coulson *et al.* 2001, Toigo *et al.* 2007).

Density effects are reflected in an individual's body condition, as competition for the remaining food resource intensifies. Density has been shown to be important in many species across most ages and stage-specific vital rates, although evidence for density dependence in adult survival remains scarce and needs to be carefully analysed (Festa-Bianchet *et al.* 2003). The effects of environmental conditions on the resource base before and after birth have been shown to have important consequences for offspring, with poor conditions during this phase potentially still evident in the adult life-stages (e.g. Gaillard *et al.* 1997, Forchhammer *et al.* 2001). These long term cohort effects can act to stabilise or destabilise a population and should thus be taken into account where possible (Lindstrom & Kokko 2002). Poor body condition also increases the vulnerability of individuals to extreme weather events and predation, which might otherwise appear to be density-independent causes of mortality (e.g. Aanes *et al.* 2000, Owen-Smith *et al.* 2005). Weather effects are likely to directly influence both herbivores and the forage resource, but also influence both indirectly through the concurrent effects of the one on the other. Untangling these effects is thus complicated. Similarly, discerning the effect of predation on a population is complicated by the interaction between the effect of competition for forage resources on body condition, and the effect of body condition on vulnerability to predation (e.g. Owen-Smith & Mills 2006). The potential for large predators to reduce adult survival rates in a population could have important consequences for the population growth trajectory.

Herbivore population dynamics are ultimately a consequence of a vast range of

stabilising and destabilising influences. The effect of environmental stochasticity on a population can depend substantially on population densities as well as the life history of the species (Clutton-Brock *et al.* 1997, Saether 1997). The slow build up of animal numbers relative to the rate at which they can crash is one mechanism by that provides a degree of buffering against temporal variability. This should allow the negative feedback between herbivores and their forage resource to become established and reduce the extent to which ‘instantaneous carrying capacity’ is exceeded (Caughley & Gunn 1993). Dramatic variation in the forage resource will however limit the effectiveness of this mechanism and should result in smaller population sizes (Georgiadis *et al.* 2003).

Spatial heterogeneity in resources is another means by which herbivores can be buffered against environmental stochasticity (Illius & O’Connor 2000, Owen-Smith 2004, Wang *et al.* 2006). Differences in the timing of plant development across a landscape, or in the accessibility of forage, create a more heterogeneous forage resource. When forage becomes limiting, animal populations can switch their diet selection to make use of previously ignored or unavailable resources, but also make use of plants in refugia by increasing their searching effort. Seasonal separation of foraging areas provides another mechanism for spatial buffering against temporal variability (Illius & O’Connor 2000). Large-scale migrations allow populations to access forage resources that are only available for parts of the year (Fryxell *et al.* 2005), but also provide benefits in terms of predator avoidance (Fryxell *et al.* 1988). However, food limitation during the plant dormancy season remains a critical factor shaping population dynamics in migratory herbivores (Sinclair 1985, Fryxell 1987, Mduma *et al.* 1999). The importance of coupling with key resources, although developed within a rangeland context (Illius & O’Connor 1999, 2000), would thus appear to be more widely relevant, indeed ubiquitous, in seasonally variable plant-herbivore systems.

This study aimed to estimate the effects of a seasonally variable forage resource on herbivore population dynamics. This involved estimating the relative importance of environmental conditions, and the accessible and used forage resources, at different stages of the seasonal cycle to herbivores in different life-stages and at different points in the reproductive cycle. It thus forms an empirical test of the idea that herbivores are coupled to a subset of their forage resource in seasonally variable environments, to establish the veracity of the predictions of the key resource model.



Figure 1.1. Looking south from Maerpoort in the Richtersveld National Park.

This was approached by studying a goat population in the arid Richtersveld region in the far west of South Africa, over a period of three years. These goats are kept by semi-nomadic Nama pastoralists, who opportunistically move their herds through the landscape in response to the requirements of their animals. Approximately 800 individually-identifiable animals from nine herds were weighed every 2-3 months over the course of the study period, to provide an estimate of their body condition. The resource base was quantified using climatic data, satellite imagery and *in situ* measurements of forage availability. Weekly herd positions and biannual census data were combined in a geographic information system to create surface maps of goat density throughout the study period. Body condition, survival rates and fecundity rates were then modelled as a response to the state of the resource base. Goat body condition and vital rates were also compared between two study sites within the Richtersveld. Finally, the long-term size and variability of the livestock population in the main Richtersveld study site was compared with livestock dynamics in an established study system at Paulshoek, 250 km south east of the Richtersveld.

2 Study sites and methods

This thesis is structured into three data chapters, followed by an essay that offers a perspective on the rangeland debate, and a general discussion of the findings of this study. The first two data chapters provide an analysis of the dynamics of the goat population in the Richtersveld National Park (RNP), in relation to resource availability and environmental conditions in the dry season (chapter 3) and the wet season (chapter 4). In the third data chapter (chapter 5), I contrast the RNP goat population dynamics with those of a population in the neighbouring Kuboes region, as well as with livestock kept in the Paulshoek region, 250 km south east of the RNP. The majority of the data that were analysed in this study were collected over the period from February 2007 to November 2009. Five fieldtrips were undertaken each year at roughly even time intervals (February, April, June, August and November), and involved data collection in both the RNP and in the Kuboes region. Data for the Paulshoek region were kindly provided by Prof. Timm Hoffman (Plant Conservation Unit, University of Cape Town).

2.1 Richtersveld National Park

2.1.1 Overview

The focal area for this study was the Richtersveld National Park (RNP) in the Northern Cape, South Africa (figure 2.1). The northern and eastern border of the RNP is formed by the Orange River, which also forms the border between South Africa and Namibia. The region is characterised by steep and largely inaccessible mountain ranges, which are separated by broad drainage basin plains that taper into narrow ravines leading to the incised Orange River valley (figure 2.2).

The climate is arid with highly variable rainfall ($80 \text{ mm} \pm 43 \text{ s.d.}$, $CV > 0.5$). Rainfall occurs most reliably in the mid-winter months (June to August), and at this time of year is associated with cold fronts moving in off the cold Atlantic Ocean

2 Study sites and methods

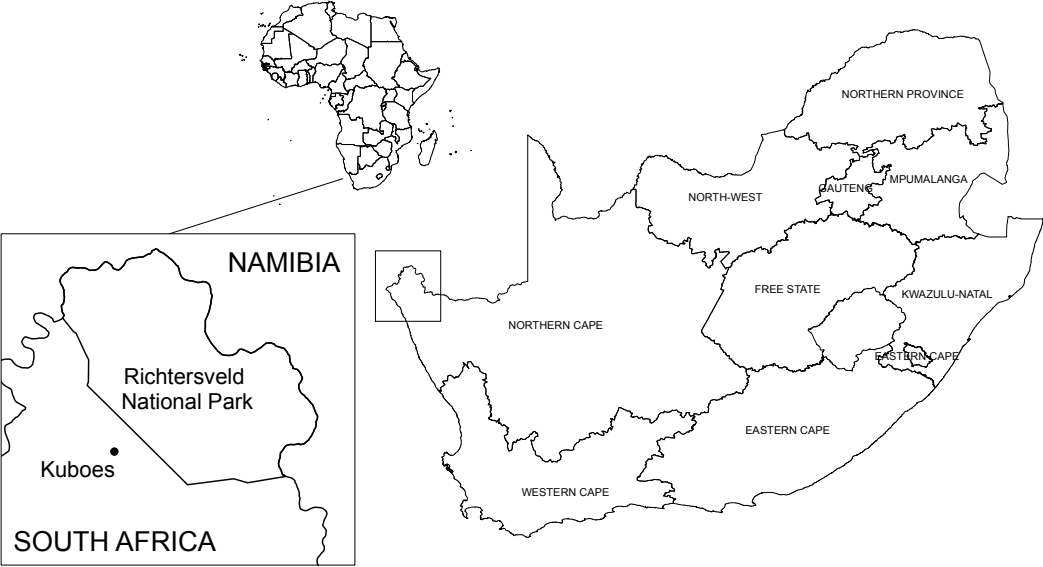


Figure 2.1: The location of the Richtersveld National Park in relation to the rest of Africa and South Africa.

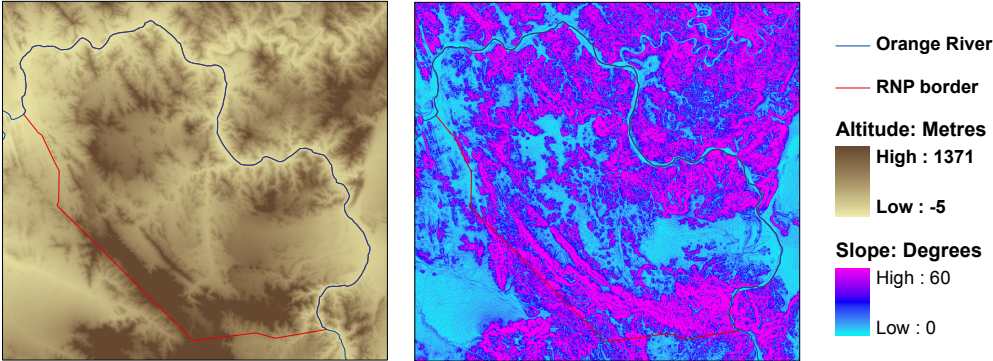


Figure 2.2: Maps showing the variation in altitude (left) and slope (right) in the RNP. Kuboes lies to the south west of the RNP.

100 km to the west. In the course of this study, the main wet season period was generally considered to be the interval from July to October in each year, with the dry season thus being from November to June. However, given that a single frontal system might be the only ‘wet season rainfall’ in a year, the exact timing of the wet and dry season is quite variable. In some years, summer thunderstorms from the east offer relief during the long dry season. These storms are at the extreme western edge of the weather system that brings summer rainfall to the majority of southern Africa. Daily maximum temperatures peak around February/March (frequently > 40°C), but monthly average maximum temperatures drop to below 20°C in the winter months (figure 2.3). Minimum temperatures seldom drop below 5°C. Rain gauges are situated at five locations within the RNP, and daily temperatures are recorded in Sendelingsdrift. Rainfall and temperature data were kindly provided by the South African Weather Service.

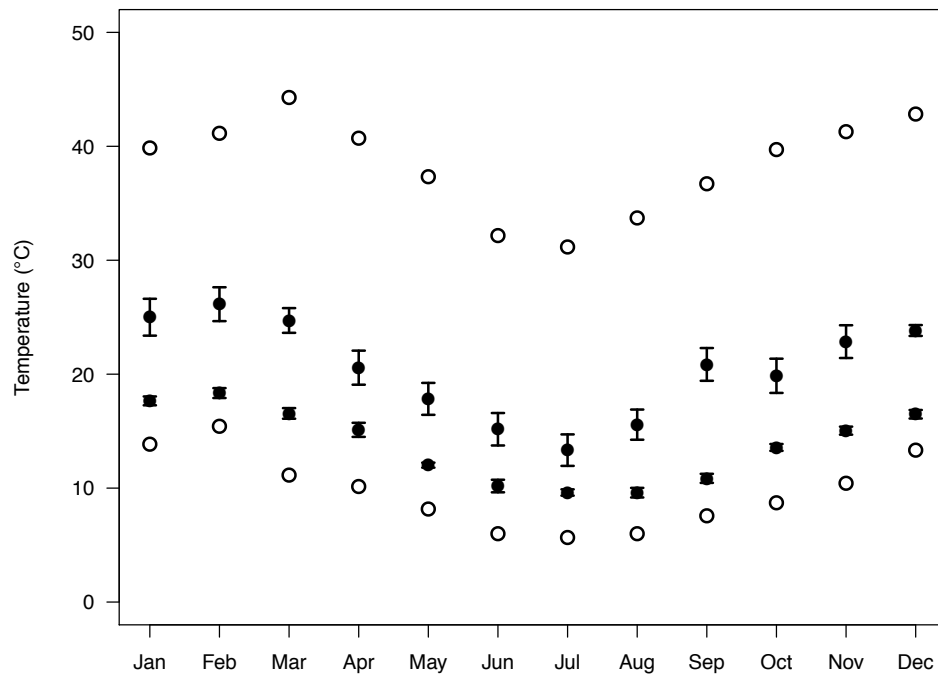


Figure 2.3: Average monthly temperatures in the RNP. Closed symbols represent average daily maximum and minimum temperatures in each month of the year (\pm s.e.). Open symbols represent the average highest and lowest temperature in each month.

The RNP vegetation is predominantly represented by two biomes, the Succulent Karoo and Desert biomes (Mucina & Rutherford 2006). Succulent Karoo vegetation occurs in the cooler, more moist regions to the west and south of the RNP, and Desert vegetation types predominate in the north and east. The narrow floodplain of the Orange River supports a well developed fringe of riparian vegetation, which is characterised by a mix of indigenous tree species that includes *Acacia karroo*, *Euclea pseudobenus*, *Maytenus linearis*, *Rhus pendulina*, *Tamarix usenoides* and *Ziziphus mucronata*, as well as the alien invasive species, *Prosopis glandulosa*.

Plant growth is strongly seasonal in the Richtersveld, with the main plant growth period occurring in the cooler winter months following rainfall (Cowling *et al.* 1999, Desmet 2007). A suite of perennial species grow and flower in this period, but the remarkable flush of annual species on the drainage basin plains in the RNP is the most striking vegetative transformation that occurs at this time. In contrast, the high potential evapotranspiration rates during the hot summers mean that most plants are dormant for a large part of the year (A. R. Palmer, pers. comm.).

The majority of the data analysed in this study were collected between February 2007 and November 2009. The 2006 wet season is the wettest on record, and the 2008 dry season was ameliorated by a good summer thunderstorm (figure 2.4). The 2009 wet season, however, received below average rainfall. On the whole, the study period can be considered as forming a relatively favourable series of years.

2.1.2 Pastoralism

The RNP is a contractual national park, with the land being under lease from the local Nama community. The local community have retained their rights to graze their livestock in the park as part of the agreement. Their livestock herds predominantly comprise mixed-breed goats (Indigenous, Boer and other goat breeds; *Capra hircus*) and fat-tailed sheep (*Ovis aries*), but one small herd of cattle (*Bos primigenius*) is also kept. Gemsbok (*Oryx gazella*) and springbok (*Antidorcas marsupialis*) were reintroduced into the RNP during the study period, but populations are still very small. Klipspringer (*Oreotragus oreotragus*), steenbok (*Raphicerus campestris*), kudu (*Tragelaphus strepsiceros*), mountain zebra (*Equus zebra*) and feral donkeys (*Equus africanus*) and horses (*Equus ferus*) also occur in the region, but the small livestock kept by pastoralists considerably outnumber these other populations. Black-

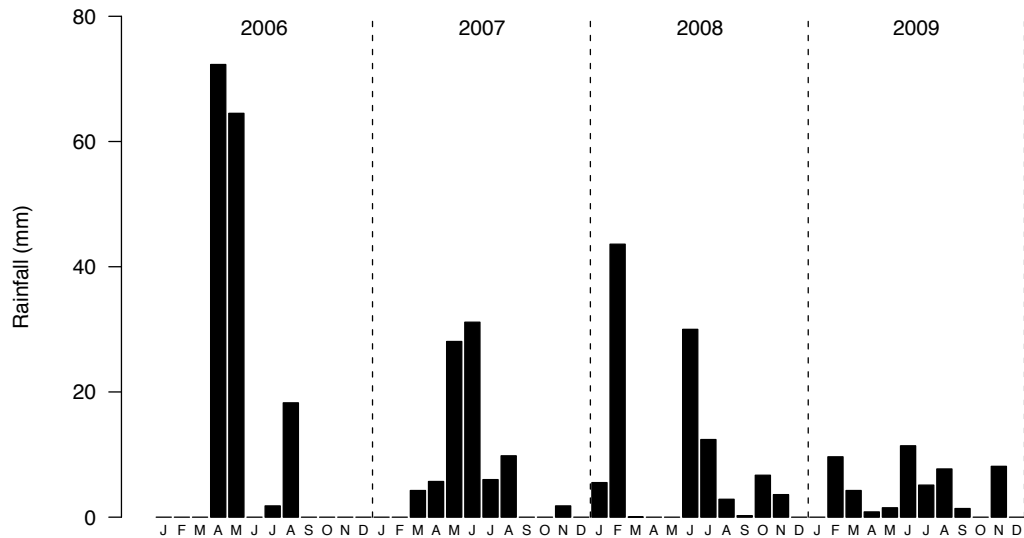


Figure 2.4: Monthly rainfall totals (mm) averaged for the five recording stations in the RNP.

backed jackal (*Canis mesomelas*), leopard (*Panthera pardus*) and unconfirmed reports of brown hyena (*Hyaena brunnea*), form a small pool of predators. Chacma baboons (*Papio ursinus*) and various raptors are also important predators, but would mainly be restricted to preying on kids and lambs.

The Nama pastoralists adopt a semi-nomadic herd management strategy, shifting the position of their stockpost every few months in response to the needs of their livestock. A stockpost traditionally consists of a 'rondehuis' (round house), a fire place with a screen to provide shelter from the wind, and sometimes a kraal (enclosure) to keep the livestock in overnight (e.g. figure 2.5). In many cases, the owner of the herd lives in town, and one or two herders (often sons of the owner) live at the stockpost, but many different arrangements occur. The general pattern of movement is to spend the dry summer months based in the Orange River valley and to move to the interior plains in the wetter winter months to make use of the flush of annual species. Some herds do not make use of the river in the dry season, but then need to be based close to a reliable water source, either springs in the mountains, or near to one of the few boreholes. There are approximately 250 recognised stockposts in the RNP, and usually 15 to 20 of these will be utilised at any one time. RNP management has requested that no new stockpost locations be developed, due to their



Figure 2.5. An example of a stockpost in the Richtersveld, with *Hoodia* sp. in the foreground.

intense local impact ('piosphere effects', Hendricks *et al.* 2005a).

2.1.3 Herd level data

Weekly updates of herd positions were obtained from the RNP field rangers for the period from August 2006 to November 2009. Herd censuses have generally been conducted between twice and four times per year since 1995, with an attempt being made to categorise individuals into age classes (0 - 3 month, 3 - 6 month, 6 - 9 month, 9 - 12 month and older than 12 months). These have almost exclusively been conducted by Dr. Howie Hendricks, who was most kind in making the data available to me for use in this study.

Goat density was mapped over the entire study period, and was based on a combination of the herd position data and the census data (figure 2.6). The average daily foraging distance of a herd from its stockpost is approximately 2.5 km, but herds may range up to 5 km from the stockpost (Hendricks *et al.* 2005b). Herd sizes were extrapolated linearly over the period between each census, to obtain an estimate of

herd size for each week of the study period. This estimate of the size of each herd was then assigned to each pixel (< 10 m²) within a 2.5 km radius of the stockpost at which each herd was located, and was summed for the areas where the zones around each herd overlapped. The weekly density value calculated for each herd was the average number of goats per pixel within 2.5 km of the stockpost. This preparation of the data was performed using ArcGIS 9.3 . The density layer for each week was imported into R version 2.10.1 (R Development Core Team 2009) using the adehabitat package (Calenge 2006), in order to allow for these densities to be combined over different time periods and time lags for use in various analyses.

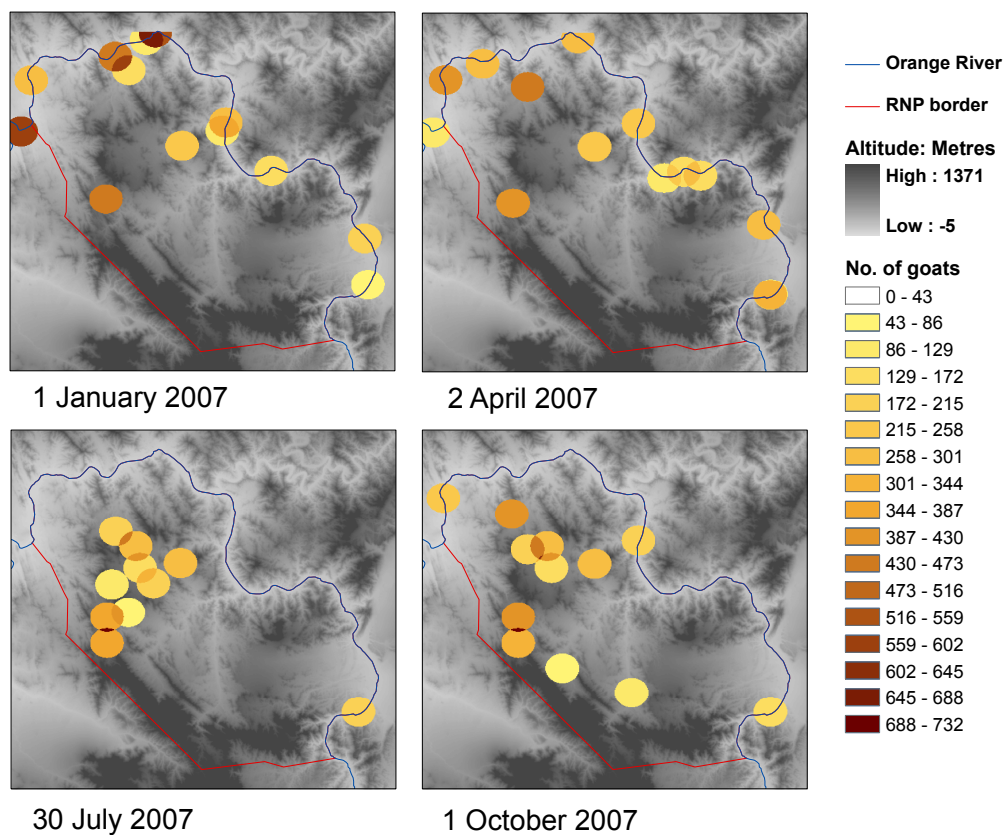


Figure 2.6: An example of the goat density maps produced for each week of the study period.

Density was expressed relative to an estimate of forage availability in each season. In the dry season analyses, this was based on the area (ha) of tree cover within 2.5 km of each stockpost within the riparian zone. Tree cover was mapped in ArcGIS using imagery from Google Earth and digital 1:50 000 maps obtained

2 Study sites and methods

from South African Surveys and Mapping. The FPAR (fraction of photosynthetically active radiation) product, produced by NASA from imagery obtained by the Terra EOS satellite, was used as the estimate of forage availability in the wet season (e.g. figure 2.7). This is available at a spatial resolution of approximately 1 km² and at an 8-day time interval, and was downloaded off the NASA website. FPAR has been shown to be highly correlated with actively growing plant biomass in semi-arid regions (e.g. Fensholt *et al.* 2004). The average FPAR value within 2.5 km of each stockpost was calculated for each 8-day time step during the study period.

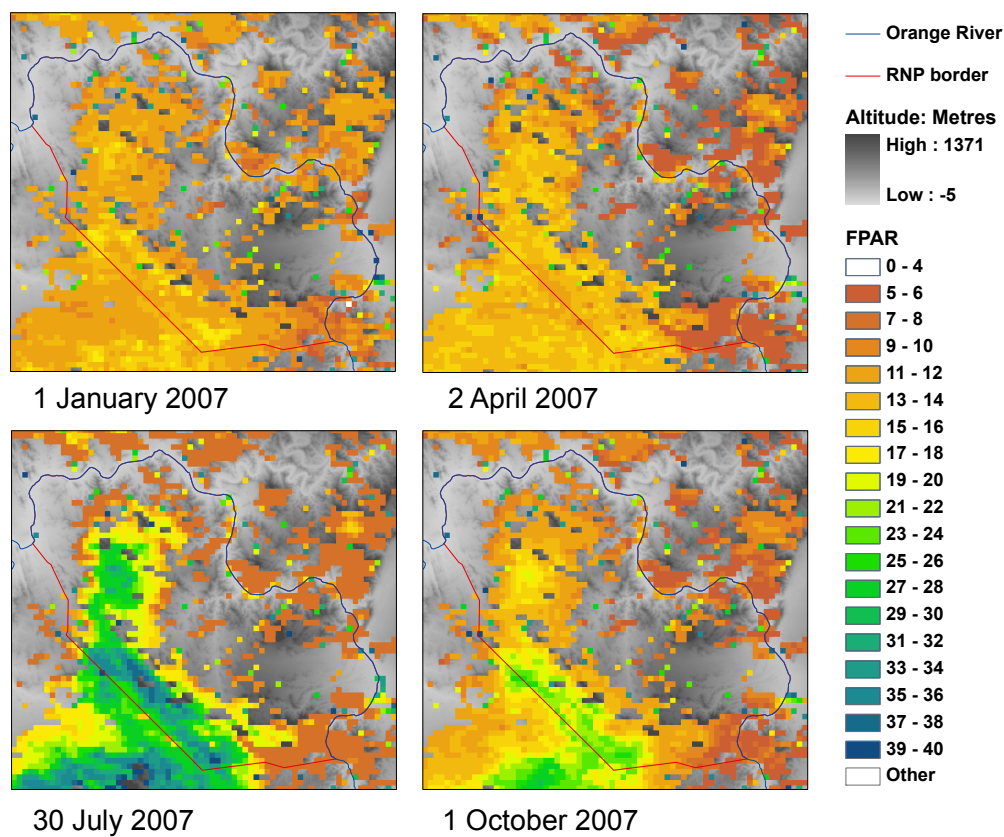


Figure 2.7: An example of the FPAR imagery obtained from the NASA website. Values below 5 and above 40 were excluded from analyses due to their unreliability.

2.1.4 Forage data

Browse availability in the riparian zone of the Orange River was estimated at the individual branch-level and at the tree-level during each fieldtrip from November 2007 to November 2009. This was carried out at five locations within the RNP: Sendelingsdrift, Potjiespram, Oena, De Hoop and at Richtersberg.

Branch-level monitoring was initially based on > 25 branches of each of three species (*Ziziphus mucronata*, *Rhus pendulina*, *Prosopis glandulosa*). A minimum of 20 branches of each of the focus species occurring at the site were being monitored at any point in the study. Branch-level browse availability was based on a visual estimate of the mass and percentage of leaf material on each branch at the time of each fieldtrip. Mass estimates for each species were calibrated by estimating leaf mass on branches not included in the study and then stripping and weighing their leaves.

Tree-level browse availability estimates were made based on trees in six 50 x 20 m plots located at 500 m intervals at each of the five study sites. Browse availability below 2 m was estimated by measuring the length, breadth and height or depth of sections of the canopy (leaf material) of each tree within the plot, an approach that was adapted from the method described in Walker (1976). Vertical measurements were made using a pole marked at 10 cm intervals, while length and breadth of canopy units were estimated to the nearest metre. These three measurements were multiplied together to get an estimate of canopy volume below two metres. For each of these canopy units, an estimate of the percentage of the maximum potential leaf density was made. Browse availability was estimated by multiplying the canopy volume estimate by the percentage of maximum leaf material estimate. This was done for all species occurring in each plot, and was summed to provide a single browse availability estimate for each species in each plot. No attempt was made to estimate the species-specific conversion factor necessary to convert this index of browse availability into an estimate of the actual mass of leaf material.

2.1.5 Goat data

Goat population dynamics were assessed by weighing and tracking the fecundity and survival rates of uniquely marked individuals over the course of the study period. An initial group of 225 female goats were marked in five study herds in the in the RNP



Figure 2.8. Ear tagged kid in the late wet season.

in February 2007. In each herd, a total of 45 individuals were marked with a uniquely numbered green ear tag (figure 2.8). This initial group consisted of 15 kids (< 1 year), 15 yearlings (1 - 2 years) and 15 adults (> 2 years) in each herd. Over the course of the study, this group was added to by marking the female offspring of these tagged individuals. This was done at as young an age as possible, but was dependent on the permission of the herder/owner. Additional individuals were included at various points in the study to supplement diminished life-stage specific sample sizes arising due to mortalities.

Goats were weighed using a portable walk-on scale. All weighing sessions were carried out early in the morning before herds went out foraging for the day (figure 2.9). At the time of weighing, the reproductive status of the individual was recorded (not pregnant, early/late pregnant, lactating), as well as any details available from the herder and from examination by myself and my locally-based field assistants (e.g. number and sex of kids, date of parturition, foetus aborted etc.). In the case of a marked goat not being present at the time of weighing, the herder was questioned as to its fate: cause of death, sales, slaughter, missing etc. If no further information



Figure 2.9. Johannes Cloete bringing a goat to be weighed.

was available, a goat that subsequently did not reappear was recorded as having died of natural causes in the first interval in which it had gone missing. There was a small amount of migration between herds, but this was usually reported due to the distinctness of the green ear tags that were fitted. The quality of information available from the herder/owner varied considerably depending on familiarity with the individual animals (e.g. an owner living with herd vs. a hired herder from town). Quality improved over time as herders and owners became more familiar with the range of questions I would ask. I attempted to standardise the baseline quality of the data included in the analyses by recording my impression of its reliability for each herd during each fieldtrip.

2.2 Kuboes

2.2.1 Overview

Kuboes is a small town (population \pm 1000) situated less than 10 km to the south west of the RNP. Livestock farming has traditionally been the main source of income for this community, but this has to a large extent shifted to a reliance on state grants and wage labour at the alluvial diamond mines along the Orange River (Berzborn 2007). The close proximity of Kuboes to the RNP means that the weather patterns in both of these study sites are very similar, particularly in terms of temperatures, and also the timing and amount of winter rainfall from frontal systems that sweep across both sites. Succulent Karoo vegetation types predominate in the landscape (Mucina & Rutherford 2006).

The major difference between Kuboes and the RNP, which forms the basis of their comparison in this study, is the lack of access to the Orange River for livestock herds during the dry season. The seasonal herd movement patterns in the Kuboes region are less marked than in the RNP. A frequently adopted strategy, used by all herds included in this study, is to locate the stockpost at the base of the escarpment. Herds graze on the plains, which extend 50 km westwards to the coast, during the wet season to make use of the seasonal flush of growth of annual and perennial species. Herds make increasing use of forage reserves in the mountains to the east of Kuboes as the dry season progresses, with some farmers moving their stockposts onto the top of the escarpment towards the end of the dry season. This poses a considerable challenge when it comes to weighing their goats.

2.2.2 Goat data

The same marking, weighing and observational protocols were used for goats in the Kuboes herds that were used in the RNP. Goats from three Kuboes herds were included in the initial group of individuals (135 goats) that were marked in February 2007, and these were monitored throughout the study period. A fourth herd was included in April 2008 to increase the sample size. Goat density was not mapped for Kuboes, as herd position and census data were not available for all herds in the region. Forage availability was not estimated in Kuboes.

2.3 Paulshoek

2.3.1 Overview

Paulshoek is located 250 km south east of the RNP, and has been the focal study site for a long term study of livestock and vegetation dynamics, as well as a large number of social studies. This research effort has mainly been led by Prof. Timm Hoffman (Plant Conservation Unit, University of Cape Town), who kindly granted me access to the monthly livestock census dataset which covers all herds in the Paulshoek region from 1997 to present (August 2010). These data were used to compare the long term trends in population size and variability between the RNP and Paulshoek (chapter 5).

The Paulshoek area has a higher and less variable annual rainfall (200 mm, CV = 32 %) than the RNP and Kuboes. This system has the same winter rainfall pattern as the Richtersveld study sites, which is associated with frontal systems that approach South Africa from the south west. Being further south than the Richtersveld, a greater proportion of these systems will result in rainfall in Paulshoek than in the Richtersveld. The vegetation comprises communities from the Succulent Karoo and Fynbos biomes, and shows a similar pattern of seasonality as in the Richtersveld (Mucina & Rutherford 2006).

2.4 Definitions

All is not necessarily as it would seem when discussing plant-herbivore dynamics, particularly the role of key resources (see chapter 6). I've attempted to maintain constant usage of the following terms:

Coupling In the sense of the consumer-resource framework developed by Alfred Lotka and Vito Volterra, which captures the dynamical interaction resulting from a functional link between herbivores and their forage resource.

Disequilibrium The situation where animal population dynamics do not match their resource dynamics perfectly due to perturbations to the system (e.g. environmental forcing) which cause the state variables (amount of forage or number of herbivores)

of the system to not presently reflect the system's inherent equilibrium. Due to the coupling between plants and animals, the equilibrium is a moving attractor; the distance between the current state of the system and that moving attractor would be considered to be the extent of disequilibrium.

Equilibrium The plant community and the animal community are coupled by a functional mechanism (herbivory), which potentiates the existence of a negative feedback between the herbivore and the forage resource. Density-dependence is generally expressed in this context.

Key factor *sensu* Varley & Gradwell (1960), the vital rate of a population that has the greatest impact in terms of determining the population trajectory. However, the methodology proposed by Varley & Gradwell (1960) for calculating the key factor has been shown to have flaws due to a failure to accurately relate variation in vital rates to variation in population size (Royama 1996).

Nonequilibrium Context dependent, see chapter 6. Either 1) a high state of disequilibrium, or 2) the lack of coupling between herbivore and forage resource.

Range The area being used by animals at a certain time of the year e.g. the dry season range.

3 The Dry Season

3.1 Introduction

The mid-summer heat in the RNP dry season can be extreme, which when combined with violent dust storms, can make it seem a truly inhospitable landscape. The Orange River effectively becomes a linear oasis under these conditions, threaded through forbidding terrain (figure 3.1). It is unsurprising that most herds make use of the riparian zone during the dry season (Hendricks *et al.* 2005*b*), as it provides both drinking water and an apparently plentiful supply of browse. Herds tend to remain in this small subset of the total area of the RNP until the onset of the winter wet season, which usually begins between May and August. In drought years, however, herds will remain in the riparian zone virtually the whole year round (Hendricks *et al.* 2005*b*). There is thus a clear reliance on the riparian zone during dry periods, but the significance of this for the goat population has not yet been investigated.

The obvious role of the Orange River is that it provides water for the herds, but it also determines what forage resources are accessible during the dry season. Water plays an important role in determining the seasonal distributions of most herbivores (e.g. Western 1975, Redfern *et al.* 2003). The provision of artificial waterpoints in a landscape has been shown to increase the abundance of herbivores, by increasing the area accessible to them during the dry season (Grant *et al.* 2002, Gaylard *et al.* 2003). Water can thus be a useful tool for managers, as it enables them to exert some degree of control over the abundance and seasonal distribution of herbivores (Smit *et al.* 2007, Chamaille-Jammes *et al.* 2007). However, the consequences of the spatial patterning of water need to be carefully considered. In a study of the effect of drought on four regions with differences in artificial water supply, herbivore mortality was highest where waterpoints were most closely spaced (Walker *et al.* 1987). These regions with high drought mortality also showed the highest depletion of forage reserves, which was considered to be an effect of both the increased concentration of herbivores and the homogenisation of the foraging landscape. Water availability and herbivore



Figure 3.1. The Orange River, flowing through the forbidding terrain of the De Hoop region of the RNP.

dynamics are thus clearly linked, but this relationship operates through the forage resource and relies on the population being food-limited. In the context of the RNP, most herds rely on the Orange River as their water source in the dry season, and the riparian forage resource is thus expected to be important for goat population dynamics.

Food limitation in the dry season is an important factor shaping population dynamics in many semiarid systems. Poor nutritional status during the dry season has been shown to be a direct cause of mortality in white-eared kob (Fryxell 1987) and wildebeest (Mduma *et al.* 1999); starvation in both cases was exacerbated in drier years. Sinclair (1985) and Mduma *et al.* (1999) both consider dry season mortality to be critical in shaping the trajectory of the Serengeti wildebeest population. Poor nutrition has also been linked to greater dry season mortality in kudu (van der Waal *et al.* 2003). The decline in body condition of impala during the dry season was shown to be density-dependent in a population in Zimbabwe (Gaidet & Gaillard 2008), providing further evidence for forage resource limitation at this time of year. There is thus considerable evidence to suggest that the dry season forage resource might have an important effect on the dynamics of the RNP goat population.

Hendricks *et al.* (2005b) suggest the Orange River riparian zone is likely to form the key resource of the RNP goat population, due to its role in sustaining animals during the dry season. In this chapter I test this contention, by assessing the evidence for:

1. Density-dependent depletion of the riparian forage resource
2. Declines in goat body condition over the dry season
3. Mortality being dependent on body condition
4. Lower survival rates over more severe dry seasons

3.2 Methods

3.2.1 Seasonal movement patterns

The role of the Orange River in the seasonal dynamics of goats in the RNP was explored using the movement patterns of the study herds and local weather data. Herd movement patterns were based on the position of the stockpost occupied by each study herd, which was updated weekly based on reports from the RNP rangers. The distance to the Orange River was calculated for each stockpost occupied between September 2006 and November 2009, and formed the basis of the analysis of herd movement patterns. A general linear mixed-effects model structure was used to analyse the proximity of herds to the Orange River, with the \log_e of the distance of the stockpost to the Orange River being entered as the response variable. Rainfall and temperature over the month prior to a move to a new stockpost were fitted as fixed effects in the model. Rainfall was entered as the \log_e of the sum of rainfall in the previous month, and average daily temperature in the previous month was fitted as a three level factor - high (32°C - 38°C), medium (26°C - 32°C) and low (20°C - 26°C). Herd identity was fitted as a random effect, to account for the preference of certain regions by some farmers. The model was fitted in R version 2.10.1 (R Development Core Team 2009) using the nlme package (Pinheiro *et al.* 2009).

Seasonal range use was further explored by splitting the RNP into a dry season range and a wet season range, and calculating the percentage of each year spent in each range. Stockposts within 2.5 km of the Orange River were considered to be in

the dry season range, as this has previously been found to be the average distance a herd in the RNP travels from its stockpost each day (Hendricks *et al.* 2005b). The remaining stockposts were classified as being in the wet season range. The average duration of stay at a stockpost was calculated for each range for each year.

3.2.2 Forage dynamics

Tree-level

Tree- and branch-level forage availability was analysed using general linear mixed-effects models fitted with the lme4 package (Bates & Maechler 2010) in R version 2.10.1 (R Development Core Team 2009). In the tree-level analyses, the \log_e of forage abundance below 2 m was entered as the response variable, and the \log_e of previous forage abundance, \log_e of adult goat density and the \log_e of rainfall were fitted as fixed effects. In preliminary analyses, adult goat density aggregated over the previous ten weeks and rainfall aggregated over six to fifteen weeks were found to have the most explanatory power and were fitted in the main models. Goat density was expressed relative to the area of total tree cover within 500 m of all study plots at each site. A distance of 500 m was chosen as this was the spacing interval between plots along the river. The random effects structure accounted for potential plot-level effects, nested within site-level effects.

Density effects on different species were assessed by comparing four models with a nested random effects structure. A null hypothesis of there being no difference in forage abundance between species in the absence of goats (model 1), was contrasted with the hypothesis that species abundance varied, by including species as a random effect (model 2). The hypothesis that goat browsing affects the abundance of browse from each tree species differently was tested by including the effect of goat density on the slope of species forage abundance as a random effect (model 3). Finally, the hypothesis that the effect of increasing goat density on species forage abundance was related to species forage abundance in the absence of goats was tested by including the effect of goat density on the slope and intercept of species forage abundance (model 4). Model 4 tests for goats switching species preference as goat density increases. The effect of density on different species was modelled in the random effects because species had fifteen factor levels, and modelling their variance uses fewer degrees of

freedom than modelling their means.

In the first step in selecting the best model, models 1-4 were paired in order of increasing complexity and compared using a χ^2 -test on twice the difference of their log-likelihood ratios. Fixed effects were dropped independently and their significance calculated as the χ^2 -probability of the resulting log-likelihood ratio. The order of model terms was based on the amount of variance explained when added sequentially in an analysis of variance; the term accounting for the highest proportion of remaining variance was selected for each position. The simplest model adequately explaining forage availability was selected as the best model, and used to estimate the main effects of goat density and rainfall. As measures of the overall fit of the best model, the correlation and residual standard deviation of the values fitted by the model and the actual values of the response variable were calculated.

Goat browsing effects are expected to vary within the forage profile and were explored by analysing the interaction between density and forage abundance at different heights in a general linear mixed-effects model. Total forage abundance (0 - 2 m) was split into five height categories: 0.0 - 1.0 m, 1.0 - 1.3 m, 1.3 - 1.5 m, 1.5 - 1.7 m and 1.7 - 2.0 m, and entered as the response variable. These categories were chosen to reflect heights at which an individual's standing reach or hind leg balancing ability might start limiting their feeding efficiency - based on observations made in the field. The main effects and interaction of density and height were fitted as fixed effects, as were rainfall and the \log_e of previous forage abundance. The density and rainfall intervals and the random effects structure fitted in model 3 - for the full profile - were fitted in this height categorised model.

Branch-level

Branch-level forage availability analyses entered the \log_e of leaf mass on a branch as the response variable, with goat density, rainfall, species and initial leaf mass being fitted as explanatory variables. Goat density was expressed at the site level as the number of goats per hectare of tree cover within 500 m of the study plots. Preliminary analyses identified adult goat density over the period five weeks prior to estimates, and rainfall over the period six to ten weeks before leaf mass estimates, as being the density and rainfall variables with most explanatory power. The \log_e values of these terms were fitted as fixed effects in the full model. Species was fitted as a main effect

in the full model, and the \log_e of previous leaf mass was fitted to account for branches with a greater initial leaf mass being able to show bigger changes in leaf mass. Site, a unique branch code and cohort were fitted as random effects. Cohort identifies branches as having been added to the study on the same fieldtrip, and had four levels. The significance of main effect terms was assessed using a χ^2 -test of log-likelihood ratio of the resultant model when the each term was dropped, and terms were ordered based on the amount of variation explained. The correlation and standard deviation of the difference between values fitted by the model and actual values of the response variable were used as measures of the goodness of fit of the model.

3.2.3 Dry season goat mass

The effect of conditions in the dry season on goat nutritional status was assessed by analysing the change in mass of the marked individuals, which were weighed approximately every twelve weeks. In order to restrict the analysis to mass changes associated with the dry season range forage resource, only the subset of cases where a herd had spent seven or more of the previous twelve weeks in the dry season range were considered. Analyses were split into life-stages - adults, yearlings and kids - because of the need for higher age estimate precision when accounting for the rapid growth rates of younger individuals, and differences in the shape of the stage-specific growth curve. General linear mixed-effects models were used to analyse the mass of the marked individuals, which were fitted using the lme4 package (Bates & Maechler 2010) in R version 2.10.1 (R Development Core Team 2009).

The effects of adult goat density, rainfall and time spent in the dry season range were of primary interest in understanding dry season range dynamics, and measures of each were fitted as main effects. Goat density was calculated as the number of adult goats per hectare of tree cover within 2.5 km of the stockpost. This was calculated for the periods 0 - 32, 0 - 64, 0 - 96, 32 - 64, 32 - 96 and 64 - 96 days prior to each mass estimate. Rainfall was assessed using a similar series of 32 day time intervals, lags and sequential combinations, but was extended to a maximum of 192 days prior to mass estimates for yearlings and adults. The maximum rainfall period considered for kids was 112 days, as longer time periods produced results which were difficult to interpret. This may in part be due to longer time periods extending beyond the date of conception for the youngest individuals. Reproductive status was fitted

as a main effect in the yearling and adult models, as it plays an important role in influencing goat mass. Various coding schemes for reproductive status were assessed - the simplest having four levels (not pregnant, pregnant, lactating or unknown), and the most detailed including coding for early pregnancy, the number of kids and aborted pregnancies. Preliminary analyses were used to identify the respective \log_e density, \log_e rainfall and reproductive status measures with the highest explanatory power, which were then included in the full model. The number of weeks spent in the dry season range over the previous twelve weeks was fitted in each full model. Age in years was fitted as a fixed effect in the adult model, while monthly age estimates were fitted in the yearling and kid models. Due to limitations in data availability, age was fitted as an eight level factor in the adult model (2-8 years and unknown). In order to allow for differences in the shape of the growth curve for yearlings and kids, the effect of fitting age as either a linear or quadratic covariate was tested. Calendar year was fitted as the final fixed effect term in the full model for each life-stage, in order to account for remaining variance not explained by the biological effects that were quantified.

The random effect component of each life-stage model took individual and herd effects into account. Individual effects were modelled by fitting tag number as a random term. This individual effect was conditioned by age in the adult (factor, age in years) and kid (quadratic, age in months) models. Conditioning the yearling individual effect by the individual's age did not improve the fit of the model, and age was thus excluded from the random component. Management differences between herds were accounted for by including herd as a random term.

The best model was chosen by dropping each fixed effect from the full model, and assessing the resulting change in fit based on a χ^2 test of twice the difference in resulting log-likelihood. Model terms were included in decreasing order of total variation explained, which was calculated by adding them sequentially in an analysis of variance. The differential impact of density, rainfall and time spent in the dry season range on different life-stages was assessed using t-tests on the respective slope estimates. As a measure of the predictive power of each model, the correlation between the fitted values and original mass estimates was calculated, as well as the standard deviation of the difference between fitted and actual mass values.

3.2.4 Vital rates

Adult survival rates over the dry season were estimated using the survival of tagged goats from the February to August fieldtrips each year. This time period was selected in order to include the mid- and late dry season in each year, while keeping the interval length the same for each year. Survival over this period was assessed for all adults alive in February each year. A binary response variable was generated, with individuals scored as 'one' if they survived through to August that year, and 'zero' if they died during the interval. A general linear mixed-effects model with binomial error structure was fitted to assess the role of various individual and environmental factors in shaping variation in survival rates over the dry season. The mass of an individual in February was fitted to assess the effect of the size of an individual on its probability of surviving the dry season. Goat mass was further used to assess the effect of the condition of a particular individual on its likelihood of survival, by fitting its change in mass from February to April, expressed as a proportion of its mass in February. The reproductive status of an individual in February was also fitted in the model. Goat density impacts on survival were tested by fitting the \log_e of the number of adult goats within 2.5 km of the stockpost each week, summed for the period from March to May and from June to August. Year was fitted as a proxy for rainfall, because only a single rainfall value was available for any time interval selected in each of the three years - meaning the rainfall slope would be estimated off only three points. Herd and individual identity were fitted as random effects in preliminary analyses, but excluded because they accounted for very low levels of the remaining variance.

3.3 Results

3.3.1 Seasonal movement patterns

Herds made use of the Orange River riparian zone during hot and dry periods, and moved into the wet season range following rainfall in cooler periods (figure 3.2). Herd distance from the Orange River was positively related to the \log_e of rainfall in the previous month ($F_{1,93} = 14.3$, $p = 0.0003$) and negatively related to temperature in the previous month ($F_{2,93} = 5.8$, $p = 0.0041$). The effect of the 26°C - 32°C level was similar to the effect of the 32°C - 36°C level (0.2503 ± 0.3975 (s.e.), $t_{(5)} = 0.63$, p

= 0.5304), but the cooler 20°C - 26°C level corresponded with herds moving further away from the river (1.3493 ± 0.4164 (s.e.), $t_{(5)} = 3.24$, $p = 0.0017$).

The amount of time spent in the dry and wet season range differed amongst years in the study period, as did the average length of stay at a stockpost (table 3.1). In 2007, herds spent equal amounts of time on average in the DSR and the WSR, and spent similar amounts of time at a stockpost in either range. A greater proportion of 2008 was spent in the WSR than the DSR, although length of stay at a stockpost remained similar for each range. In contrast, 2009 saw herds spending almost two-thirds of the year in the DSR, and moved between stockposts more frequently than in 2007 or 2008.

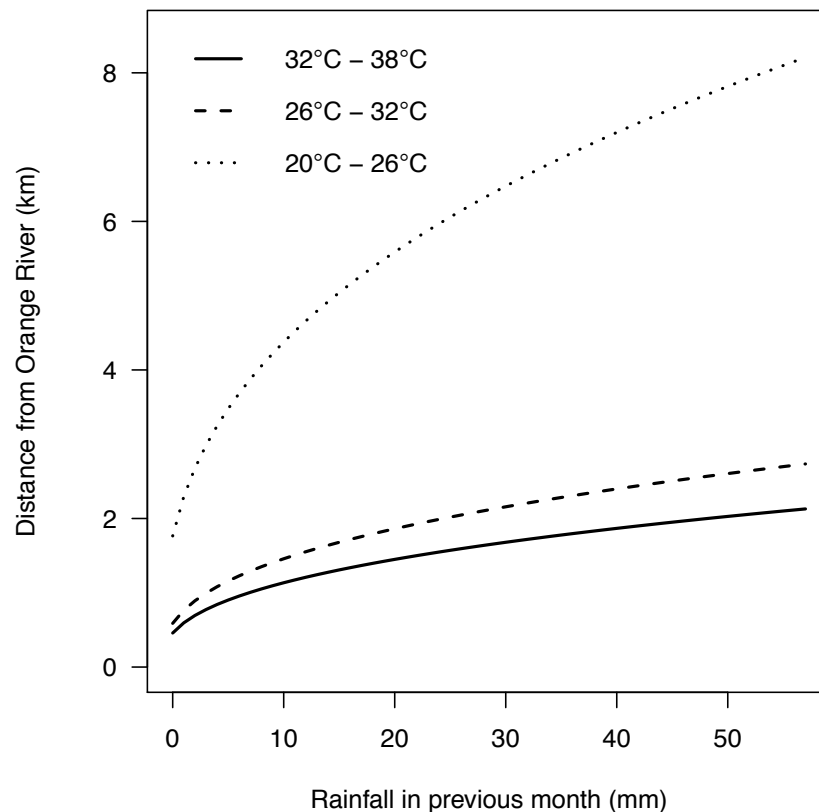


Figure 3.2: Distance of the stockpost from the Orange River in response to the effects of rainfall and temperature in the previous month. Temperature was entered as a three level factor.

Table 3.1: Amount of time spent in the dry and wet season range for each year of the study (%), and the average duration of stay at a stockpost (weeks, mean \pm s.d.) in each seasonal range for each year.

Year	Dry season range		Wet season range	
	Percentage of year	Duration of stay	Percentage of year	Duration of stay
2007	51.6 %	7.5 \pm 6.0	48.8 %	8.0 \pm 6.3
2008	41.8 %	8.9 \pm 5.0	58.2 %	8.9 \pm 4.5
2009	65.1 %	4.7 \pm 3.9	34.9 %	6.5 \pm 3.9

3.3.2 Forage dynamics

Tree-level

Tree-level browse availability varied amongst tree species, and forage depletion rates also differed amongst species in response to goat density (table 3.2). The log-likelihood ratio of model 1 vs. model 2 indicates that, in the absence of goats, forage availability differed between species ($\chi^2 = 20.7$, d.f. = 1, $p < 0.001$). The comparison of model 2 to model 3 shows that species were utilised differentially by goats ($\chi^2 = 29.4$, d.f. = 1, $p < 0.001$). There is however no evidence of goats switching between browse species in response to increasing goat densities ($\chi^2 = 0.0$, d.f. = 1, $p = 0.984$). The random effects structure of model 3 was further simplified by dropping the species intercept term and nested plot effect, which had no effect on the log-likelihood of the model. The remaining terms in model 3 were significant, which was thus selected as the best model explaining tree-level forage availability (table 3.3).

Forage abundance was positively related to previous forage abundance ($\chi^2 = 1599.8$, d.f. = 1, $p < 0.0001$), but the slope was less than one (0.8727 ± 0.0148 s.e.), indicating a decline in overall forage abundance over the study period in the absence of rain and goats. Forage abundance was increased by rainfall ($\chi^2 = 89.8$, d.f. = 1, $p < 0.0001$) and reduced in response to higher goat densities ($\chi^2 = 12.4$, d.f. = 1, $p = 0.0004$). Site and density effects on the slope of species accounted for small parts of the remaining variation, but most of this was unexplained. The approximate goodness of fit estimate (fitted vs. actual response values) had an r^2 value of 0.81, and residual standard deviation of 0.7086.

Goat density effects on tree-level forage abundance vary amongst species in the

Table 3.2: Candidate models accounting for tree-level forage availability by the effects of previous forage abundance, goat density and rainfall. The different random effects structures show an increase in complexity from model 1 to model 4. Overall species effects are first ignored (model 1) and then included (models 2 - 4). Density effects on individual species responses are ignored in model 2, allowed to affect the slope of the individual species response (model 3) and finally allowed to influence the slope and intercept of each species (model 4). The main effects are \log_e of previous forage abundance, \log_e of adult goat density per hectare of trees over the previous ten weeks and \log_e of rainfall in the period 6 - 15 weeks previously. Refer to text for further details.

Model	d.f.	Log ratio	Test	p value
Model 1: Main effects + (1 Site/Plot)	7	-1301.3		
Model 2: Model 1 + (1 Species)	8	-1290.9	1 vs. 2	< 0.001
Model 3: Model 2 + (Density-1 Species)	9	-1276.2	2 vs. 3	< 0.001
Model 4: Model 1 + (Density Species)	10	-1276.2	3 vs. 4	0.984

Table 3.3: Summary of the general linear mixed-effects model of tree-level forage availability ($n = 1169$) as the response to previous forage abundance, rainfall and adult goat density. The random structure accounts for site effects ($n = 5$) and a density-conditioned slope for each species ($n = 15$).

Fixed effects	Estimate	S.E.	t-value	F-ratio	d.f.	p-value
Intercept	0.1278	0.0742	1.72			
Previous forage				3532.7	1	< 0.0001
\log_e of previous forage	0.8727	0.0148	59.15			
Rainfall				103.8	1	< 0.0001
\log_e rainfall 6-15 weeks	0.1462	0.0152	9.65			
Density				14.5	1	0.0004
\log_e density 0-10 weeks	-0.0916	0.0240	-3.82			
Random effects	Variance	Percentage				
Species						
Density _(slope)	0.0041	0.79				
Site	0.0070	1.35				
Residual	0.5089	97.86				
Total variance	0.5200					

dry season range (figure 3.3). *Ziziphus* abundance shows the steepest decline in response to an increase in goat densities, and is commonly perceived by pastoralists as being an important browse species (pers. comm.). *Prosopis*, an alien invasive species, is widely considered as being an important forage species. However, it would appear that its value is largely restricted to its pods, as leaf forage abundance shows no evidence of a decline in response to an increase in goat densities. *Tamarix* is the most abundant species in the riparian zone, but is little utilised as a source of browse.

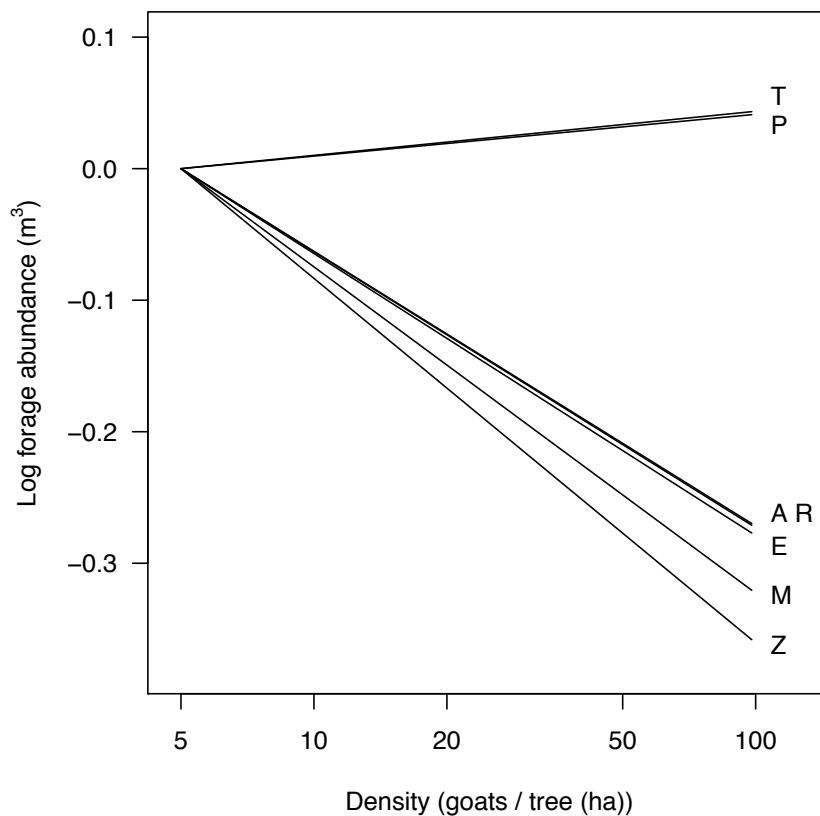


Figure 3.3: Slope of the tree-level response of \log_e forage abundance (m^3) to adult goat density (goats / tree (ha)) for six common species in the dry season range, based on estimates from the best model. T = *Tamarix usenoides*, P = *Prosopis glandulosa*, A = *Acacia karroo*, R = *Rhus pendulina*, E = *Euclea pseudobenus*, M = *Maytenus linearis* and Z = *Ziziphus mucronata*.

The negative effect of goat browsing on forage abundance differed substantially through the forage profile, being strongest lower down and diminishing with height above 1.3 m (figure 3.4). In the height categorised model, variation in forage

abundance was significantly influenced by height ($\chi^2 = 65.0$, d.f. = 4, $p < 0.0001$), density ($\chi^2 = 4.9$, d.f. = 1, $p = 0.0264$) and the interaction between the height and density terms ($\chi^2 = 26.3$, d.f. = 4, $p < 0.0001$). Forage abundance in the 0.0 - 1.0 m and 1.0 - 1.3 m height classes showed the steepest, and similar, negative responses to increased goat density. Above 1.3 m, the slope of the response to goat density decreased as height in the profile increased, being smallest in the 1.7 - 2.0 m height class.

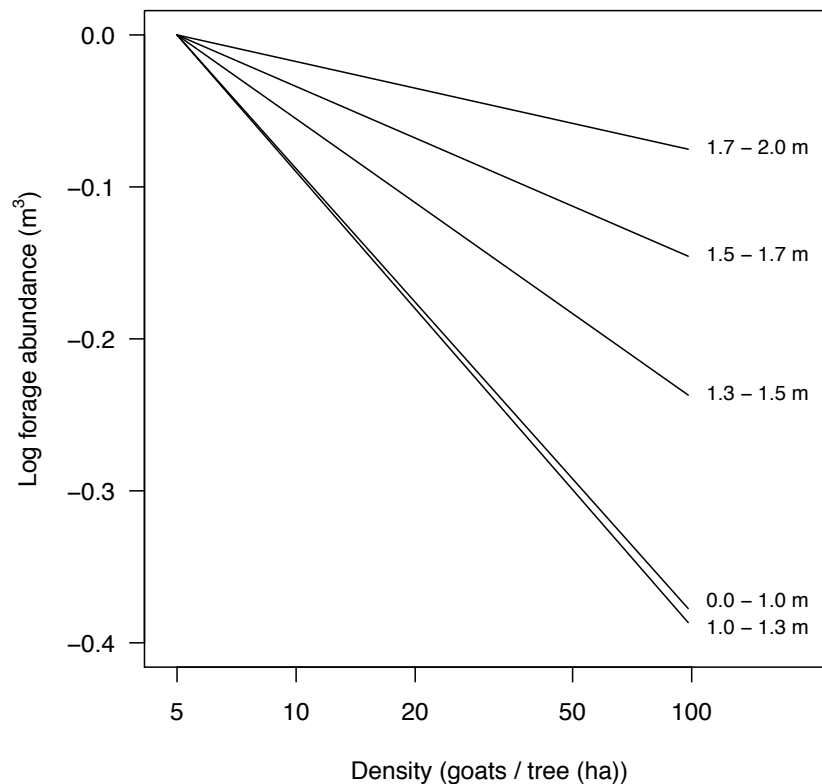


Figure 3.4: Slope of the tree-level response of \log_e forage abundance (m^3) to adult goat density (goats / tree (ha)) at five heights in the forage profile, based on estimates from the height categorised model.

Branch-level

Branch-level forage abundance differed between species in response to adult goat density, but all species showed a positive response to rainfall and previous leaf mass.

Table 3.4: Summary of the general linear mixed-effects model of branch-level forage abundance (n = 2460) in response to previous leaf mass, rainfall, species, adult goat density and the interaction between species and density effects. The random component accounts for variance attributable to individual branch effects (n = 386), site effects (n = 5) and branch cohort effects (n = 4).

Fixed effects	Estimate	S.E.	t-value	F-ratio	d.f.	p-value
Intercept	0.9187	0.2145	4.28			
Previous mass				4009.2	1	< 0.0001
log _e of previous mass	0.6302	0.0159	39.66			
Rainfall				304.2	1	< 0.0001
log _e rainfall 6-10 weeks	0.1490	0.0158	9.42			
Species				248.5	2	< 0.0001
Prosopis	0					
Rhus	-0.1017	0.1613	-0.63			
Ziziphus	-0.5407	0.0948	-5.70			
Density				33.5	1	< 0.0001
log _e density 0-5 weeks	0.1334	0.0297	4.49			
Species x Density				87.3	2	< 0.0001
Prosopis x Density	0					
Rhus x Density	-0.7086	0.0589	-12.04			
Ziziphus x Density	-0.3289	0.0348	-9.46			
Random effects	Variance	Percentage				
Branch	0.0148	1.39				
Site	0.0438	4.11				
Cohort	0.1037	9.73				
Residual	0.9034	84.77				
Total variance	1.0657					

All terms included in the full model were significant (table 3.4). Leaf mass was positively related to the previous leaf mass estimate ($\chi^2 = 928.5$, d.f. = 1, $p < 0.0001$), but the slope was much less than one (0.6309 ± 0.0159 s.e.), indicating that branch biomass decreased over time. Rainfall in the previous 6 - 10 weeks had a positive effect on leaf mass estimates ($\chi^2 = 87.3$, d.f. = 1, $p < 0.0001$). Prosopis branches included in the study had the highest leaf mass and Ziziphus branches the lowest ($\chi^2 = 547.6$, d.f. = 4, $p < 0.0001$). Goat densities had a significant effect on forage estimates ($\chi^2 = 200.1$, d.f. = 3, $p < 0.0001$), but the response differed amongst species ($\chi^2 = 169.2$, d.f. = 2, $p < 0.0001$; figure 3.5). Prosopis responded positively to goat densities, confirming its low desirability as a browse species. Rhus and Ziziphus both

responded negatively to goat densities, but the *Rhus* response was steeper. This may indicate a preference for *Rhus* over *Ziziphus* (although both are perceived as being highly desirable), but may be an artefact of the smaller size of *Ziziphus* branches included in the study. Branch, site and cohort effects accounted for increasing amounts of the remaining variance, but the majority was unexplained. The correlation between the values fitted by the model and the response variable was reasonable ($r^2 = 0.77$), with a residual standard deviation of 0.9412.

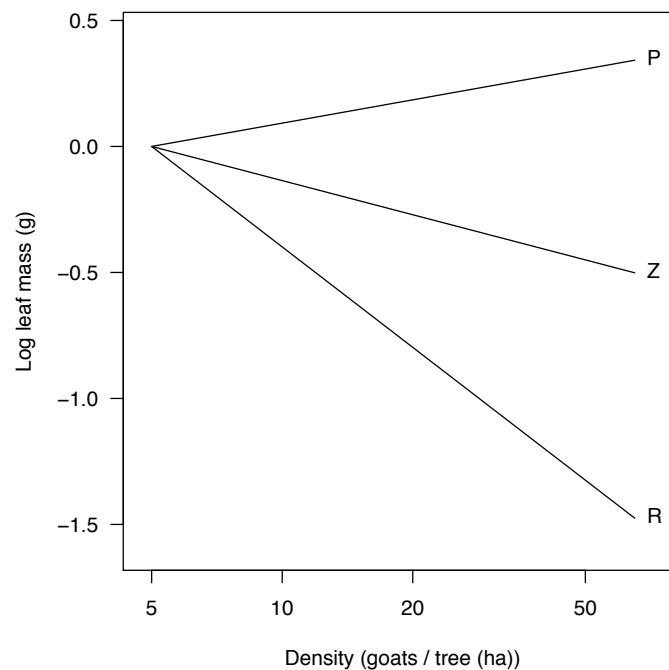


Figure 3.5: Slope of the branch-level response of \log_e leaf mass (g) to adult goat density (goats / tree (ha)) for three species, based on estimates from the best model. P = *Prosopis glandulosa*, R = *Rhus pendulina* and Z = *Ziziphus mucronata*.

3.3.3 Dry season goat mass

The qualitative effect on mass of density, rainfall and duration of residence in the dry season range was the same for all life-stages: goat mass was negatively related to goat density and the amount of time spent in the dry season range, but was positively related to rainfall. The best model for each life-stage included all fixed terms entered in the full model, although the details and ordering of these terms differed. Reproductive

status accounted for the largest amount of variation in the adult model, followed by the rainfall, age, time in dry season range and the density terms (table 3.5). Age and reproductive status were the first two terms fitted in the yearling model, after which rainfall, density and time in the dry season range were fitted (table 3.6). In the best kid model, age accounted for most variation in body mass, followed by the time in dry season range, rainfall and density terms (table 3.7). Calendar year, fitted as the final term in each model, accounted for a significant proportion of the remaining variation in body mass in each life-stage model.

The negative relationship between goat body mass and adult goat density and time spent in the dry season range was consistent across life-stages (figure 3.6a and 3.6b). The best fit density term for adults was \log_e density in the previous 32 days ($\chi^2 = 9.5$, d.f. = 1, $p = 0.0021$) and \log_e density over the previous 96 days for yearlings ($\chi^2 = 49.8$, d.f. = 1, $p < 0.0001$) and kids ($\chi^2 = 22.5$, d.f. = 1, $p < 0.0001$). The slope of the yearling mass response to density was significantly steeper than the kid ($t_{(74)} = -4.37$, $p < 0.001$) or adult response ($t_{(74)} = 6.99$, $p < 0.001$). Adults showed the smallest mass response to density (vs. kids: $t_{(133)} = 5.54$, $p < 0.001$). Despite the differences in time periods over which density was measured, the slopes were deemed comparable because the same units were used in each case (goats/tree (ha)), which did not include time.

Goat mass was significantly and negatively impacted by time spent in the dry season range in the adult ($\chi^2 = 23.9$, d.f. = 1, $p < 0.0001$), yearling ($\chi^2 = 23.9$, d.f. = 1, $p < 0.0001$) and kid models ($\chi^2 = 22.2$, d.f. = 1, $p < 0.0001$). The slopes of the life-stage response to time spent in the dry season range were ranked in the same order as density effects were, but the size of the mass response was smaller. The yearling response to time spent in the dry season range was steeper than the kid response, but the difference between the slopes was not significant ($t_{(74)} = -0.79$, $p > 0.1$). The slope of the adult mass response was significantly shallower than the kid response ($t_{(133)} = 4.39$, $p < 0.001$).

Table 3.5: Summary of the best fit general linear mixed-effects model of adult goat mass (n = 1166) in response to reproductive status, rainfall, age, time spent in the dry season range, adult goat density and calendar year. The random component takes into account an individual's identity (n = 255), conditioned by its age in years (n = 8), and herd level effects (n = 5).

Fixed effects	Estimate	S.E.	t-value	F-ratio	d.f.	p-value
Intercept	43.3003	1.4477	29.91			
Reproductive status				114.8	8	< 0.0001
Early pregnant single	0					
Early pregnant twins	1.0826	0.4995	2.17			
Early pregnant unknown	-0.1994	0.5718	-0.35			
Pregnant single	4.1138	0.4050	10.16			
Pregnant twins	6.1041	0.4742	12.87			
Pregnant unknown	2.9643	0.5358	5.53			
Lactating	-1.6704	0.3670	-4.55			
Not pregnant	-0.8830	0.4525	-1.95			
Unknown	-0.4339	1.1488	-0.38			
Rainfall				111.7	1	< 0.0001
Rainfall 64-160 days	0.8578	0.0952	9.01			
Age				60.7	7	< 0.0001
2 years	0					
3 years	7.6891	0.5563	13.82			
4 years	11.2088	0.6722	16.68			
5 years	12.8230	0.8113	15.81			
6 years	13.1883	1.0346	12.75			
7 years	11.0015	1.0739	10.24			
8 years	11.7016	1.0796	10.84			
Unknown	11.7046	0.9809	11.93			
Time in DSR				4.8	1	< 0.0001
No. weeks in last 12	-0.3519	0.0715	-4.93			
Density				10.9	1	0.0021
Goat adults 0-32 days	-0.2007	0.0655	-3.07			
Year				18.1	2	< 0.0001
2007	0					
2008	-2.7508	0.5216	-5.27			
2009	-3.0192	0.5330	-5.67			

Table 3.5: (continued on next page)

Table 3.5: (continued)

Random effects	Variance	Percentage
Tag		
Age (Intercept)	19.8471	13.09
Age 3 years	16.0288	10.57
Age 4 years	26.9419	17.77
Age 5 years	13.5458	8.94
Age 6 years	13.6746	9.02
Age 7 years	12.4941	8.24
Age 8 years	12.3637	8.16
Age unknown	26.2709	17.33
Herd	4.1189	2.72
Residual	6.2875	4.15
Total variance	151.5733	

Goat mass responded positively to rainfall (figure 3.6c) in the adult ($\chi^2 = 78.5$, d.f. = 1, $p < 0.0001$), yearling ($\chi^2 = 36.2$, d.f. = 1, $p < 0.0001$) and kid models ($\chi^2 = 21.9$, d.f. = 1, $p < 0.0001$). The best fit rainfall term in the adult model was the \log_e of rainfall in the preceding 64 - 160 days (i.e. approx. 3 - 5 months), while \log_e rainfall in the preceding 64 - 96 days (i.e. approx. 3 month) was the best rainfall term in the yearling and kid models. The slope of the yearling mass response to rainfall was significantly steeper than the kid mass response ($t_{(74)} = 2.86$, $p < 0.001$). In figure 3.6c, the units of the adult response to rainfall in the model (\log_e (rainfall/96 days)) have been recalculated as \log_e (rainfall/32 days), to allow comparison of the slope with that for yearlings and kids. However, the slopes of the terms in the models cannot be compared with a t-test. Adult mass appears to be less sensitive to rainfall effects than yearling or kid mass.

Adult and yearling mass was strongly influenced by the individual's reproductive status. The best fit term in the adult model included coding for individuals as non-pregnant, early-pregnant, pregnant, lactating or unknown, as well as whether they were carrying singletons, twins or an unknown number of kids ($\chi^2 = 603.7$, d.f. = 8, $p < 0.0001$). Non-pregnant and lactating adults were lighter than pregnant adults; pregnant adults were heavier depending on the number of kids they were carrying. The best fit yearling reproductive status term did not include details of the number of kids being carried, and had five levels - non-pregnant, early-pregnant, pregnant, lactating and unknown ($\chi^2 = 131.7$, d.f. = 4, $p < 0.0001$). Mass increased through

Table 3.6: Summary of the best fit general linear mixed-effects model of yearling goat mass (n = 208) in response to age, reproductive status, rainfall, adult goat density, time spent in the dry season range and calendar year. The random component takes into account an individual's identity (n = 76) and herd level effects (n = 4).

Fixed effects	Estimate	S.E.	t-value	F-ratio	d.f.	p-value
Intercept	43.2885	3.0196	14.34			
Age				74.2	1	< 0.0001
Age in months	0.7272	0.0706	10.31			
Reproductive status				44.6	4	< 0.0001
Early pregnant	0					
Pregnant	3.2530	0.4281	7.60			
Lactating	-1.4438	0.4225	-3.42			
Not pregnant	-2.3183	0.4556	-5.09			
Unknown	-0.2154	1.7790	-0.12			
Rainfall				34.7	1	< 0.0001
Rainfall 64-96 days	1.1987	0.1940	6.18			
Density				3.9	1	< 0.0001
Goat adults 0-96 days	-5.0005	0.6691	-7.47			
Time in DSR				24.5	1	< 0.0001
No. weeks in last 12	-0.7707	0.1566	-4.92			
Year				70.1	1	< 0.0001
2008	0					
2009	-4.4431	0.5305	-8.38			
Random effects	Variance	Percentage				
Tag	14.7812	63.99				
Herd	5.9202	25.63				
Residual	2.3984	10.38				
Total variance	23.0998					

the pregnancy, and non-pregnant and lactating yearlings were lighter than pregnant yearlings.

Goat mass was significantly affected by age in each of the adult ($\chi^2 = 242.1$, d.f. = 7, $p < 0.0001$), yearling ($\chi^2 = 85.2$, d.f. = 1, $p < 0.0001$) and kid models ($\chi^2 = 273.4$, d.f. = 2, $p < 0.0001$). Adult mass appears to increase markedly up until an individual is about four years old, whereupon it then plateaus, with suggestion of a slight decline after six years. Age was best fitted as a linear term in the yearling model, as the added complexity of the quadratic term did not improve the model ($\chi^2 = 0.0$, d.f. = 1, $p = 0.8667$). However, including age as a quadratic term improved the fit of the kid model

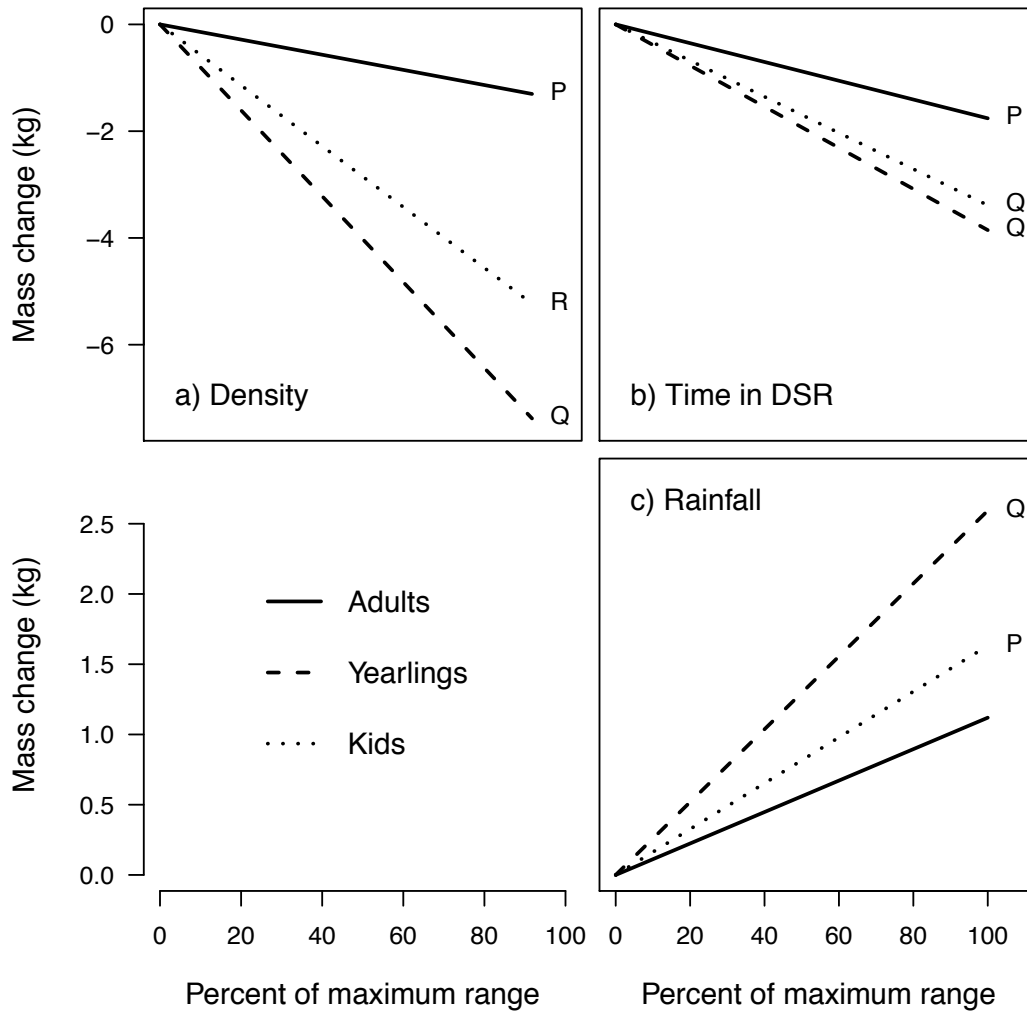


Figure 3.6: Change in body mass (kg) of adults, yearlings and kids in response to a) goat density, b) time spent in the dry season range, and c) rainfall, as estimated by the best model for each life-stage. Lines on the same axes with different letters (P, Q or R) are significantly different from one another ($p = 0.05$). The adult response to rainfall has different units to the kid and yearling response, but has been rescaled appropriately for comparison.

Table 3.7: Summary of the best fit general linear mixed-effects model of kid goat mass (n = 347) in response to age, time spent in the dry season range, rainfall, adult goat density and calendar year. The random component takes into account an individual's identity (n = 135) conditioned by its age in months (n = 11) as a second order polynomial, and herd level effects (n = 5).

Fixed effects	Estimate	S.E.	t-value	F-ratio	d.f.	p-value
Intercept	20.1975	2.2053	9.16			
Age				623.3	2	< 0.0001
Age in months (x)	3.2689	0.1683	19.43			
Age in months (x ²)	-0.1139	0.0136	-8.36			
Time in DSR				15.0	1	< 0.0001
No. weeks in last 12	-0.6775	0.1030	-6.58			
Rainfall				27.2	1	< 0.0001
Rainfall 64-96 days	0.7543	0.1158	6.51			
Density				15.0	1	< 0.0001
Goat adults 0-96 days	-3.5439	0.5803	-6.11			
Year				44.6	1	< 0.0001
2008	0					
2009	-2.6086	0.3949	-6.61			
Random effects	Variance					
Tag (intercept)	0.7148					
Age in months (x)	0.9042					
Age in months (x ²)	0.0056					
Herd	2.2045					
Residual	1.3748					
Total variance	5.2040					

($\chi^2 = 58.8$, d.f. = 1, $p < 0.0001$).

Adults, yearlings and kids were all heavier in 2008 than 2009, and adults were heaviest in 2007. These annual effects on goat mass were significant in each of the adult ($\chi^2 = 32.7$, d.f. = 2, $p < 0.0001$), yearling ($\chi^2 = 61.0$, d.f. = 1, $p < 0.0001$) and kid models ($\chi^2 = 30.1$, d.f. = 1, $p < 0.0001$). The difference in mass between 2008 and 2009 was largest in yearlings and smallest in adults.

The partitioning of the remaining variation in goat mass between the random effects suggests that herd effects decrease with age, while individual effects are relatively more important in older life-stages. Herd effects accounted for 42 % of the remaining variance in the kid model, 26 % in the yearling model, and 3 % in the adult

model. In contrast, individual effects accounted for 93 % of the remaining variation in the adult model, and 64 % and 31 % in the yearling and kid models respectively.

The best model for each life-stage generally provided a good description of the data. The adult model had the lowest correlation between fitted and actual mass values ($r^2 = 0.93$, d.f. = 1164, $p < 0.001$), with a residual standard deviation of 2.0 kg or 4.6 % of the mean adult mass. The fitted values in the yearling model were slightly better correlated with the actual mass values ($r^2 = 0.95$, d.f. = 206, $p < 0.001$), but not as well correlated as for the kid model ($r^2 = 0.99$, d.f. = 345, $p < 0.001$). The residual standard deviation of fitted vs. actual mass values was relatively smaller for yearlings (1.2 kg, 3.8 %) than for kids (0.8 kg, 4.2 %).

3.3.4 Vital rates

The probability of an adult goat surviving the whole dry season was strongly influenced by its condition in the early to mid-dry season. The reproductive status of an individual and year effects also influenced adult dry season survival rates (table 3.8). Adult goats that lost mass in the period from February to April each year were less likely to survive the dry season than goats that gained mass during this interval ($\chi^2 = 7.6$, d.f. = 1, $p = 0.0058$; figure 3.7). Reproductive status in February had a significant effect on dry season survival, with pregnant goats being more likely to survive than lactating or non-pregnant goats ($\chi^2 = 10.0$, d.f. = 2, $p = 0.0069$). Year effects had a marginally significant effect on adult survival over the dry season, and were retained in the best model ($\chi^2 = 6.0$, d.f. = 2, $p = 0.0510$). Goat survival over the dry season was highest in 2007 and lowest in 2009. The size of an individual and density effects did not have a significant influence on dry season survival rates.

3.4 Discussion

The analysis of dry season processes shows that there is considerable reliance on the Orange River riparian zone during the hot and dry periods of the year, and that plant-herbivore dynamics there are dependent on environmental conditions. Both forage abundance and goat mass dynamics are responsive to the effects of rainfall and goat density, and survival over the dry season is linked to goat mass dynamics. There were consistent differences between years in these variables which could not wholly be

Table 3.8: Summary of the best fit generalised linear model of adult survival over the dry season in the RNP ($n = 468$), in response to proportional mass change from February to April, reproductive status and year effects. A binomial error structure was fitted, with individuals scored as 1 if they survived the dry season, and 0 if not.

Effects	Estimate	S.E.	z-value	Deviance	d.f.	p-value
Intercept	3.2683	0.6100	5.36			
Mass change				7.6	1	0.0058
Proportion (Feb - Apr)	6.8751	2.5572	2.69			
Reproductive status				10.0	2	0.0069
Lactating	0					
Non-pregnant	-0.6180	0.4561	-1.36			
Pregnant	1.8431	0.9221	2.00			
Year				6.0	2	0.0510
2007	0					
2008	-0.7136	0.5607	-1.27			
2009	-1.2109	0.5211	-2.32			

explained by rainfall. This reliance on the riparian zone during the dry season suggests that this spatial and temporal subset of the greater RNP plant-herbivore system might limit goat numbers, and it thus potentially operates as the key resource. However, establishing this conclusively requires the demonstration of coupling, or, the existence of a tendency towards equilibrium, between this spatio-temporally delimited subset of resources and the goat population, which shapes their population dynamics.

Landscape use patterns

The landscape use patterns of herds in the RNP were strongly tied to seasonal temperature and rainfall effects (figure 3.2). Temperature, in particular, appears to play an important role in herders decision-making process regarding where a herd should be based. During the hottest parts of the year, and also during more moderate periods, herds were largely located within 2.5 km of the river, giving them comfortable access to drinking water and the vegetation growing along the river bank. Rainfall during these moderate to hot periods generally was insufficient cause for herds to leave the riparian zone. In contrast, rainfall during the cooler winter months was strongly associated with movements away from the Orange River. Winter rainfall

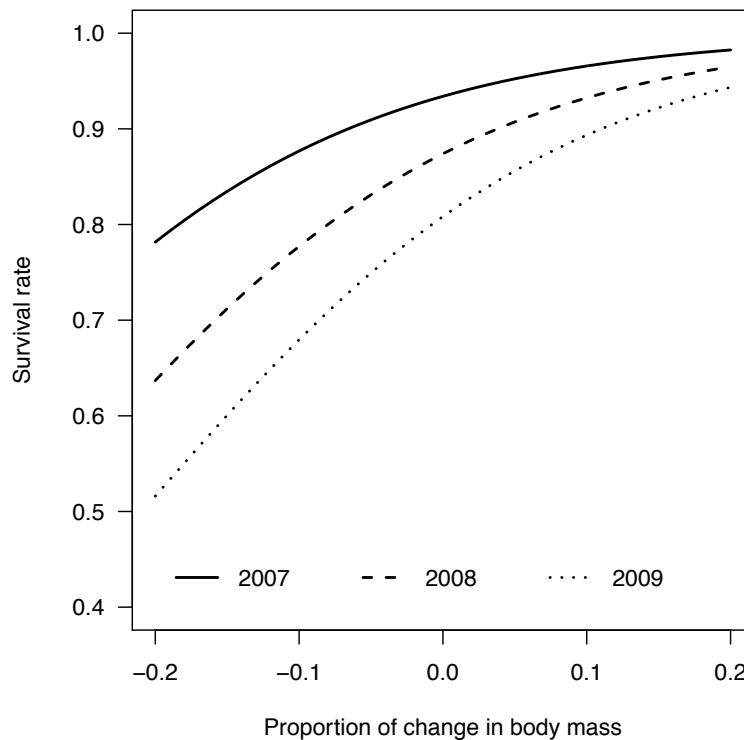


Figure 3.7: Comparison of adult survival rate over the dry season in response to the proportion of change in body mass of an individual between February and April each year. Estimates were calculated for each year, using the best adult survival model, and are for a four-year old, non-pregnant individual.

is typically associated with the main plant growth season in the Succulent Karoo vegetation, which dominates the regions that are used in the winter (Cowling *et al.* 1999; chapter 4, figure 4.4). The riparian zone thus clearly forms the primary spatial subset of forage resources in the RNP that are relied upon during the season of plant dormancy.

The different landscape use patterns in each year of the study highlights further the role of the riparian zone during less favourable periods (table 3.1). In 2008, which received a good dry season summer thunderstorm, the study herds spent almost 60 % of the year based more than 2.5 km from the river. In strong contrast to this, in 2009 - the year with least rainfall - 65 % of the year was spent based in the riparian zone. 2007 had little rainfall in the hottest part of the year, but the winter rains arrived early in the season and were above average. This resulted in a 50/50 split in the time

spent based in the riparian zone and away from it. This pattern of greater reliance on the riparian zone during dry periods was also reported during the 1998 - 1999 drought, when herd movements away from the riparian zone were particularly limited (Hendricks *et al.* 2005b).

Within the riparian zone, stockpost choice and the duration of stay at a particular stockpost is assumed to be provisional on the condition of the forage resource in the area. Water is freely accessible in the riparian zone, and moving to a new stockpost requires considerable effort - breaking camp, transporting belongings, fixing the new kraal, collecting firewood etc. Any decision to move to a new stockpost is thus expected to be forced by the needs of the livestock (Hendricks 2004). If all herds have fair access to the riparian zone, then, as the dry season progresses, the distribution of herds in the riparian zone would be anticipated to reflect the abundance of the remaining forage reserves (Fretwell & Lucas 1969). The average length of stay at a stockpost in the riparian zone was shorter in 2009 (approx. 5 weeks) than in 2007 and 2008 (approx. 8 weeks). The 2009 dry season is considered to have been the most severe of the three dry seasons during the study period, and when the forage resource is likely to have been most heavily utilised. The higher movement rate between stockposts in 2009 may thus reflect herds being forced to space themselves more evenly relative to a diminishing forage resource. Hendricks *et al.* (2005b) also found that larger herds moved more frequently, and although this analysis was not constrained to the riparian zone, lends support to the notion that relative resource abundance affects the distribution of herds in the RNP.

Forage resource

Adult goat density, which was expressed relative to tree cover, had a negative impact on forage abundance that was detectable at both the tree- and branch-level. The time interval over which these respective forage depletion signals were observed are reconcilable with the average length of stay of a herd at a stockpost (approx. 5 - 9 weeks). Branch-level depletion was correlated most strongly with adult goat density over the previous five weeks, and over the previous ten weeks at the tree-level. The difference in this time interval is likely to be due to the relative sensitivity of each measure, which affects the degree of browsing effort required to produce a detectable difference at each scale of measurement.

Browsing impacts were however not uniform between species, with distinct differences in species preference being observed at both the tree- (table 3.2, figure 3.3) and branch-level (figure 3.5) scale of enquiry. This diet selectivity is likely to reflect differences in nutritional quality and defences of the tree species assessed in this study (Cooper & Owen-Smith 1986, Cooper *et al.* 1988, Lu 1988, Illius *et al.* 1999, Papachristou *et al.* 2005). *Ziziphus mucronata* is widely perceived by herders as being a highly favoured browse species in the riparian zone of the RNP (pers. comm.). This is well supported by the tree-level analysis, where *Ziziphus* showed the steepest negative response to adult goat density. *Rhus pendulina*, which is also considered a favoured browse species, showed a steeper response to adult goat density than *Ziziphus* at the branch-level. This difference may reflect the sensitivity of each measurement: *Ziziphus* is well defended with spines and hooks, and complete defoliation at the branch-level is thus less likely, but could be scored as such at the tree-level. The longer time interval considered in the tree-level model may also allow more time for factors other than the specific diet preferences of goats to have an effect, such as the accessibility of browse in the forage profile.

The accessibility of forage was found to have a marked effect on the likelihood of it being utilised as browse (figure 3.4). The formation of a browse-line is a frequently observed response to high browsing intensity (e.g. Bond & Loffell 2001). Height was found to have a strong modifying influence on the response of total browse abundance to goat density. The strong effect of goat presence on forage abundance below 1.3 m, which gradually decreases with increased height, was interpreted as being due to differential browsing by goats from the ground up. Head height of an adult goat in the RNP is in the approximate range of 1.0 - 1.3 m, which would thus be expected to be the most convenient - and probably also the most efficient - browsing height range. However, by stretching its neck, placing its fore-legs on a supporting branch or by balancing only on its hind-legs, a goat is able to browse successively higher up the forage profile. This access to higher levels in the forage profile would be expected to come with trade-offs in terms of energy expenditure and decreased mobility, and thus reduced overall foraging efficiency, which would account for the bottom-up pattern of forage depletion that was observed.

The bottom-up depletion of the forage profile is likely to be disadvantageous to younger goats during the dry season, as suggested by their greater mass loss. The smaller stature of kids, and possibly yearlings, is likely to place physical constraints

on the proportion of the forage resource that is accessible to them. The ability to utilise forage at higher levels in the canopy has been shown to influence kudu to preferentially feed above the reach of impala, where the leaf:wood ratio of their larger bite size is likely to be better (de Garine-Wichatitsky *et al.* 2004). Makhabu (2005) recorded stratification in the feeding height range of the browser guild in the riparian zone of the Chobe River in Botswana, where the feeding height range of each species was also shown to shift higher in the profile during the dry season. This separation in feeding height is hypothesised to be driven from below, with smaller species with smaller bite sizes able to make more efficient use of the forage resource within their reach (Woolnough & du Toit 2001, Cameron & du Toit 2007). Smaller body size could possibly constrain an individual to selecting a higher quality, more easily digestible diet than larger-bodied individuals, whose longer gut passage time hypothetically allows them to extract greater benefit from a lower quality diet (Demment & Van Soest 1985). In the RNP, the small difference in bite size between kids and adults may allow kids to make better use of the forage within their reach. However, the main nutritional limitation late in the dry season is likely to be the quantity of forage that an individual can reach, rather than its quality.

Rainfall had a regenerative effect on forage abundance in the riparian zone. Like the density effect, the influence of rainfall was detectable over a shorter timescale at the branch-level than at the tree-level. This was again considered to likely be as a consequence of the sensitivity of each scale of measurement. The slope of the relationship between previous forage abundance and the current forage measurement was less than one at both the tree- (0.87) and branch-level (0.63). This suggests that forage depletion occurred more frequently than growth over the interval between measurements. The higher value for this slope at the tree-level may point to better recovery at the tree-level. Marked branches that experienced high levels of depletion frequently failed to recover, and many trees were observed to have a 'skirt' of dead branches. The overall trend during the study period of forage depletion occurring more frequently than recovery over an interval, may be balanced by rates of regrowth being higher than depletion rates. Alternately, it may have been exacerbated by the experiment having been started at the beginning of the rather wet 2008 dry season, and terminated at the end of the driest year in the study period.

The effect of differential browsing pressure on different tree species is predicted to have consequences for community composition in the riparian zone. Most species

possess some form of mechanical (e.g. spines, growth form) or chemical (e.g. tannins, toxicity) defence against herbivory, which should generally be reflected in herbivore diet preferences and feeding rates (e.g. Cooper & Owen-Smith 1985, 1986). The low browsing pressure on *Tamarix usenoides* and *Prosopis glandulosa* is likely to reflect these species being better defended than other species in the riparian zone. The high abundance of *Tamarix* may thus be a result of differential browsing pressure allowing it to become more widely established. *Prosopis* is an alien invasive species that has rapidly spread through the riparian zone, although much work is now being done to eradicate it. This rapid spread would appear to have been greatly facilitated by the low palatability of its foliage but also by the high palatability of its pods, with seeds being dispersed widely through the riparian zone by goats. If browsing pressure is able to induce a shift in community composition towards less palatable species, then the consequences of supporting high numbers of goats should be monitored. This would be relevant from both a biodiversity-centred conservation approach, but also from the perspective of pastoralists, who rely heavily on the riparian zone for their livelihoods.

Mass

I found good indirect evidence that the negative effect of goat density on forage abundance in the riparian zone has a negative feedback on goat mass. This evidence can be grouped into four parts: a) the negative effect of goat density on goat mass (figure 3.6a), b) the corresponding time-lags of rainfall on forage regrowth and its positive effect on goat mass (table 3.3 to table 3.7), c) the differences in goat mass response in dry seasons with different severity (table 3.5 to table 3.7), and d) the negative relationship between time spent in the riparian zone and goat mass (figure 3.6b). In addition, these findings were consistent for all life-stages, although the magnitude of the mass response differed between life-stages. It was hoped that direct evidence of the negative feedback of forage depletion by goats on goat mass would be obtained by comparing changes in goat mass to changes in forage availability in the branch- and tree-level study areas. This was severely complicated by movements of the focal and other herds into and out of the forage study areas intermittently in the period between fieldtrips, and the differential effect of rainfall at different times of year on browse recovery.

The negative effect of high adult goat density, expressed relative to tree cover, on

both browse abundance and goat mass is a strong indication that a negative feedback mechanism exists between goat condition and the dry season forage resource. The time interval over which the density-dependent mass response was most strongly detected was shorter in adults than in yearlings or kids. Adult mass was most strongly related to density measured over the shortest interval that was tested (approx. one month), while kids and yearlings responded most markedly to density over the preceding three months. Adult body condition has been shown to generally be less sensitive to environmental effects than in younger individuals (Gaillard *et al.* 1998). I thus infer that the body condition of yearlings and kids took longer to recover from periods of high density, and that the ‘ghost of density past’ signal was thus detectable for a greater period of time after the event in these younger individuals. The absolute magnitude of the mass response to density was greatest in yearlings and smallest in adults (figure 3.6a). When this mass response is considered as a proportion of an individual’s body mass, it appears that the density-dependent loss of body condition in the dry season is greatest in kids, followed by yearlings and then by adults. This trend of greater sensitivity of earlier life-stages to their environment has been widely observed in large mammals, e.g. roe deer (Gaillard *et al.* 1993, Pettorelli *et al.* 2003); Soay sheep and red deer (Clutton-Brock *et al.* 1997).

Rainfall had a positive influence on goat mass (figure 3.6c), which became apparent at a similar time lag to that at which the positive effect on forage was also detected (approx. 6 - 9 weeks). The mass analyses were restricted to cases where a herd had spent a minimum of seven of the preceding twelve weeks in the riparian zone. It is thus possible that in some instances the positive mass response will correspond to utilisation of forage growth outside of the riparian zone, but the more general case should reflect a mass response to improvement in the riparian forage resource. It is also worth noting that riparian forage regrowth would occur more widely than the herd’s current location, presenting the opportunity to move back to sections of the river that had previously been depleted. The best fit rain interval for yearlings and kids (64 - 96 days) was shorter than that for adults (64 - 160 days), which may again illustrate the greater sensitivity of earlier life-stages to environmental effects. Given that yearlings and kids are likely to be in a worse condition than adults, any rainfall that improves the forage resource has a detectable effect on yearling and kid mass. This effect would be magnified by the skew in the ability of different life-stages to access the remaining forage. If rainfall results in regrowth at all heights in the profile,

then kids and yearlings should disproportionately benefit from this growth. Forage regrowth lower down in the profile may be of little consequence to adults if reserves higher up, but still within reach, are still adequate. This may explain why adult mass was less sensitive to isolated rainfall events, and that a longer history of rainfall events was more closely related to changes in adult mass.

Year was fitted as a factor in the mass analyses in order capture the combined effect of the many permutations of events that contribute to the severity of a dry season. Factors that affect the severity of a particular dry season include the amount of rainfall, but also the specific sequence and timing of rainfall events, temperature extremes and other weather phenomena. The duration of the dry season - or when the wet season starts - will also be important to consider when retrospectively assessing the severity of a particular dry season. There was a consistent pattern in the mass response of each life-stage to year effects, with mass in 2009 being lower than in 2008. The adult analysis also included the 2007 dry season, where equivalent individuals were heavier than in the following two years. Based on the absence of a substantial mid-summer thunderstorm (as in 2008) and the dry season not ending early (as in 2007), 2009 was considered to be the most severe of the dry seasons during the study period. The generally lower mass of goats in the 2009 dry season provides further evidence of the link between the goat population and the dry season resource.

Goat mass in all life-stages was lower when a greater proportion of the previous twelve weeks (minimum seven weeks) had been spent in the dry season range. This measure was fitted to capture the extent to which each herd had relied on the riparian zone since the last fieldtrip, and also to exclude situations where a herd had been based outside of the dry season range. Increased reliance on the riparian zone had the greatest negative impact on kids' relative mass loss and the least effect on adults (figure 3.6b). The finding that this increase in pressure on the dry season resource has a negative feedback on goat condition supplements the evidence from the density, rainfall and year effects, and provides a compelling basis from which to conclude that the goat population is coupled to the dry season forage resource.

Age and reproductive status had a marked influence on the mass of an individual, and were largely in accordance with what would be anticipated. Mass increases up to about four to five years of age and then plateaus. There was a very weak suggestion that mass began to decrease after six years in age. This possible early

sign of senescence could not be explored further because only a few goats in these older age classes were identifiable. Senescence in large herbivores is considered to partially be a response to tooth wear (e.g. Skogland 1988, Kojola *et al.* 1998). Tooth wear can cause individuals to shift their diet and spend more time masticating (Perez-Barberia & Gordon 1998), as poorly masticated food is less digestible (Bjorndal *et al.* 1990). Kid and yearling growth rates, which would be expected to be sensitive to environmental effects, were not compared between years, but this effect should be explored in future analyses. It was interesting to note that herd effects accounted for a greater proportion of the remaining variance in the mass of earlier life-stages, while individual effects dominated in adults. This may indicate that herd management decisions are of more consequence to kids e.g. the exact choice of stockpost (shade, topography) and the timing of movements to a new stockpost.

Survival

The final stage in identifying the riparian zone as being a dry season key resource in the RNP is to assess whether the coupling between the forage resource and goat mass translates into an effect on population survival rates. The finding that goats that lose a greater proportion of their body mass during the mid-dry season are less likely to survive to the end of the dry season is a clear link between goat body condition and survival (figure 3.7). Testing the effect of body condition on survival was complicated by not having a mass estimate at the time of death for the individuals that died. However, the previous finding that goats lose mass with increasing time spent in the dry season range suggests that goats that lost condition in the mid-dry season would continue to do so, or at least be unlikely to regain condition, over the remaining portion of the dry season. There would thus seem to be a strong link between a decline in body condition and a decreased likelihood of survival in the dry season.

The link between mass and survival is further supported by the consistent ranking of year effects on adult mass and survival. Both adult mass and adult survival were highest in 2007 and lowest in 2009. The weather data suggests that the 2009 dry season was the most severe, and accordingly - if goats are coupled to the dry season resource - we would expect to see the biggest negative effect on mass and survival during this period. It would appear that from a goat's perspective that the 2007 dry season was more favourable than the 2008 dry season. This may indicate that

curtailing the length of the dry season does more to release the dry season bottleneck than the moderating effect of rainfall in the mid-dry season, but which does not yet signal an end to the dry season.

The reproductive status of an individual in the mid-dry season was also found to have a significant impact on its probability of surviving the dry season. Survival rates were highest in pregnant individuals, followed by lactating goats, and were lowest in non-pregnant individuals. Reproduction places considerable strain on an individual's body reserves, and it would thus be anticipated that facing this cost in the mid-dry season would be detrimental to survival probability, as opposed to improving survival rates. These effects were not extensively explored, but two potential explanations are offered. Firstly, individuals under reproductive strain earlier in the dry season might not be facing these costs later in the dry season - when conditions are more severe - particularly if the pregnancy fails to come to term. Secondly, the small number of individuals reproducing at this stage of the year may only be able to do so because of being in better condition already, and thus may have had an improved chance of surviving the dry season *a priori*.

Summary

The riparian zone in the RNP forms the dry season range of the study population, and functions as a key resource whereby forage supply has a regulating effect on the goat population. Over the course of the dry season, density-dependent depletion of the forage resource occurs, which leads to the development of a density-regulated negative feedback on goat mass. The loss of body condition is directly related to a decline in adult survival rates. This dry season bottleneck is exacerbated in years when conditions during the dry season are more severe. Asymmetric competition as a result of forage resources being depleted from the bottom-up is predicted to have a strong effect on goat demography by contributing to differences in body condition and survival rates between life-stages.

4 The Wet Season

4.1 Introduction

The cool wet winter sparks life into the RNP, a striking contrast with the heat and dust of the dry season (figure 4.1). The winter months bring cooler temperatures and generally reliable frontal rainfall that triggers the plant growth season (Desmet 2007). Herds move away from the riparian zone to take advantage of the flush of growth in perennial species and the profusion of annual species that carpet the interior plains (Hendricks *et al.* 2005*b*). The wet season is also the focus of the reproductive calendar, which allows lactating mothers to take advantage of an apparently plentiful forage supply (Hendricks 2004). An important question to address from a plant-herbivore perspective is whether this time of apparent abundance plays an essential role in shaping herbivore population dynamics, as one might expect. One hypothetical mechanism is that population size is determined by the quality of the wet season each year. This effect on recruitment is predicted to act through improved maternal nutrition and hence lactation, thus improving the body condition and survival rates of neonates (Parker *et al.* 2009*e.g.*). A second expected mechanism might be that the extent to which animals regain body condition during the wet season could have a direct impact on survival over the following dry season (Cook *et al.* 2004*e.g.*).

Births are generally timed for the start of the wet season, which focuses attention on how conditions in early life impact on an individual's probability of survival. Neonates are heavily reliant on their mothers, who face the double burden of lactation and recovery from the dry season bottleneck (Therrien *et al.* 2007). Mothers thus face a trade-off between investing in their current offspring and their own welfare, which has been shown to result in reduced maternal care when resources are limiting (Festa-Bianchet & Jorgenson 1998, Therrien *et al.* 2007). These early developmental phases are likely to be important in determining kid survival rates, both through the wet season and over the subsequent dry season (Gaillard *et al.* 1997). Studies on roe deer have shown that habitat quality early in life can have an effect on fawn body size that



Figure 4.1. Yellow ‘knoppiesopslag’, an annual species, covering the plains in the wet season.

is still detectable when they are adults (Pettorelli *et al.* 2001, 2002). Recruitment into the RNP goat population would thus be expected to be influenced by conditions during the wet season. However, the dry season is also likely to play a role in determining annual recruitment, due to the effects of environmental conditions during pregnancy. Goats have low fat reserves (Tshabalala *et al.* 2003) and thus function more as income breeders, which increases the potential for pre-partum effects (Jonsson 1997). Poor environmental conditions during pregnancy could thus decrease the mass of kids at birth resulting in lower neonate survival rates (e.g. Soay sheep, Clutton-Brock & Pemberton 2004).

The wet season could also affect goat population dynamics by determining body condition at the start of the dry season. Dry season survival is dependent on body condition (chapter 3), and the carryover effect of wet season mass gain could thus play an important role in determining dry season survival rates. Cook *et al.* (2004) have shown this effect in experiments with elk, where winter survival rates (i.e. over the plant dormancy season) were related to the effect of summer-autumn nutrition on an individual’s mass at the onset of winter. These effects were most apparent in

earlier life-stages. Caribou have also been shown to be affected by the adequacy of nutrition during the plant growth season, which was found to have a regulatory effect through decreased fecundity and survival (Crete & Huot 1993). Therrien *et al.* (2007) suggest that the role of forage availability during the plant growth season has generally been overlooked, as it plays an important role not only in lactation and the extent of maternal care, but also in determining growth and the subsequent reproductive success of an individual.

The aim of this chapter is to explore the effect of the wet season in shaping goat population dynamics in the RNP. The key resource determines the size of the key factor acting on a population, and if the wet season was able to drive goat population dynamics through its impact on recruitment, then it would be regarded as the key resource. This was examined by assessing the wet season influence on recruitment rates, but also its role in determining dry season survival rates. Specifically, the following hypotheses are tested:

1. Wet season quality determines annual recruitment through its effect on maternal condition and neonate survival rates
2. Goat body condition is coupled to the wet season forage resource, and/or
3. Goat body condition at the end of the wet season determines survival rates over the dry season

The role of the dry season in determining annual recruitment rates is also considered.

4.2 Methods

4.2.1 Identifying the wet season range

The wet season is defined as the main plant growth season, the exact timing and duration of which varies between years depending on environmental conditions. Forage availability in the wet season range was estimated using the FPAR product produced by NASA from imagery obtained from the Terra EOS satellite. The FPAR product is the fraction of photosynthetically active radiation (400 - 700 nm) absorbed by green vegetation, and has been shown to be highly correlated with actively growing

plant biomass (e.g. Fensholt *et al.* 2004). The product is available at eight day intervals and approximately 1 km² spatial resolution. The quality of the FPAR imagery available for the Richtersveld is very high, due to the low cloud cover. However, its utility is to some extent limited by the very sparse vegetation cover in some areas, which fails to produce a signal detectable by the satellite. Higher values than are plausible for the region were also occasionally returned. Based on the distribution of values obtained for all pixels in the study period, and consultation with researchers familiar with the product, pixel values lower than 6 and greater than 40 were excluded from analyses (A. R. Palmer, pers. comm.).

Suitable plant growth conditions were identified by correlating the mean FPAR value for the RNP with the 8-day daily temperature mean and various rainfall time lags. This allowed for the start of the wet season to be defined, and hence the classification of fieldtrip dates with respect to the existent duration of the wet season. The average distance of the five study herds from the Orange River was also correlated with FPAR, in order to determine whether a threshold FPAR value was required before herds would move into the wet season range.

4.2.2 Wet season goat mass

The impact of resource availability on goat performance in the wet season was assessed using the response of goat mass to duration of the wet season, goat density relative to FPAR and year effects. Goat mass was analysed using a general linear mixed-effects model fitted using the lme4 package (Bates & Maechler 2010) in R version 2.10.1 (R Development Core Team 2009). The precision of individual age estimates decreased with age, and accordingly, mass analyses were split into three life-stages - adults, yearlings and kids - to allow for differences due to stage-specific growth trajectories to be assessed. Two measures of the degree of progression of the wet season were considered for inclusion in the full model - the number of days since the start of the wet season (wet season duration), or a three-level factor identifying wet season stage (early, mid- or late wet season; < 30 days, 31 - 90 days or > 90 days). Goat density was included in the model as the number of adult goats divided by the mean FPAR value for the area within 2.5 km of the stockpost, the average daily foraging range of RNP goats. Density was calculated for the periods 0 - 32, 0 - 64, 0 - 96, 32 - 64, 32 - 96 and 64 - 96 days prior to

weighing. Longer intervals were not considered, due to the increased lag meaning that dry season effects would be predominant in the analysis. The interaction between density and wet season stage (factor) was fitted to determine whether density effects changed through the season. Reproductive status affects goat mass, and was included in the full model. Reproductive status was coded using various schemes, with the simplest having four levels (not pregnant, pregnant, lactating or unknown), and the most detailed accounting for early and late pregnancy, the number of kids and aborted pregnancies. Calendar year was fitted as the last fixed effect term in the full model, in order to account for any remaining variation due to inter-annual differences. Rainfall and temperature effects were inferred to be included in the FPAR value, and thus not fitted independently in the model. The random effects structure accounted for individual, herd and age effects. In the adult and kid models, the individual effect was conditioned by age (adults in years, kids in months). Including age in the random effect structure did not improve the fit of the yearling model. Differences arising from herd management decisions were accounted for by fitting herd as a random effect.

The wet season duration, density and reproductive status terms with highest explanatory power were identified in preliminary analyses, and were included in the full model. Simplification of the full model was performed by excluding each fixed effect and assessing the resulting change in fit with a χ^2 -test of twice the change in log-likelihood. The simplest model not compromising explanatory power was selected as the best model. In situations where different density intervals or time lags produced statistically equivalent results ($p > 0.05$), the term with the smallest or no time lag was preferred, and then the term with the shorter time interval. This was perceived as being the most parsimonious approach, as increased time lags and interval lengths require more complex interpretations of the effects. The order of fixed effect terms was determined using an analysis of variance, with terms being ranked according to the amount of total variation that they accounted for. As a measure of the predictive power of each model, the correlation between the fitted values and original mass estimates was calculated, as well as the standard deviation of the difference between fitted and actual mass values.

In order to further explore year effects on goat dynamics in the wet season, the interaction between wet season duration and calendar year was fitted in each life-stage model. The purpose of fitting this interaction was to ascertain whether goats ended each wet season in a similar condition, or whether the quality of a wet season

determined goat performance over that time period. The main effects and interaction between calendar year and the number of days since the start of the wet season were fitted in the model, as well as the age, reproductive status and density terms fitted in the best model. To simplify interpretation of the results, the density by wet season stage interaction was not fitted when assessing the year by wet season duration effect.

4.2.3 Fecundity

In the Richtersveld, as in many other systems, the timing of births is concentrated around the time of year when resources are most abundant - in this case the winter wet season. There is, however, considerable variability in the timing of the onset of the wet season in the Richtersveld, which presents the possibility that when and where goats are during the main kidding period might have a considerable impact on reproductive success in any year. This was tested by analysing the effect of conditions leading up to and during the kidding period on three aspects of fecundity: pregnancy rate, birth rate and the survival rate of kids in the period shortly after birth.

The data for these analyses was based on the tagged individuals. The reproductive status of each goat was assessed when it was weighed, with individuals recorded as being pregnant, lactating or not pregnant. If a goat had given birth in the period since it was last weighed, the herder or herd owner was questioned as to the number of kids that were born, and their ensuing fate. This was supplemented by direct observation of the goats in the kraal, and also from records from subsequent fieldtrips. The quality of this information improved through the study, particularly with respect to herders' reporting of the number of kids born, and their fate. As such, pregnancy rates were analysed for the entire study period, but birth rates and the survival rates of kids shortly after birth were only considered for 2008 and 2009. Although considerable effort was made to determine accurately the number of kids born to each pregnant female, and the fate of those kids, there is still likely to be bias towards kids that survived. This would skew the results towards lower birth rates and higher survival rates, but is almost unavoidable in a study where it is not possible to document 100% of births. Variation in each of the three fecundity parameters was modelled using a general linear mixed-effects model with a binomial error structure.

Pregnancy rate

Pregnancy rate was analysed using reproductive status data from all the marked goats and over the entire study period. The binary response variable was created by scoring goats as ‘one’ on the last occasion in each pregnancy that they were observed to be pregnant (c.f. early pregnant in the mass analyses), and ‘zero’ otherwise. Life-stage was fitted as a fixed effect, to account for differences in the stage of development of an individual. Season-stage was fitted to account for variation in pregnancy rate with respect to the timing of rainfall and the general favourability of conditions for plant growth. The fieldtrips labelled C7, D8 and D9 in figure 4.4, were classified as ‘early wet season’; D7, E7, E8 and E9 as ‘late wet season’; A7, A8, B8 and A9 as ‘mid-dry season’; and B7, C8, B9 and C9 as ‘late dry season’. Calendar year was fitted to capture effects possibly operating over longer time scales than the season-stage levels. Density was fitted simply as the number of adult goats within the average daily foraging range from a stockpost (2.5 km), and was calculated for the periods 0 - 32, 0 - 64 and 0 - 96 days prior to each fieldtrip. Density was not expressed relative to forage abundance because no measure was available for both the dry and wet season range. The average distance of a herd from the Orange River in the period since the last fieldtrip was fitted to estimate the effect of being in the dry and wet season range on pregnancy rates. Herd and individual identity were fitted as random effects.

Birth rate

Birth rate was modelled for all tagged adult and yearling goats with reliable birth records in 2008 and 2009. Although ostensibly aimed at modelling the actual number of kids born per pregnancy, the analysis was simplified to considering only two cases - singletons, which were scored as zero, and twins or triplets, which were scored as one. This structure was adopted because of the difficulty of dependably recording a pregnancy in which the foetus was reabsorbed - i.e. no kids born - and there were no instances where this was felt to have been reliably reported. Grouping triplets and twins considerably simplified the error structure of the model, and given that triplets were only recorded on four occasions, was felt to be acceptable. Life-stage was fitted to determine whether adults and yearlings showed different birth rates - with births to goats classed as kids having been omitted due to low sample size. Season-stage - using the same coding as in the pregnancy rate model - was fitted as a fixed effect,

with calendar year again fitted to potentially account for conditions operating over longer time-scales. Density and distance from the Orange River were also fitted as fixed effects, using the same measures that were fitted in the pregnancy rate model. Herd and individual identity were fitted as random effects in the full model.

Neonate survival rate

The survival rate of kids in the period immediately after birth - the neonate survival rate - was modelled for kids born to tagged adults and yearlings in 2008 and 2009. A binary response variable was generated, with neonates that survived the period from their birth to the first fieldtrip after their birth scored as 'one' and those that died during this period scored as 'zero'. Births were thus assumed to be randomly distributed between fieldtrip intervals, and the reporting of the birth of a kid and its subsequent fate needed to be deemed reliable. The life-stage of the mother of each kid was fitted as a fixed effect, and in addition to this maternal effect, whether a kid was singleton or a twin was also fitted in the model. Season-stage - coded as for the pregnancy rate model - was fitted as a fixed effect, as was calendar year. Density - again expressed simply as the number of adult goats, and using the same time intervals as in the pregnancy rate model - was fitted as a fixed effect. The average distance of the stockpost from the Orange River in the period during which the kid was born was also fitted as a fixed effect. Herd identity was fitted as a random effect.

4.3 Results

4.3.1 Identifying the wet season range

FPAR - the plant biomass estimate - was positively related to rainfall and negatively to temperature (figure 4.2). The best-fit rainfall time lag was an eighty day window lagged by 16 days ($r^2 = 0.48$, d.f. = 129, $p < 0.0001$). The correlation of FPAR with average daily temperature showed a negative relationship between these variables ($r^2 = 0.34$, d.f. = 129, $p < 0.0001$). Examination of figure 4.2 revealed three generalisations regarding the relationships between FPAR, rainfall and temperature in the Richtersveld region - 1) FPAR was below about seventeen for much of the year; FPAR values higher than seventeen were usually associated with: 2) cumulative

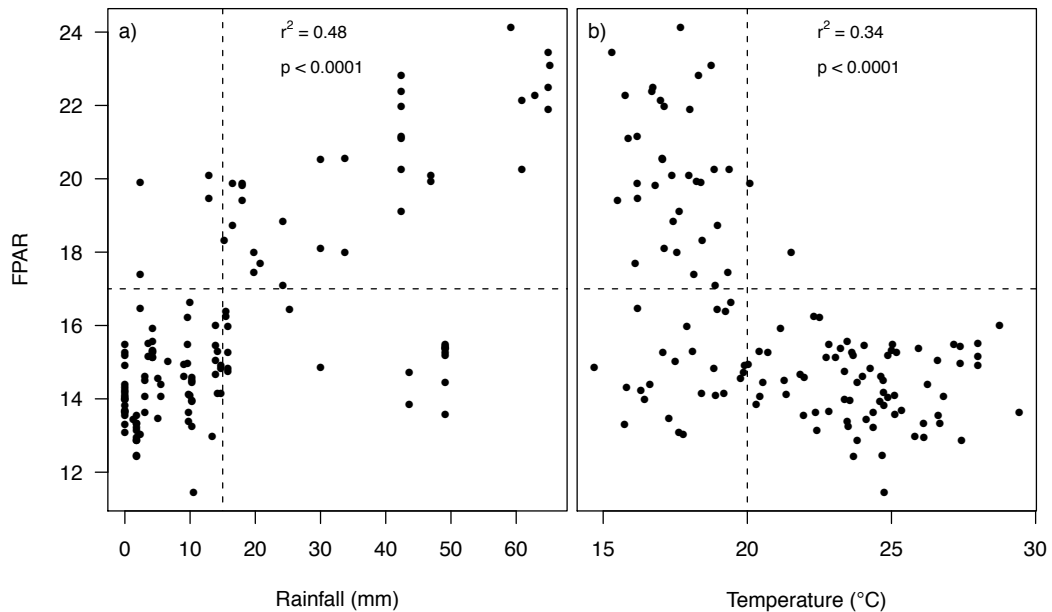


Figure 4.2: Linear regression of FPAR on a) rainfall (mm) and b) temperature (°C). Rainfall measures are 80-day cumulative figures following a 16-day time-lag, and temperature is the daily average over an 8-day time period. Dashed lines indicate FPAR = 17, rainfall = 15 mm and temperature = 20°C.

rainfall events above 15 mm, and 3) average daily temperatures below about 20°C. This combination of conditions typically occurs in what is commonly regarded as the growing season in Succulent Karoo - i.e. the winter months (June - September). Summer thunderstorms presumably don't trigger major plant growth episodes due to the high temperatures (frequently > 40°C) and associated high evapotranspiration rates. Based on these results, the growing season was defined as the period when rainfall in the previous three months exceeded 15 mm, and average daily temperatures were below 20°C.

Herd movements away from the Orange River were largely associated with high FPAR values (figure 4.3). The average distance of the five study herds from the river was highly correlated with FPAR ($r^2 = 0.66$, d.f. = 129, $p < 0.0001$), and is again useful for drawing out a number of generalisations about the role of the wet season. The clearest observation is that when FPAR is greater than 17, all herds move away from the river to take advantage of the plant growth. In contrast, at low FPAR values, herds tend to stay within daily foraging range (< 5 km) of the river, although this is

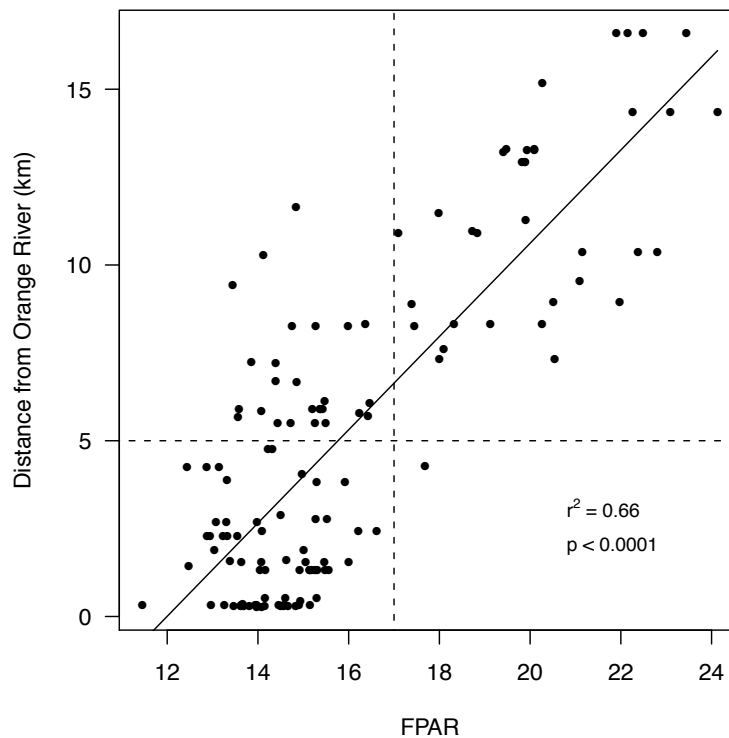


Figure 4.3: Herd distance from the Orange River in response to FPAR, an index of plant growth rates ($r^2 = 0.66$, d.f. = 129, $p < 0.0001$). Herd distance is the average position of the five study herds each week and FPAR is averaged for the whole RNP. The dashed line at 5 km indicates the maximum distance at which the Orange River could generally be reached in the course of daily foraging.

by no means the rule. The ability of herds to utilise areas > 5 km from the river when FPAR values are low indicates that despite plants largely being dormant, forage is still available in these areas.

Time series plots of FPAR, temperature, rainfall and average herd distance from the Orange River (figure 4.4) were used to classify fieldtrips with respect to existent duration of the wet season. Using the labels in figure 4.4b, fieldtrips C7 and D8 were coded as ‘early wet season’, D7 and D9 as ‘mid-wet season’ and E7, E8 and E9 as ‘late wet season’. D8 is a marginal classification between early and mid-wet season, but is less than a month after FPAR increased to above 17 in 2008.

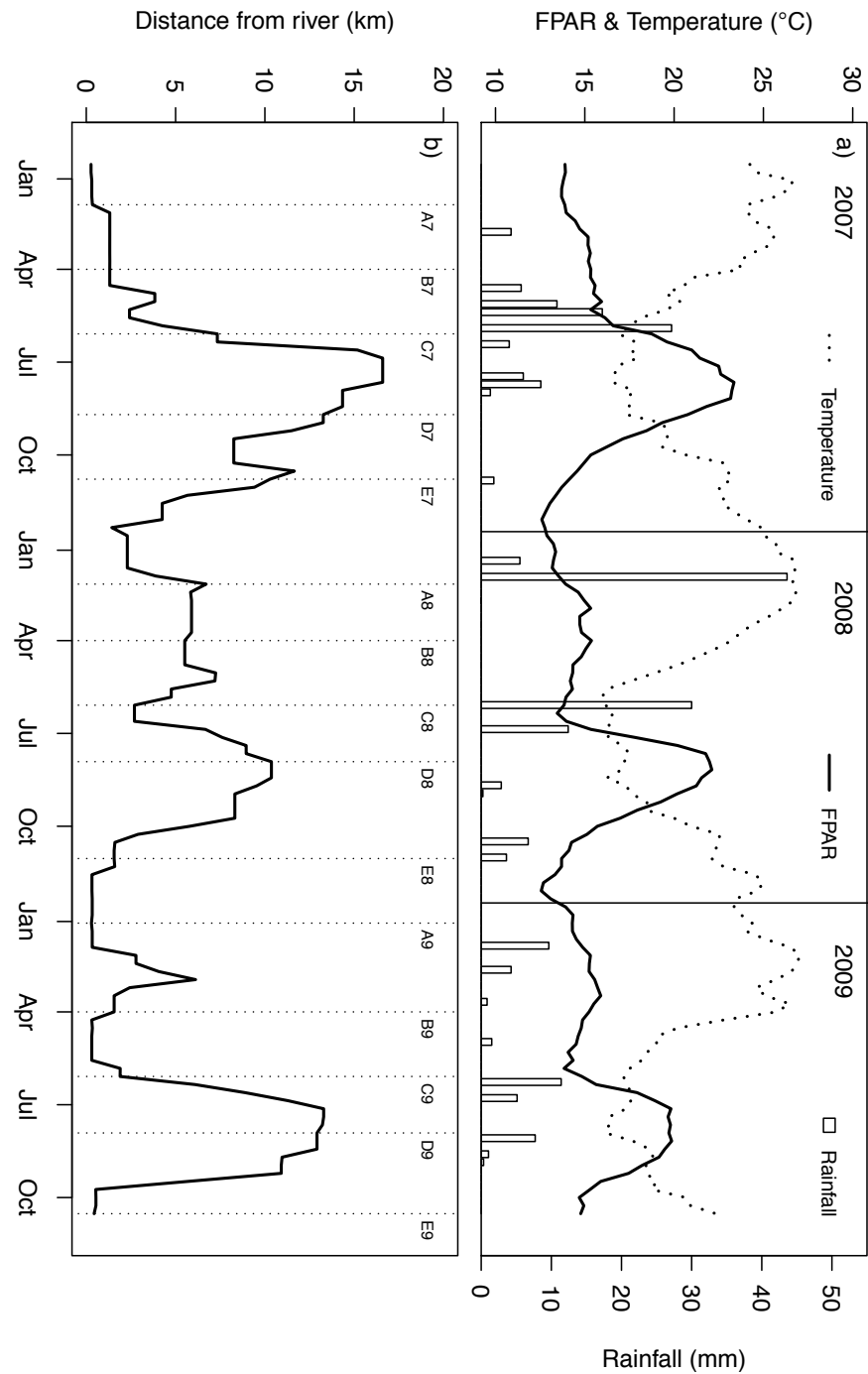


Figure 4.4: Time series plots of a) FPAR, average daily temperature, 8-day rainfall and b) average herd distances from the Orange River. Fieldtrip dates are labelled and marked with vertical dotted lines in b). Fieldtrips C7 and D8 were coded as ‘early wet season’, D7 and D9 as ‘mid-wet season’ and E7, E8 and E9 as ‘late wet season’.

4.3.2 Wet season goat mass

The wet season would appear to be a time of plenty for goats in the RNP - mass increased during this period in each life-stage. Negative density effects were detected in the adult and kid models, but not for yearlings, and adults were only affected by density early in the wet season. The best adult mass model included all terms fitted in the full model, as well as the interaction between wet season stage (early, mid- and late wet season) and density over the previous 64 days (table 4.1). Wet season stage accounted for the largest amount of explained variance in the dataset, followed by reproductive status, age and density. The best yearling mass model did not include a density term ($\chi^2 = 2.0$, d.f. = 1, $p = 0.1533$). Wet season duration (number of days since start of wet season) was preferred to wet season stage (table 4.2) and accounted for most of the explained variation in the yearling model, followed by age and reproductive status. The kid mass model included goat density over the previous 96 days (table 4.3), but not the interaction with wet season stage ($\chi^2 = 2.4$, d.f. = 2, $p = 0.3026$). Age accounted for the most explained variation in kid mass, followed by wet season duration and density. Calendar year was retained in the best model for each life-stage.

Body mass in each life-stage responded positively to wet season duration (figure 4.5), with adults gaining about 6 kg over periods of about 100 days. Wet season stage and the number of days since the start of the wet season provided an equally good fit to the data in the adult model ($\chi^2 = 2.7$, d.f. = 1, $p = 0.1031$). Adult mass was strongly influenced by wet season stage ($\chi^2 = 226.2$, d.f. = 2, $p < 0.0001$), which was preferred to wet season duration in the best model in order to ease the interpretation of the interaction between density and length of time spent in the wet season range. The response of yearling and kid mass to wet season duration was positive and significant (yearling: $\chi^2 = 88.5$, d.f. = 1, $p < 0.0001$, kid: $\chi^2 = 84.8$, d.f. = 1, $p < 0.0001$), but the slope of the yearling response was significantly steeper than the slope of the kid response ($t_{(80)} = 6.15$, $p < 0.0001$).

Table 4.1: Summary of the best fit general linear mixed-effects model of adult goat mass (n = 937) in response to wet season stage, reproductive status, age, goat density and calendar year. The random component takes into account an individual's identity (n = 271), conditioned by its age in years (n = 8), and herd level effects (n = 5).

Fixed effects	Estimate	S.E.	t-value	F-ratio	d.f.	p-value
Intercept	44.2213	1.8044	24.51			
Wet season stage				97.4	2	< 0.0001
Early wet season	0					
Mid-wet season	0.7284	1.4146	0.52			
Late wet season	0.2159	1.5303	0.14			
Reproductive status				110.6	4	< 0.0001
Early pregnant						
Pregnant	4.8190	0.5309	9.08			
Lactating	-2.8430	0.5051	-5.63			
Not pregnant	-2.2294	0.5688	-3.92			
Unknown	2.4847	1.1796	2.11			
Age				46.8	7	< 0.0001
2 years	0					
3 years	5.5147	0.3868	14.26			
4 years	8.9693	0.5743	15.62			
5 years	10.2211	0.7856	13.01			
6 years	10.7243	0.8921	12.02			
7 years	8.8279	1.2021	7.34			
8 years	11.5427	1.5649	7.38			
Unknown	8.2168	1.1130	7.38			
Density				8.3	1	0.0014
Goats/FPAR 0-64 days	-0.6622	0.2607	-2.54			
Year				35.6	2	< 0.0001
2007	0					
2008	0.8133	0.4235	1.92			
2009	-2.3632	0.5434	-4.35			
Density x wet season stage				5.4	2	0.0054
Density x early wet season	0					
Density x mid-wet season	0.1819	0.3908	0.47			
Density x late wet season	1.0812	0.4066	2.66			

Table 4.1: (continued on next page)

Table 4.1: (continued)

Random effects	Variance	Percentage
Tag		
Age (Intercept)	17.4511	10.59
Age 3 years	7.4533	4.52
Age 4 years	16.6795	10.12
Age 5 years	19.2440	11.68
Age 6 years	12.7424	7.73
Age 7 years	17.5705	10.66
Age 8 years	24.6419	14.95
Age unknown	31.6284	19.19
Herd	9.6191	5.84
Residual	7.7805	4.72
Total variance	164.8107	

Density effects were detected in adults and kids during the wet season, but not in yearlings (figure 4.5). Adult goat mass was negatively affected by adult goat density over the period 64 days prior to weighing ($\chi^2 = 5.1$, d.f. = 1, $p = 0.0238$). Fitting the interaction between density and wet season stage improved the adult model ($\chi^2 = 10.4$, d.f. = 2, $p = 0.0054$), and revealed density effects to be strongest early in the wet season and probably irrelevant late in the wet season (figure 4.6). Kid mass was negatively related to goat density over the previous 96 days ($\chi^2 = 5.1$, d.f. = 1, $p = 0.0242$), but the interaction between density and wet season stage was not significant ($\chi^2 = 2.4$, d.f. = 2, $p = 0.3026$).

Adult and yearling mass was significantly affected by an individual's reproductive status (adult: $\chi^2 = 324.4$ d.f. = 4, $p < 0.0001$, yearling: $\chi^2 = 77.1$, d.f. = 6, $p < 0.0001$). Adult reproductive status was adequately described by a five level factor - early pregnant, pregnant, lactating, not pregnant and unknown - but including the number of kids being carried improved the yearling model. Mass increased through the duration of the pregnancy, with lactating and non-pregnant goats being the lightest categories.

Body mass variation was significantly related to an individual's age in all life-stages (adult: $\chi^2 = 231.1$, d.f. = 7, $p < 0.0001$, yearling: $\chi^2 = 37.5$, d.f. = 1, $p < 0.0001$, kid: $\chi^2 = 215.4$, d.f. = 2, $p < 0.0001$), which had a positive influence on body mass up to approximately 5-6 years in age. Fitting age as a simpler linear term was

Table 4.2: Summary of the best fit general linear mixed-effects model of yearling goat mass (n = 151) in response to wet season duration, age, reproductive status and calendar year. The random component takes into account an individual's identity (n = 82) and herd level effects (n = 4).

Fixed effects	Estimate	S.E.	t-value	F-ratio	d.f.	p-value
Intercept	21.5897	1.9756	10.93			
Wet season duration				225.1	1	< 0.0001
Days since start of WS	0.0500	0.0043	11.57			
Age				72.3	1	< 0.0001
Age in months	0.7550	0.1086	6.96			
Reproductive status				20.5	6	< 0.0001
Early pregnant singleton	0					
Early pregnant unknown	3.3193	2.1223	1.56			
Pregnant singleton	6.5061	1.4305	4.55			
Pregnant twins	5.8681	2.6350	2.23			
Lactating	-1.5596	1.2071	-1.29			
Not pregnant	-2.3798	1.2196	-1.95			
Unknown	4.1635	1.6473	2.53			
Year				15.7	1	0.001
2008	0					
2009	-4.0244	1.0016	-4.02			
Random effects	Variance	Percentage				
Tag	14.7587	67.21				
Herd	4.6422	21.14				
Residual	2.5582	11.65				
Total variance	21.9591					

preferred to age as a quadratic term in the yearling model ($\chi^2 = 2.7$, d.f. = 1, $p = 0.0986$), but not in the kid model ($\chi^2 = 19.0$, d.f. = 4, $p = 0.0008$).

Individuals from each life-stage were heaviest in 2008 and lightest in 2009, with adults and kids being intermediate in 2007 (adult: $\chi^2 = 57.7$, d.f. = 2, $p < 0.0001$, yearling: $\chi^2 = 10.9$, d.f. = 1, $p = 0.0010$, kid: $\chi^2 = 18.7$, d.f. = 2, $p < 0.0001$). The difference in body mass between 2008 and 2009, due to year effects, was greatest in yearlings and smallest in kids. The interaction between year and wet season duration was only significant in the adult model ($\chi^2 = 14.9$, d.f. = 2, $p = 0.0006$; figure 4.7). Adults started the 2007 and 2008 wet seasons at a similar average mass, but were approximately 2.5 kg heavier than adults in 2009. Over the duration of the wet season,

Table 4.3: Summary of the best fit general linear mixed-effects model of kid goat mass ($n = 237$) in response to age, wet season duration, goat density and calendar year. The random component takes into account an individual's identity ($n = 148$), conditioned by its age in months ($n = 12$) as a second order polynomial, and herd level effects ($n = 5$).

Fixed effects	Estimate	S.E.	t-value	F-ratio	d.f.	p-value
Intercept	8.6040	2.1822	3.94			
Age				795.5	2	< 0.0001
Age in months (x)	2.7240	0.2015	13.52			
Age in months (x^2)	-0.0762	0.0183	-4.17			
Wet season duration				223.5	1	< 0.0001
Days since start of WS	0.0302	0.0029	10.48			
Density				16.5	1	0.0242
Goats/FPAR 96 days	-1.1667	0.5059	-2.31			
Year				9.8	2	< 0.0001
2007	0					
2008	1.1527	0.5953	1.94			
2009	-1.0182	0.7593	-1.34			
Random effects	Variance					
Tag (intercept)	0.5466					
Age in months (x)	0.7122					
Age in months (x^2)	0.0026					
Herd	3.7365					
Residual	1.4227					
Total variance	6.4207					

adults gained similar amounts of mass in 2008 and 2009 (approx. 5 kg), but only half of that in 2007. The result is that after 4 months, adults in 2007 and 2009 had attained a similar average mass, but were approximately 3 kg heavier in 2008.

Individual effects explain more of the remaining variation in body mass of older individuals, while herd effects appear to be more important in younger individuals. Individual effects accounted for approximately 89 %, 67 % and 20 % of the remaining variance in the adult, yearling and kid datasets respectively; herd effects accounted for 6 %, 21 % and 58 % of remaining variance.

The best model for each life-stage provided a good description of the respective datasets. Fitted values from each life-stage model were highly correlated with the actual mass values (adults: $r^2 = 0.92$, d.f. = 935, $p < 0.001$; yearlings: $r^2 = 0.97$, d.f. =

149, $p < 0.001$; kids: $r^2 = 0.99$, d.f. = 235, $p < 0.001$). The residual standard deviation of the difference between the fitted and actual mass values from the adult model was 2.2 kg, or 4.7 % of mean adult mass. The residual standard deviation of fitted vs. actual mass values was relatively smaller for yearlings (1.1 kg, 3.4 %) than for kids (0.8 kg, 4.8 %).

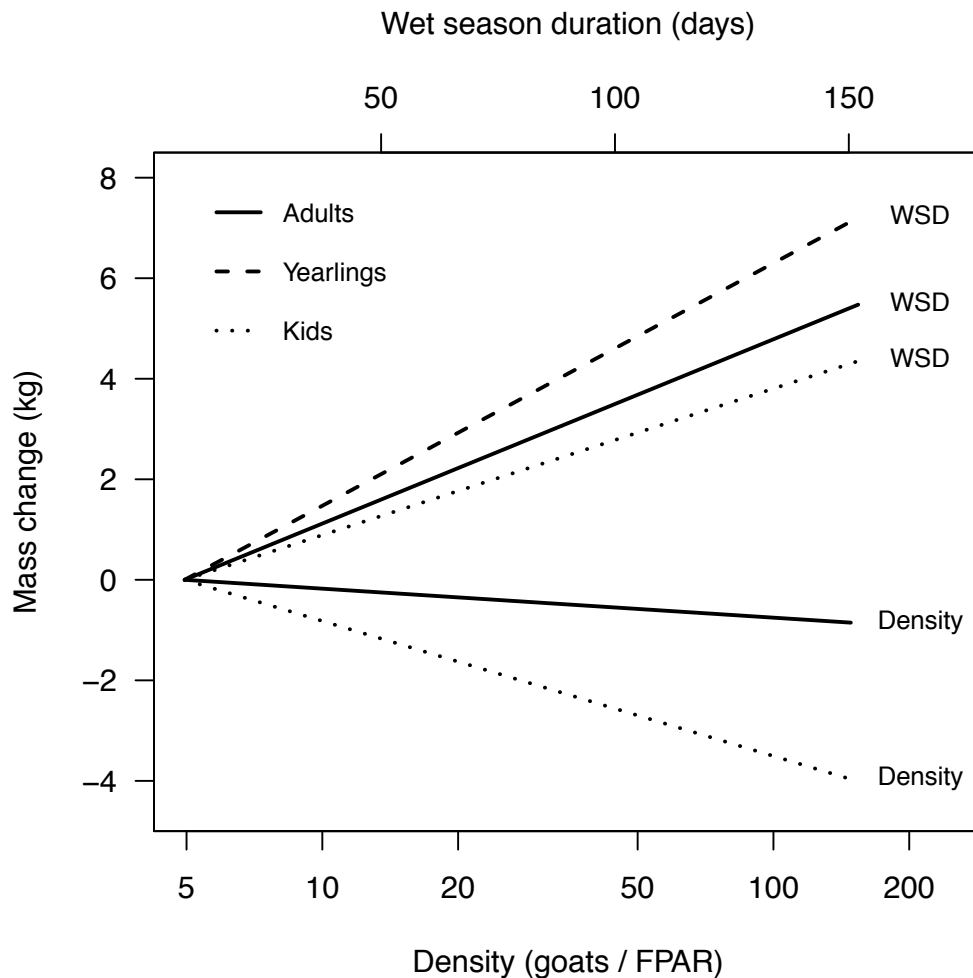


Figure 4.5: Change in body mass in response to wet season duration (days) and density (goats/FPAR) during the wet season. Estimates were obtained using the best model for each life stage; modified for adults by substituting wet season duration for wet season stage, with no density interaction. Density did not have a significant influence on yearling mass. Note that the density axis has been log-scaled.

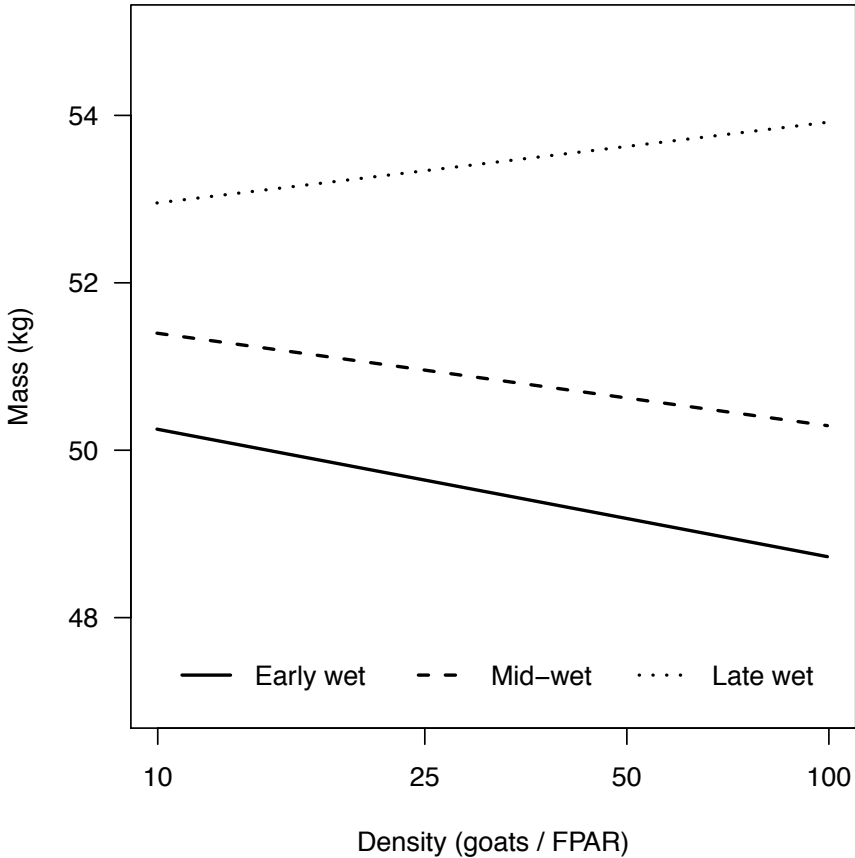


Figure 4.6: Adult mass response to density (goats/FPAR) at three stages in the wet season. Estimates were calculated using the best adult mass model, for a four year old non-pregnant goat in the 2008 wet season. The year by wet season duration interaction effect was excluded from this model. Note that the density axis has been log-scaled.

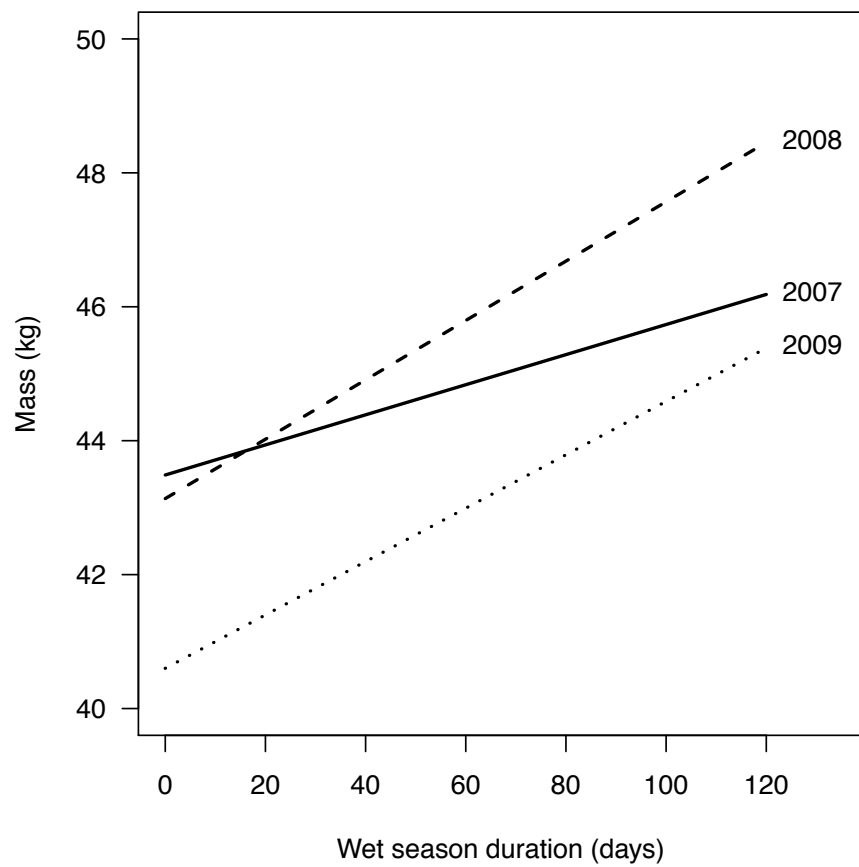


Figure 4.7: Adult mass response to wet season duration for each year of the study. The density by wet season stage interaction effect was excluded from this model.

4.3.3 Fecundity

Pregnancy rate

Goat pregnancy rates in the RNP differed between life-stages, seasons and years, and also in response to adult goat density and distance from the Orange River. All of the fixed effects fitted in the full model were significant (table 4.4). Life-stage had a significant effect on pregnancy rates ($\chi^2 = 184.3$, d.f. = 2, $p < 0.0001$), with adults being more likely to be pregnant than yearlings, and kids having very low pregnancy rates. For example, early in the 2007 wet season at 10 km from the river and average adult goat density, the predicted probability of being pregnant was 0.21 for adults,

Table 4.4: Summary of the best fit general linear mixed-effects model of goat pregnancy rates in the RNP (n = 4053). Life-stage, year, season, distance from the Orange River and adult goat density were fitted as fixed effects, and herd (n = 5) and individual identity (n = 502) were fitted as random effects. A binomial error structure was fitted, with individuals scored as pregnant (1) or not pregnant (0).

Fixed effects	Estimate	S.E.	z-value	χ^2	d.f.	p-value
Intercept	-0.7680	0.4016	-1.91			0.0558
Life-stage				184.3	2	< 0.0001
Adult	0					
Yearling	-0.4745	0.1219	-3.89			
Kid	-2.1325	0.2052	-10.39			
Year				7.2	2	0.0270
2007	0					
2008	0.2330	0.1341	1.74			
2009	-0.0663	0.1288	-0.52			
Season				205.4	3	< 0.0001
Early wet	0					
Late wet	-0.6163	0.1680	-3.67			
Mid-dry	-0.2482	0.1647	-1.51			
Late dry	1.2234	0.1467	8.34			
Distance to river				20.1	1	< 0.0001
Distance to river (km)	0.0734	0.0149	4.94			
Density				10.0	1	0.0015
log _e adult goats 0-64 days	-0.1696	0.0491	-3.45			
Random effects	Variance					
Herd	0.0427					

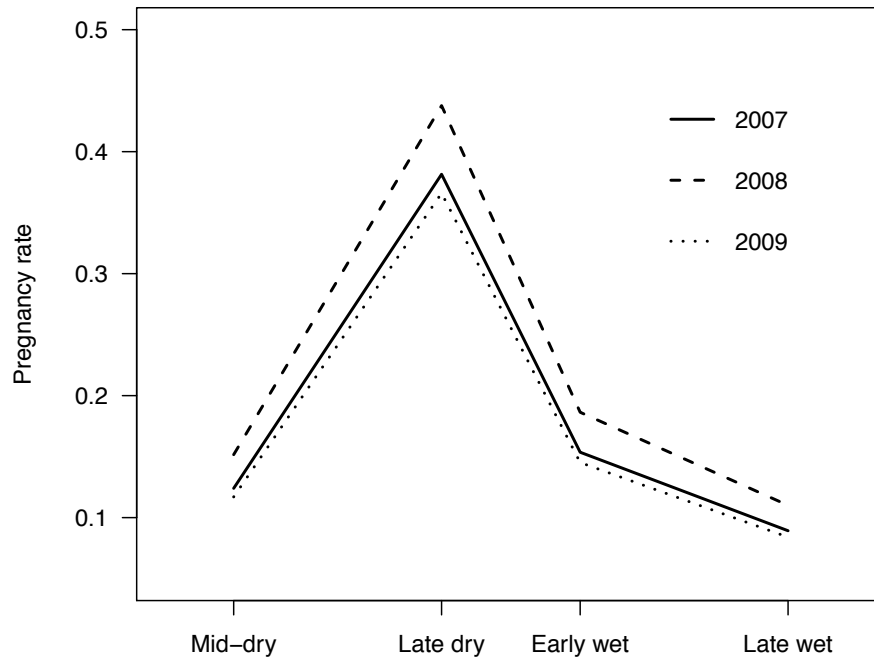


Figure 4.8: Comparison of pregnancy rates in the RNP between years and seasons. Estimates were obtained using the pregnancy rate model and were calculated for an adult goat at the average adult goat density and 5 km from the river.

0.14 for yearlings and 0.03 for kids.

The high seasonality of goat pregnancies in the Richtersveld was captured by the model ($\chi^2 = 205.4$, d.f. = 3, $p < 0.0001$), with pregnancy rates peaking in the late dry season (figure 4.8). There were also significant differences in pregnancy rates between years, which were highest in 2008 and lowest in 2009 ($\chi^2 = 7.2$, d.f. = 2, $p = 0.0270$). Pregnancy rates were positively related to distance from the Orange River ($\chi^2 = 20.1$, d.f. = 1, $p < 0.0001$). Density in the previous two months (0 - 64 days) had a negative effect on pregnancy rates, which were lower when individuals had shared the area within 2.5 km of their stockpost with higher numbers of adult goats ($\chi^2 = 10.0$, d.f. = 1, $p = 0.0015$). Individual effects were dropped from the full model as they accounted for virtually none of the remaining variance.

Birth rate

Birth rates in the RNP appear to be strongly influenced by the life-stage of the mother and also adult goat density during the previous three months (table 4.5). Life-stage had a significant effect on birth rates, with yearlings producing fewer kids per pregnancy than adults ($\chi^2 = 19.4$, d.f.=1, $p < 0.0001$). Birth rates were also negatively affected by the \log_e of adult goat density in the previous three months ($\chi^2 = 4.66$, d.f. = 1, $p = 0.0308$; figure 4.9). Year effects were excluded from the best model, but there was some evidence to suggest that birth rates were higher in 2009 than in 2008. Season and the distance to the river had little discernable impact on birth rates, and were excluded from the best model. Herd and individual effects accounted for very little of the remaining variance, and a generalised linear model structure was preferred for the best model.

Table 4.5: Summary of the generalised linear model of birth rates in the RNP ($n = 273$), which included life-stage and adult goat density as fixed effects. Year, distance to the Orange River and season were excluded from the best model, but their fit when included in the best model is shown for comparison. A binomial error structure was fitted, with individuals scored as a singleton (0) or a twin or triplet (1).

Fixed effects	Estimate	S.E.	z-value	Deviance	d.f.	p-value
Intercept	10.1167	4.8368	2.09			0.0365
Life-stage				19.4	1	< 0.0001
Adult	0					
Yearling	-1.9600	0.5451	-3.60			
Density				4.7	1	0.0308
\log_e adult goats 0-96 days	-1.2749	0.5943	-2.15			
Excluded	Estimate	S.E.	z-value	Deviance	d.f.	p-value
Year				2.0	1	0.1623
2008	0					
2009	0.3664	0.2628	1.39			
Distance to river				0.5	1	0.4841
Season				2.3	3	0.5092

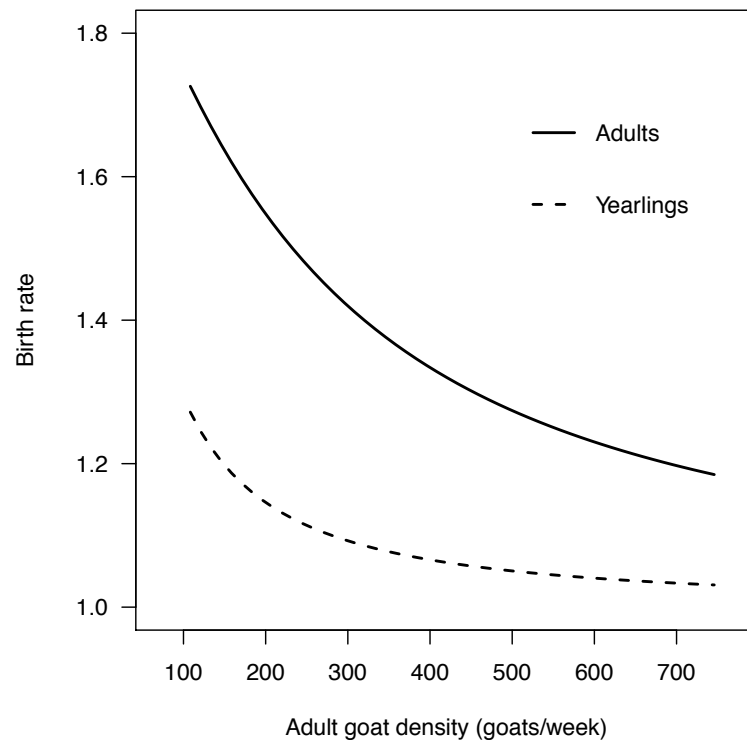


Figure 4.9: Response of the birth rates of adults and yearlings to adult goat density in the RNP. Birth rate is expressed as the number of kids per pregnancy, and was calculated using the birth rate model.

Neonate survival rate

Neonate survival rates in the RNP were strongly influenced by whether a kid was a twin or a singleton, but also differed in response to the distance of a herd from the river (table 4.6). The significant effect of sibling status on neonate survival rate suggests that singletons had a much higher chance of surviving than neonates born as a twin ($\chi^2 = 20.0$, d.f. = 1, $p < 0.0001$). This effect was modified by proximity to the Orange River, with higher neonate survival rates predicted closer to the river ($\chi^2 = 5.7$, d.f. = 1, $p = 0.0167$). Combining these effects would suggest that a singleton born 10 km from the river - in the wet season range - would be twice as likely to survive as a twin would be (figure 4.10). There was weak evidence for the existence of seasonal and year effects on neonate survival rates, but the standard error of these estimates was high, and the terms were thus excluded from the best model. Life-stage of the mother

Table 4.6: Summary of the generalised linear model of neonate survival rates in the RNP (n = 245). The sibling status of a kid and the distance of the herd to the Orange River were included in the best model. Season, year, mother's life-stage and adult goat density effects were excluded from the best model, but are shown for comparison, when included individually in the best model. A binomial error structure was fitted, with individuals scored as 1 if they survived to the first fieldtrip after their birth and 0 if not.

Fixed effects	Estimate	S.E.	z-value	Deviance	d.f.	p-value
(Intercept)	3.0070	0.4301	6.99			< 0.0001
Sibling status				20.0	1	< 0.0001
Singleton	0					
Twin	-1.7188	0.4371	-3.93			
Distance to river				-5.7	1	0.0167
Distance to river (km)	-0.1549	0.0639	-2.42			
Excluded	Estimate	S.E.	z-value	Deviance	d.f.	p-value
Season				3.1	2	0.2140
Early wet	0					
Mid-dry	-1.8240	1.1986	-1.52			
Late dry	-1.9875	1.2581	-1.52			
Year				0.8	1	0.3617
2008	0					
2009	0.3565	0.3959	-0.90			
Life-stage				0.1	1	0.7601
Density 0-96 days				0.0	1	0.9026

and adult goat density appear to have little effect on neonate survival rates, and were also excluded from the best model. A generalised linear model structure was adopted after herd and individual effects were found to be very low.

4.4 Discussion

The wet season provides obvious relief from the strain of the dry season, with goats in all life-stages shown to regain body condition during this period. However, the extent of wet season mass gain is not clearly associated with wet season quality. Goat pregnancy rates peak in the late dry season and births coincide with the start of the wet season. There is thus the potential for a complex interplay between dry and wet season conditions on annual recruitment rates. The potential for carryover effects from the

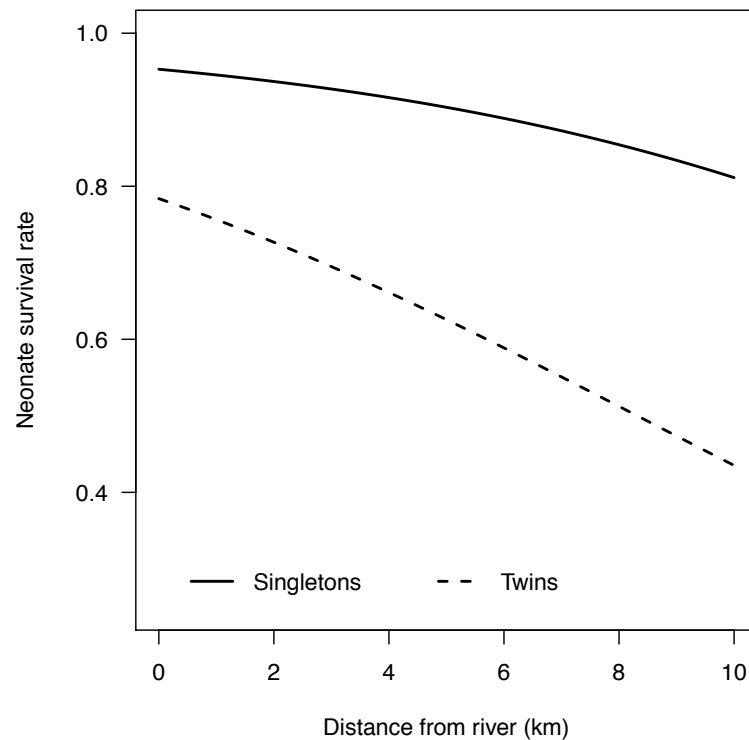


Figure 4.10: Comparison of the predicted neonate survival rate of singletons and twins in response to distance from the Orange River (km). Predictions were made using the neonate survival rate model.

wet season to the dry season was also examined by assessing whether wet season mass influenced subsequent dry season survival rates.

Wet season range

There was a clear relationship between FPAR and variation in rainfall and temperature over the study period (figure 4.2). FPAR has previously been shown to be closely related to vegetation cover in semi-arid environments, and to capture accurately seasonal fluctuations in the amount of photosynthesising plant biomass (Fensholt *et al.* 2004). The relationship between FPAR and the distance of herds from the Orange River provides formal evidence that herd movements away from the river are predominantly associated with the main plant growth season (figure 4.3). This rationale is frequently presented by herders, and confirms the findings of Hendricks

et al. (2005b). The main focal areas for herds during the wet season are the wide drainage basin plains that lie between the steep and rocky mountain ranges (Hendricks 2004). These plains are thus considered to form the core of the wet season range in the RNP. Hendricks *et al.* (2005b) suggest that the general movement back to the riparian zone at the end of the wet season is due to a shortage of adequate daily drinking water in the wet season range, which becomes necessary when the forage resource begins to dry out. This was corroborated in discussions with herders. It is also of interest to note that herds moved away from the Orange River during the mid-dry season in 2008, in response to plant growth following the February 2008 summer thunderstorm.

The duration of the wet season differed between years, as did the peak FPAR and total amount of rainfall in each wet season (figure 4.4). The 2006 wet season is the wettest on record and is regarded as being better than those during the study period. During the study period, the 2007 wet season was considered to be the best wet season, based on it having the highest total rainfall and peak FPAR and also the longest duration. The 2008 and 2009 wet seasons were of similar duration, but total rainfall and peak FPAR were notably higher in 2008. Wet season quality was thus considered to decline in each successive year of the study period.

Recruitment

Wet season quality did not affect the rate of recruitment into the goat population in a particular year. However, dry season conditions would appear to influence annual recruitment through effects on pregnancy and birth rates. The incidence of pregnancy peaked in the late dry season, and inter-annual differences were detected (figure 4.8). The timing of births is not a reflection of a herd management strategy as males are kept in the herd throughout the year. Pregnancy rates were highest in 2008, which had good rainfall in the mid-dry season. The timing of this boost to the dry season forage reserves is likely to have had a positive effect on the number of pregnancies coming to term (Jonsson 1997). Year effects on birth rates (table 4.5) and neonate survival rates (table 4.6) were not significant, which suggests that they are not constrained by wet season forage limitations. Rather, variation in the state of the dry season forage resource is expected to be more important in determining recruitment in each year, through its direct effect on pregnancy rates and foetal development (Byers & Hogg 1995, Keech *et al.* 2000, Wilson *et al.* 2009).

The relevance of dry season conditions to annual recruitment is established further through the effect of density on pregnancy (table 4.4) and birth rates (figure 4.9). Pregnancy rates were negatively related to adult goat density in the preceding two months, and birth rates to density in the previous three months. Births are timed for the beginning of the wet season, shortly after the nutritional bottleneck in the mid- to late dry season. The negative effect of density over this time period on both pregnancy and birth rates is thus likely to reflect a decline in the body condition of the mother (Keech *et al.* 2000). The combination of an income breeding strategy and a long life-span is likely to result in the mother compromising reproductive success in an unfavourable year in order to reduce her risk of mortality in that year (Tavecchia *et al.* 2005, Parker *et al.* 2009). This effect would also explain differences in life-stage specific pregnancy and birth rates, which were highest in adults, as sensitivity to environmental conditions decreases with age (mass, chapter 3) leading to lower variability in survival rates (Gaillard *et al.* 2000, Eberhardt 2002). Interestingly, there was no effect of density on neonate survival rates, which supports the conclusion that lactation is adequate in the wet season as a consequence of a plentiful forage resource (Landete-Castillejos *et al.* 2003, Therrien *et al.* 2008).

Neonate survival rates were strongly affected by competition with siblings (figure 4.10). The favourability of conditions both pre- and post-partum has been shown to influence neonate survival rates (e.g. Forchhammer *et al.* 2001), with twins being at a disadvantage to singletons by having to compete with each other for their mother's resources (Clutton-Brock *et al.* 1992, Johnstone-Yellin *et al.* 2009). Neonate survival rates were higher closer to the river, which is suspected to be a post-partum effect. Neonates remain at the stockpost all day while the herd goes out foraging, and the cooler shadier conditions in the riparian zone are thought to improve neonate survival rates. The positive effect of distance from the river on pregnancy rates, once having accounted for life-stage, year, season-stage and density effects, may reflect the better foraging conditions in the wet season range.

Carry over effects between seasons

The mass analysis showed that goat body condition in all life-stages improved as the wet season progressed (figure 4.5), as would be expected. This period of mass gain was however moderated by density effects on adults and kids. Adult mass

responded to density over the two month interval prior to weighing, but this only had a negative effect on mass gain during the early and mid-wet season (figure 4.6). This adult density signal probably still reflects conditions during the late dry season forage resource bottleneck, rather than there being true density-dependence of wet season mass gain. Density effects on kids were only evident when considering a longer interval (3 months), but were evident throughout the wet season. Interpreting this effect is complicated by the progression of older kids into the yearling life-stage during the wet season, and the long time interval that was necessary to detect it. The dry season bottleneck had a relatively greater impact on the body condition of kids than of adults (chapter 3, figure 3.6), and may be detectable over a longer time interval in kids. The average age of individuals in the kid life-stage is likely to be younger at the end of the wet season than early in the wet season, due to the progression of the previous year's cohort into the yearling life-stage. Thus, in the latter stages of the wet season, kid mass is likely to reflect the adequacy of lactation, rather than direct competition for forage by the kid itself (Landete-Castillejos *et al.* 2003). The consistent mass gain in all life-stages through the wet season suggests that forage resources do not become limiting, which is also the impression gained in the field. The forage resource begins to dry out towards the end of the wet season, which forces herds to make use of the few available artificial waterpoints at this stage. The density effect on kids in the late dry season might well be a true reflection of competition for the forage resource by their mothers (Festa-Bianchet & Jorgenson 1998, Therrien *et al.* 2008), but may also reflect greater competition for access to a point source water supply in larger herds.

Inter-annual differences in goat body condition during the wet season allow for the extent of coupling between goat population dynamics and the wet season forage resource to be assessed. The relative performance of goats in each year might reflect the quality of the wet season, suggesting a degree of coupling, which could also affect survival rates over the following dry season (Crete & Huot 1993, Cook *et al.* 2004). In terms of evidence for direct wet season coupling, the most informative year appears to be 2008 (figure 4.11). The 2008 wet season appeared to be of poorer quality than the 2007 wet season (longer, wetter and higher FPAR peak; figure 4.4), yet adult and kid mass were highest in the 2008 wet season (yearlings not estimated in 2007). This suggests that goat mass is likely to be responding to conditions outside of the wet season, or factors other than just the amount of forage growth e.g. reproductive costs

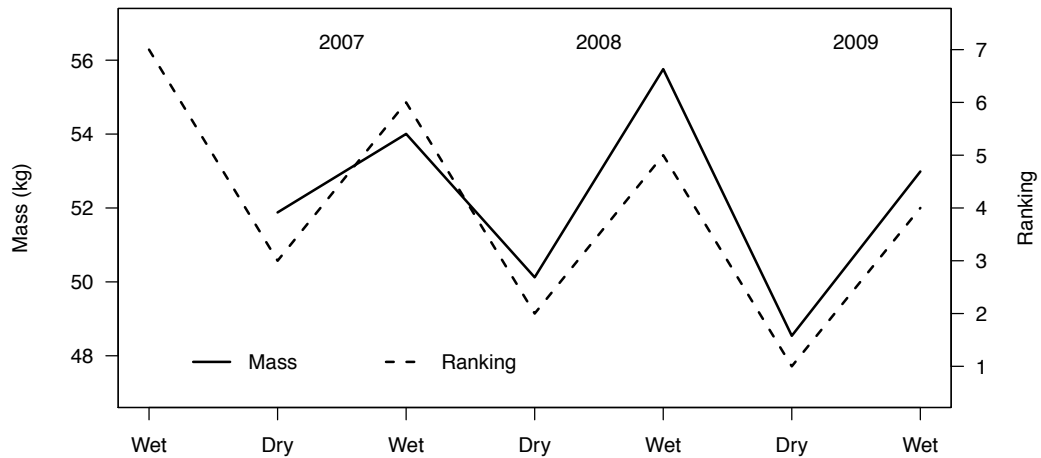


Figure 4.11: Seasonal variation in adult mass and the perceived favourability of each season during the study period. The mass estimate is for a non-pregnant five year old goat at the end of each season in each year. Estimates were made using the best model for the dry and wet season respectively. Yearlings and kids showed a similar pattern of seasonal mass change. Season rankings were based on the perceived favourability of each dry (1 - 3) and wet (4 - 7) season, with one considered the least favourable and seven the most favourable.

(Therrien *et al.* 2007). The 2009 wet season was ranked as the worst wet season (figure 4.11) and all life-stages were in their poorest 'wet season condition' in this year. The evidence for direct effects of apparent wet season quality on goat body condition thus shows some degree of contradiction. Hence, the conclusion drawn from this analysis is that goat body condition does not appear to be closely related to the quality of the wet season forage resource. However, a longer time series would be useful to test this conclusion.

The effect of body condition at the end of the wet season - irrespective of whether it reflects wet season quality - does not appear to have a strong effect on adult survival rates over the following dry season. Dry season survival was not analysed for yearlings and kids, due to a missing cohort that precluded inter-annual comparisons. The pattern of mass change in yearlings and kids matched that of adults, and although their survival rates are expected to be lower than adults, the relative pattern should match that of adults (Gaillard *et al.* 2000). This analysis is also limited by the short time series that is available, but 2008 is again an informative year. Adult survival over the dry season decreased with each year of the study period, in accordance with

their mass and the perceived quality of each dry season (figure 4.11). The 2008 wet season stands out in this trend as it is the point where goat mass was the highest during the study period, but was followed by the dry season with the lowest adult survival rates. However, the short time series once again leads to a contradiction that cannot currently be resolved, as the highest adult survival rates and mass followed the apparently highly favourable 2006 wet season which is the wettest on record. The adult survival rate over the dry season corresponds to the perceived quality of the dry season, but may also relate to conditions in the preceding wet season (Owen-Smith 1990, Ogutu *et al.* 2008). It is difficult to quantify the relative quality of each dry and wet season, but it would appear that the effect of a severe dry season can override the effect of a favourable preceding wet season (2008 wet - 2009 dry). However, if a dry season is more moderate, a carryover effect from the wet season may be discernable (2006 wet - 2007 dry; 2007 wet - 2008 dry). The wet season carryover effect is thus concluded to potentially have a modifying effect on dry season survival, but that the primary determinant of dry season survival rates is the quality of that dry season.

Summary

Herds move away from the riparian zone in the wet season, in order to take advantage of the pulse of forage resources on the interior plains. Annual recruitment rates appear to be more strongly influenced by the effects of dry season conditions on pregnancy and birth rates than by the favourability of the wet season. Neonate survival rates did not differ between years, and were most sensitive to sibling effects. Goats gain mass throughout the wet season, but this does not closely match wet season quality, and can be influenced by conditions in the preceding dry season. Adult survival rates in mild dry seasons might be modified by wet season mass carryover effects, but more severe dry season conditions override this effect. Dry season conditions are virtually the sole driver of recruitment and goat population dynamics.

5 Landscape structure

5.1 Introduction

The riparian zone in the RNP functions as a key resource, with goat population dynamics being regulated via density-dependent feedback with their dry season forage resource (chapter 3). There is thus empirical evidence to support the argument of Illius & O'Connor (1999) that, despite high environmental variability in the system at large, a link must still exist between a herbivore population and its forage resource, but that this equilibrium would exist over a spatially and temporally delimited subset of resources. The key resource is defined in dynamical terms, being the resource whose supply determines the size of the key factor that determines population growth. By definition, all systems thus have a key resource, but the nature of that key resource is not expected to be the same in each system. For example, riparian browse constitutes the key resource in the RNP, but perennial shrubs on isolated hilltops may form the key resource in another system.

The relative size and variability of the key resource has been shown to have consequences for the animal population, directly as a result of the coupling between herbivores and this resource (Illius & O'Connor 2000). Thus, an increase in the size of the key resource should result in an increase in herbivore population size, whereas an increase in the variability of primary production in the key resource would be expected to reduce the herbivore population size. This reduction in herbivore numbers is a consequence of the growth rate of herbivore populations being slower than the rate at which they can potentially decline under a severe forage resource bottleneck (Caughley & Gunn 1993, Georgiadis *et al.* 2003). Increased key resource variability would thus lead to more frequent and potentially more severe bottlenecks, reducing the long-term average population size.

An alternative view of the functioning of systems in variable environments is that plant and consumer dynamics are uncoupled by high environmental variability,



Figure 5.1. Oom Gert Joseph's stockpost in the Kuboes region.

leading to a qualitatively different relationship between herbivores and their forage resource (Ellis & Swift 1988, but see chapter 6). This perspective suggests that *'livestock populations may decline because of a lack of fodder, but fodder is scarce because there is too little rain rather than too many animals'* (page 8 - 9, Behnke & Scoones 1993). Herbivore impacts on plant dynamics are thus predicted to be irrelevant in systems where drought frequency is high, which is suggested to occur where the annual rainfall CV exceeds 33 % (Ellis & Galvin 1994). However, there is no formal evidence for fundamentally different dynamics, or qualitatively distinct characteristics, which might operate in these highly variable systems to suggest that herbivore effects on their forage resource can sometimes be ignored. The system in which this apparently alternative view was first conceived (Turkana, Kenya; Ellis & Swift 1988), based on the authors' findings (but not terminology), functions as a system that is frequently at a high state of disequilibrium, and which can begin to be understood by focussing on dry phases (chapter 6). There is thus little evidence to suggest that herbivore populations are not being regulated by the availability of their key resource during these dry phases.

The Kuboes and Paulshoek pastoral systems (figure 5.1 and figure 5.2) that are examined in this chapter are thus expected to function according to the same ecological principles shown to operate in the RNP. However, the nature of the key resource in each system may well differ. The key resource model suggests that some degree of seasonal segregation in forage resources is required in order for the impact of the key resource to become evident (Illius & O'Connor 2000). This is very likely to be the case in both Kuboes and Paulshoek, where strong seasonality in plant growth provides a similar flush of forage in the winter wet season that is not available during the dry season. Identifying the key resource is simpler in the RNP than in Kuboes or Paulshoek, because it is large and highly spatially concentrated. In contrast, the key resource in Kuboes and Paulshoek is more diffuse, and animals tend to rely on growth along minor drainage lines and forage reserves in the cooler and wetter high-lying areas during the dry season (Samuels *et al.* 2007).

The nature of the key resource in the RNP and in Kuboes and Paulshoek is thus predicted to be considerably different. The relative size of the key resource in the RNP is likely to be greatest, largely as a consequence of the stability provided by the perennial flow of the Orange River, which has resulted in the establishment of a well-developed riparian zone. The relatively smaller key resources in Kuboes and Paulshoek are anticipated to both be more variable than the RNP key resource, due to their expected primary reliance on precipitation. However, the higher and less variable annual rainfall in Paulshoek could buffer the degree of variability in the Paulshoek key resource relative to the Kuboes key resource.

These hypothesised differences in the nature of the key resource in each study site can be used to predict the relative herbivore population dynamics in each region. These predictions were tested using marked goats and census records from the RNP, marked goats in Kuboes and census records from Paulshoek.

RNP vs. Kuboes

1. Goat population dynamics are expected to be more stable in the RNP
2. Long-term average herbivore density is expected to be higher in the RNP

The mass, fecundity and survival rates of the individually marked goats in each region were used to test the first prediction. However, the second prediction could not be tested due to the absence of census data for Kuboes.

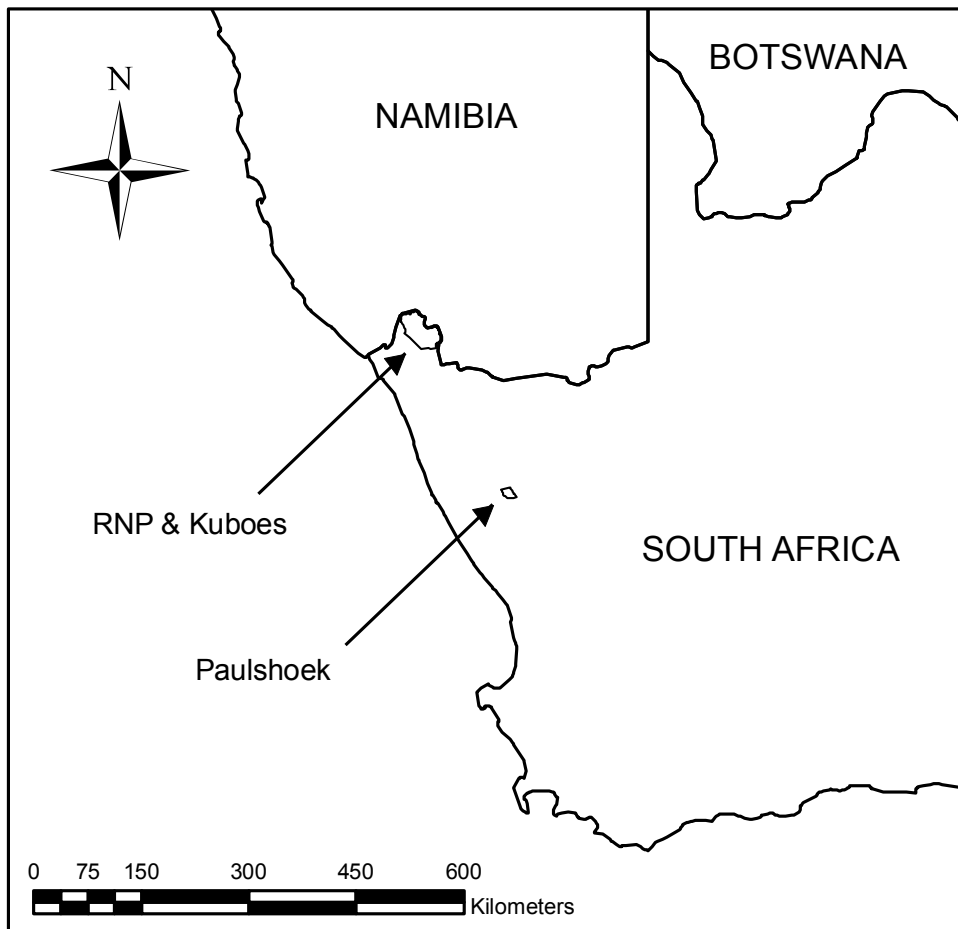


Figure 5.2: Locations of the RNP, Kuboes and Paulshoek. Kuboes is situated on the south western border of the RNP, and does not have access to the Orange River, which forms the border between South Africa and Namibia.

RNP vs. Paulshoek

1. Livestock numbers are expected to be relatively more stable in the RNP
2. Livestock numbers are expected to be relatively higher in the RNP

The comparison between the RNP and Paulshoek needs to take into account the higher annual rainfall in Paulshoek. This would be expected to increase primary production and result in higher potential animal densities (Coe *et al.* 1976, Fritz & Duncan 1994).

5.2 Methods

5.2.1 RNP-Kuboes: goat mass comparison

Goat body condition during the study period was compared between Kuboes and the RNP using mass data from the marked individuals. Two sets of analyses were performed - the first aimed to model variation in mass, and by fitting region as a fixed effect, to assess whether goat mass dynamics differed substantially between the study sites. The second set of analyses was aimed at obtaining a mass estimate for each life-stage in each region for each of the fifteen fieldtrips. These estimates could then be plotted against time to compare a time series of goat performance for each life-stage in each region over the course of the study period. As in chapter 3 and 4, the mass analyses were split into adult, yearling and kid life-stages, due to differences in the availability and resolution of age data. The data were analysed using general linear mixed-effects models, fitted using the lme4 package (Bates & Maechler 2010) in R version 2.10.1 (R Development Core Team 2009). Goat density data were not available for the Kuboes region, and could thus not be fitted in these models.

In the first analysis for each life stage, in which the primary objective was to test for regional effects on mass variation, the response of goat body mass to region and region-specific rainfall was modelled. Mass was thus entered as the response variable in the model for each life-stage, with a two-level factor - Kuboes or RNP - fitted as an explanatory variable. The \log_e of regional rainfall summed over the period 96 - 160 days prior to weighing was found to have the highest explanatory power across all life-stages, and was fitted in the full model for each life-stage. The interaction between region and the rainfall term was also fitted, in order to test whether the same amount of rainfall had the same ultimate effect on goat mass in each region. The age and reproductive status of each individual at the time of weighing was also included in the full model for each life-stage, as both have been shown to have a significant effect on goat mass (chapter 3 and 4). Herd identity and individual identity - conditioned by age - were fitted as random effects in each model. The significance of terms in the full model was tested by dropping each individually and assessing the log-likelihood ratio of the full and updated model using a χ^2 -test.

The objective of the second analysis was to obtain an estimate of the mass of an adult, yearling and kid for both regions at the time of each fieldtrip. The mass dataset

was thus split into six parts - three life-stages by two regions - and a separate model was fitted for each. Fieldtrip was fitted as a fixed effect in each model, to obtain a mass estimate at the time of each weighing session. Given that the objective of this analysis was to obtain a mass estimate as the product of the different environment and resource characteristics of each region, rainfall was omitted from each model. In contrast, variation in goat mass due to internal processes - age and reproductive status - was not the focus of this analysis, and both were accounted for by fitting them as fixed effects. Herd and individual identity conditioned by age were fitted as random effects. The models were then used to estimate the mass of an individual of the same age and reproductive status for each life-stage in both Kuboes and in the RNP. These estimates were plotted against time and compared between regions. The variance of the mass estimates for each life-stage was compared between study sites using a Levene's test for homogeneity of variance.

5.2.2 RNP-Kuboes: vital rates

Pregnancy, birth and neonate survival rates were compared between Kuboes and the RNP to determine whether regional differences in resources and conditions influenced population fecundity parameters. These analyses were structured similarly to the analyses of fecundity parameters in chapter 4, with a general linear mixed-effects model with binomial error structure being fitted for each rate. The data obtained from herders' reports and from direct observation of the marked goats was used to compare fecundity parameters of the goat populations in each region. The reproductive status of an individual was recorded at the time of weighing, and, if it had given birth in the period since it was last weighed, every effort was made to accurately determine how many kids had been born, and how many of them were still alive. As noted in chapter 4, given the difficulty in obtaining perfect reporting for every individual, bias towards lower birth rates and higher neonate survival rates is probable. Birth rates and neonate survival rates were again only calculated for 2008 and 2009, due to the improvement in reporting over this period. Density effects were not included in these comparisons due to the lack of census and herd position data for all herds in the Kuboes communal grazing areas.

RNP-Kuboes: pregnancy rates

Goats in Kuboes and the RNP were scored as ‘one’ on the last occasion that they were observed to be pregnant during each gestation period, and as ‘zero’ otherwise. Region was fitted as a fixed effect, to account for differences between Kuboes and the RNP. Life-stage was fitted to capture variation due to an individual’s developmental stage. Seasonal effects on pregnancy rates were modelled by categorising fieldtrips as early wet, late wet, mid-dry or late dry using the same classifications for each fieldtrip as used in chapter 4. Calendar year was fitted to capture any remaining variation attributable to conditions in each year. Herd and individual identity were fitted as random effects.

RNP-Kuboes: birth rates

The birth rates of goats in Kuboes and the RNP were modelled for adults and yearlings in 2008 and 2009. As in chapter 4, a binary response variable with singletons scored as ‘zero’ and twins and triplets scored as ‘one’, was generated. The low frequency of triplets, and the lack of reliability in reporting of aborted pregnancies, was used to justify this approach. Differences in birth rates between the study sites were assessed by fitting region as fixed effect. Life-stage was fitted to model differences in the number of kids born to adults and yearlings. Season-stage - using the same classifications as fitted in the pregnancy rate model - was fitted as a fixed effect, as was calendar year. Herd and individual effects were accounted for by fitting them in the random structure of the birth rate model.

RNP-Kuboes: neonate survival rates

Neonate survival rates in Kuboes and the RNP were compared for kids born in 2008 and 2009 to marked adult and yearling goats. Births were assumed to occur randomly through the period between fieldtrips; kids surviving to the first fieldtrip after their birth were scored as ‘one’, and those that died, ‘zero’. Region was fitted as a fixed effect in the model. The life-stage of the mother of each neonate - either adult or yearling - was fitted to assess whether this influenced its likelihood of survival in the period immediately after birth. In addition to this maternal effect, whether a neonate was born as a singleton or a twin was fitted, to determine whether competition for

a mother's resources - either in the womb or post-parturition - had an influence on survival rates. Season-stage and calendar year were fitted to assess the impact of conditions at the time of birth on a neonate's probability of survival. Herd identity was fitted as a random effect in the neonate survival model.

RNP-Kuboes: adult survival rates

Dry season survival rates were compared between Kuboes and the RNP based on the survival of marked adult goats from February to August in each year of the study. Yearlings and kids were omitted from the analysis due to there being very low sample sizes in the cohort of kids in February 2007 and consequently yearlings in February 2008. A general linear mixed-effects model with binomial error structure was fitted to the data, with adult goats present in February and surviving to August scored as 'one', and those dying in the interval scored as 'zero'. Region was fitted as a fixed effect, in order to test for differences in survival rates between study sites. Rainfall effects were fitted in the full model, because separate values were available for each study site - meaning that slopes would be estimated off six points as opposed to three in the RNP dry season range model (chapter 3). The \log_e of rainfall summed over three intervals - February to April, May to July and February to July - was calculated for each year, and fitted in the model. Overlapping intervals were not fitted simultaneously. The mass and reproductive status of an individual at the start of each dry season interval - February - was also fitted in the model. Individual identity was fitted as a random effect, but herd identity was omitted as it accounted for very low levels of variance.

5.2.3 RNP-Paulshoek: long-term population dynamics

The long-term dynamics of herbivore populations in variable environments are anticipated to - at least to some degree - reflect the factors shaping population dynamics that operate over seasonal timescales. In the absence of the availability of long-term census data for the Kuboes region, Prof. Timm Hoffman (Plant Conservation Unit, University of Cape Town) was approached to request access to the long-term livestock dataset that he and his colleagues have generated for the Paulshoek region, and which was kindly provided. Paulshoek is situated approximately 250 km SSE of the RNP, and has a wetter and less variable climate than the Richtersveld region. Paulshoek

is similar to the Kuboes region in that it lacks a distinct dry season range (c.f. the riparian zone in the RNP), and herds tend to rely on forage reserves in the less utilised high-lying areas during the dry season. Livestock censuses have been carried out in Paulshoek for every month from August 1998 to present (August 2010).

Long-term livestock dynamics in the RNP and Paulshoek were compared based on four characteristics of each system: 1) livestock density, 2) the variability of livestock density, 3) the relationship between environmental variability and animal population variability and 4) the predicted animal biomass for each region. Mixed herds of goats and sheep are kept in both the RNP and in Paulshoek. However, relatively more sheep are kept in Paulshoek, and thus the total number of livestock (i.e. goats plus sheep) was used to compare animal density and variability between the systems. Livestock density for each system was expressed as the number of animals per unit area (animals/ha), but was also calculated relative to FPAR. Mean FPAR was calculated for each study site at two points - day 49 (mid-February) and day 225 (mid-August) - in each year from 2000 to 2009. For Paulshoek, the total number of livestock counted in the respective month was divided by mean FPAR, and multiplied by the area of Paulshoek (ha). FPAR values were only available for about 50 % of the area of the RNP. The closest total livestock census figure (max. 3 months difference) was divided by the mean FPAR value and multiplied by the area (ha) of the RNP with a detectable FPAR signal. The RNP estimate is thus likely to represent an overestimate of actual animals per FPAR, as half of the region was effectively considered barren and ignored.

The variability of the Paulshoek and RNP livestock populations was compared using the population variability (PV) metric derived by Heath (2006). This measure of variability calculates the average percent difference of all possible pairs of population size estimates for each region. PV is considered to be robust to data which are not normally distributed, and is useful for comparisons because it is based on a proportional scale (Fraterrigo & Rusak 2008). A single population size estimate was calculated for each region for each year from 1998 to 2009 by taking the average of all censuses undertaken in each year. The RNP situation is complicated by the regular movement of herds across the park boundaries, and difficulties in reaching all herds on each census trip. The PV of livestock numbers in the RNP was thus also calculated at the individual herd level for the eleven 'resident' herds that were counted in twenty or more of the 38 RNP censuses. The coefficient of variation (CV) in annual rainfall

(standard deviation / mean) was calculated for both regions for the period from 2000 to 2009. This measure was used as an estimate of the environmental stochasticity of each region, as both systems would typically be considered to be water-limited.

Animal biomass was predicted for Paulshoek and the RNP using the regression equation for ‘medium soil nutrient availability’ derived by Fritz & Duncan (1994):

$$\log_{10}(\text{biomass}) = 1.78 * \log_{10}(\text{rainfall}) - 1.32$$

where biomass is expressed as kg/km² and rainfall is the annual mean rainfall in mm (RNP = 80 mm, Paulshoek = 200 mm). This was compared with the observed animal biomass in each region, which was calculated using the average population size of sheep and goats in each area over the study period, and a conversion factor of 45 kg. Two values were calculated for the RNP, the first for the whole area, and the second using the area of the park that was used by herds during the period 1995 to 2001 (Hendricks 2004).

5.3 Results

5.3.1 RNP-Kuboes: goat mass comparison

Seasonal variation in rainfall was the main environmental driver of body mass change in each life stage (Adults: $\chi^2 = 751.51$, d.f. = 1, $p < 0.0001$, Yearlings: $\chi^2 = 122.01$, d.f. = 1, $p < 0.0001$, Kids: $\chi^2 = 35.623$, d.f. = 1, $p < 0.0001$). The interaction between region and rainfall was significant in each life-stage model (Adults: $\chi^2 = 92.33$, d.f. = 1, $p < 0.0001$, Yearlings: $\chi^2 = 12.41$, d.f. = 1, $p = 0.0004$, Kids: $\chi^2 = 7.42$, d.f. = 1, $p = 0.0065$). In each case, a goat in Kuboes gained more weight per unit of rainfall than an equivalent individual in the RNP. When region and rainfall were fitted as additive terms (i.e. no interaction), region was not found to account for any differences in goat mass.

The second analysis of goat mass in each region suggested that the body condition of adult goats was more variable in Kuboes than in the RNP, but that yearling and kid mass variability was similar in both regions over the study period (figure 5.3). The variance of the mass estimates for a four-year old goat, over the fifteen fieldtrips, was significantly greater in Kuboes than in the RNP ($F_{1,28} = 5.2039$, $p = 0.03034$). Visual inspection of the yearling and kid mass plots suggests that the

degree of variation in each region is similar, which was supported by the Levene's test for homogeneity of variance for these life-stages (Yearlings: $F_{1,14} = 1.3279$, $p = 0.2685$, Kids: $F_{1,22} = 2.5559$, $p = 0.1241$).

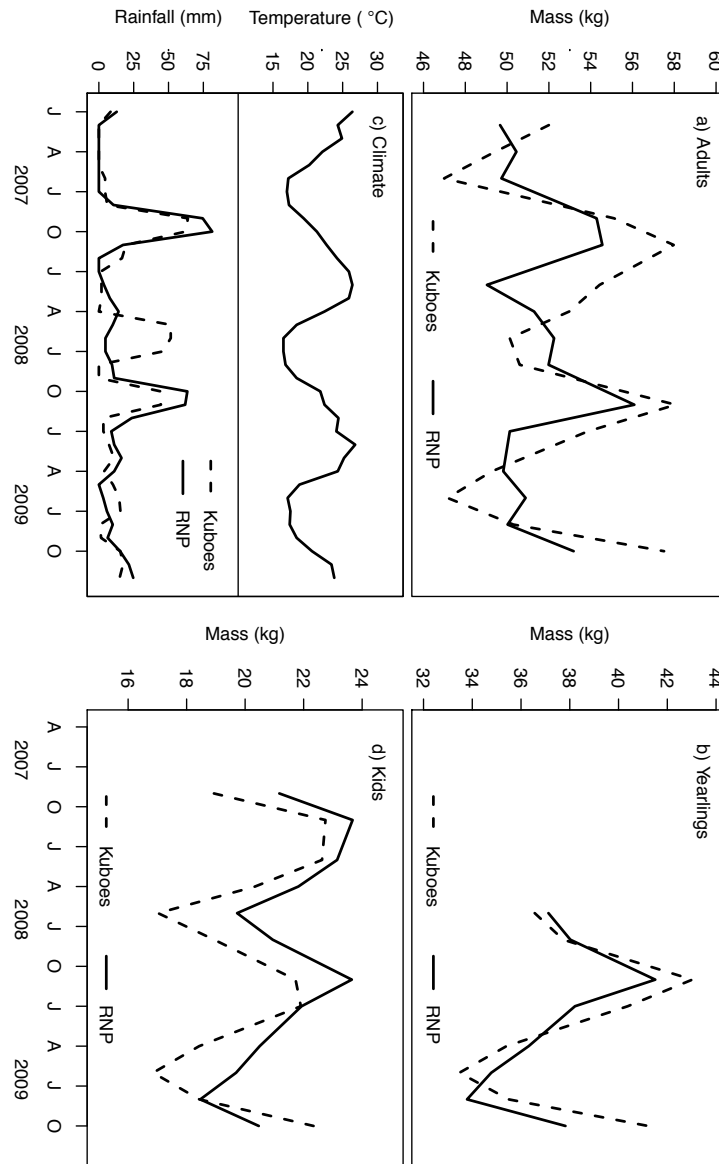


Figure 5.3: Mass estimates over the study period for goats in each region, a) adults (4-years), b) yearlings (18-months) and d) kids (6-months). Climate data is provided in c) for comparison with the goat mass dynamics. The rainfall measure provided is the sum of rain in the previous 96 - 160 days, and the temperature value is the mean daily temperature for each month.

5.3.2 RNP-Kuboes: vital rates

RNP-Kuboes: pregnancy rates

Pregnancy rates did not appear to differ between Kuboes and the RNP (table 5.1). Rather, it would appear that factors identified as being associated with pregnancy rates in the RNP (chapter 4) - life-stage, season and year - were in operation in both regions. Life-stage had a significant effect on pregnancy rates, with adults having higher pregnancy rates than yearlings, and kids having much lower pregnancy rates in both regions ($\chi^2 = 286.0$, d.f. = 2, $p < 0.0001$). The seasonal effect on pregnancy rates was apparent in both regions, peaking in the late dry season and early wet season ($\chi^2 = 210.6$, d.f. = 3, $p < 0.0001$). Pregnancy rates were highest in 2008 and lowest in 2009 ($\chi^2 = 20.9$, d.f. = 2, $p < 0.0001$). Herd and individual effects were omitted from

Table 5.1: Summary of the generalised linear model of pregnancy rates in Kuboes and the RNP ($n = 6127$). Life-stage, season and year effects were retained in the best model, but the regional effect - which did not account for variation in pregnancy rates - was excluded from the model.

Fixed effects	Estimate	S.E.	z-value	Deviance	d.f.	p-value
Intercept	-1.2807	0.1145	-11.19			< 0.0001
Life-stage				286.0	2	< 0.0001
Adult	0					
Yearling	-0.4116	0.0928	-4.44			
Kid	-2.2631	0.1829	-12.37			
Season				210.6	3	< 0.0001
Early wet	0					
Late wet	-0.7430	0.1227	-6.06			
Mid-dry	-0.7219	0.1187	-6.08			
Late dry	0.5424	0.1012	5.36			
Year				20.9	2	< 0.0001
2007	0					
2008	0.2342	0.1004	2.33			
2009	-0.1706	0.1003	-1.70			
Excluded	Estimate	S.E.	z-value	Deviance	d.f.	p-value
Region				0.7	1	0.4201
Kuboes	0					
RNP	0.0643	0.0800	0.81			

the best model - which took the form of a generalised linear model - as they accounted for very little of the remaining variance in pregnancy rates.

RNP-Kuboes: birth rates

Birth rates differed between Kuboes and the RNP, but were more strongly influenced by the life-stage of the mother (table 5.2). As observed in chapter 4, adults produced on average more offspring per pregnancy than yearlings ($\chi^2 = 55.3$, d.f. = 1, $p < 0.0001$). The evidence for regional differences in birth rates ($z = -1.98$, $p = 0.0475$) was considered sufficient to justify retaining this effect in the best model, despite only providing a marginally better fit to the data ($\chi^2 = 3.0$, d.f. = 1, $p = 0.0844$). The best model estimated birth rates of approximately 1.61 for adults in Kuboes and 1.45 for adults in the RNP, while yearling birth rates were predicted to be lower - approximately 1.13 in Kuboes and 1.07 in the RNP. Individual effects accounted for about twice as much of the remaining variation than herd effects did. Seasonal and year effects on birth rates were not significant, and were excluded from the best model.

Table 5.2: Summary of the generalised linear mixed-effects model of birth rates in Kuboes and the RNP ($n = 452$). Life-stage and regional effects were included in the best model, and year and seasonal effects were excluded, but are provided for comparison.

Fixed effects	Estimate	S.E.	z-value	χ^2	d.f.	p-value
Intercept	0.4400	0.2555	1.72			0.0850
Life-stage				55.3	1	< 0.0001
Adult	0					
Yearling	-2.3575	0.3814	-6.18			
Region				3.0	1	0.0844
Kuboes	0					
RNP	-0.6481	0.3270	-1.98			
Random effects	Variance					
Tag	0.2323					
Herd	0.1125					
Excluded	χ^2	d.f.	p-value			
Year	0.0434	1	0.8350			
Season	0.4695	3	0.9255			

RNP-Kuboes: neonate survival rates

Neonate survival rates do not appear to differ between regions (table 5.3). In accordance with the RNP-only analysis (chapter 4), whether an individual was a singleton or a twin was a significant factor in determining whether a neonate would survive the first few months after birth ($\chi^2 = 16.9$, d.f. = 1, $p < 0.0001$). The evidence for seasonal differences in neonate survival rates was considered sufficient to justify the inclusion of the season-stage effect in the best model, despite the overall effect only being significant at the 90 % confidence limit ($\chi^2 = 4.7$, d.f. = 2, $p = 0.0973$). Neonate survival rates were significantly higher in the early wet season than in the mid-dry ($z = -2.12$, $p = 0.0338$) or late dry season ($z = -1.76$, $p = 0.0784$). The neonate survival rate model selected for the RNP (chapter 4) did not include the seasonal effects on neonate survival. However, when the data from both study sites were combined, neonate survival rates were predicted to be highest for singletons born in the early wet season and lowest for a twin born in the mid-dry season (table 5.4).

Table 5.3: Summary of the generalised linear mixed-effects model of neonate survival rates in Kuboes and the RNP ($n = 446$). Whether a kid was a singleton or a twin and season-stage were included in the best model; mother's life-stage, year and regional effects were excluded, but are provided for comparison.

Fixed effects	Estimate	S.E.	z-value	χ^2	d.f.	p-value
Intercept	2.5902	0.5321	4.87			< 0.0001
Sibling status				16.9	1	< 0.0001
Singleton	0					
Twin	-1.1473	0.2927	-3.92			
Season				4.7	2	0.0973
Early wet	0					
Mid-dry	-0.9367	0.4413	-2.12			
Late dry	-0.7606	0.4322	-1.76			
Random effects	Variance					
Herd	0.8170					
Excluded	χ^2	d.f.	p-value			
Life-stage	1.5	1	0.2251			
Year	0.4	1	0.5330			
Region	0.3	1	0.5938			

Neonate survival was not significantly influenced by the life-stage of the mother or year effects, which were thus excluded from the best model.

Table 5.4: Neonate survival rates for singletons and twins born in different seasons. Estimates were made using the neonate survival model.

Season	Singleton	Twin
Mid-dry	0.84	0.62
Late dry	0.86	0.66
Early wet	0.93	0.81

RNP-Kuboes: adult survival rates

Adult survival over the dry season was higher in the RNP than in Kuboes and was positively influenced by rainfall (table 5.5). Region had a significant effect on adult survival through the dry season, with survival rates predicted to be higher in the RNP than in Kuboes ($\chi^2 = 7.3$, d.f. = 1, $p = 0.0068$; figure 5.4). Rainfall in the period from February to July was included in the best model, as it provided the best overall fit to the data. Rainfall over this period had a positive and significant effect on adult survival ($\chi^2 = 8.5$, d.f. = 1, $p = 0.0036$). When fitted independently, rainfall in the period from May to July also had a significant positive effect on survival ($\chi^2 = 7.4$, d.f. = 1, $p = 0.0065$), but the standard error of the model intercept was much larger. Rainfall from February to April was also positively related to survival, but the effect was not significant ($\chi^2 = 1.3$, d.f. = 1, $p = 0.2567$). The mass and reproductive status of an individual in February did not explain its probability of surviving to August that year.

Table 5.5: Summary of the general linear mixed-effects model of adult survival rates in Kuboes and the RNP, and in response to rainfall (n = 721). A binomial error structure was fitted, with individuals scored as one if they survived the dry season and zero if not. Individual identity was fitted as a random effect (n = 336).

Fixed effects	Estimate	S.E.	z-value	χ^2	d.f.	p-value
Intercept	-2.3183	1.2603	-1.84			0.0658
Rainfall				8.5	1	0.0036
log _e rainfall (Feb - Jul)	1.0630	0.3108	3.42			
Region				7.3	1	0.0068
Kuboes	0					
RNP	0.8513	0.3205	2.66			
Random effects	Variance					
Individual	1.6723					

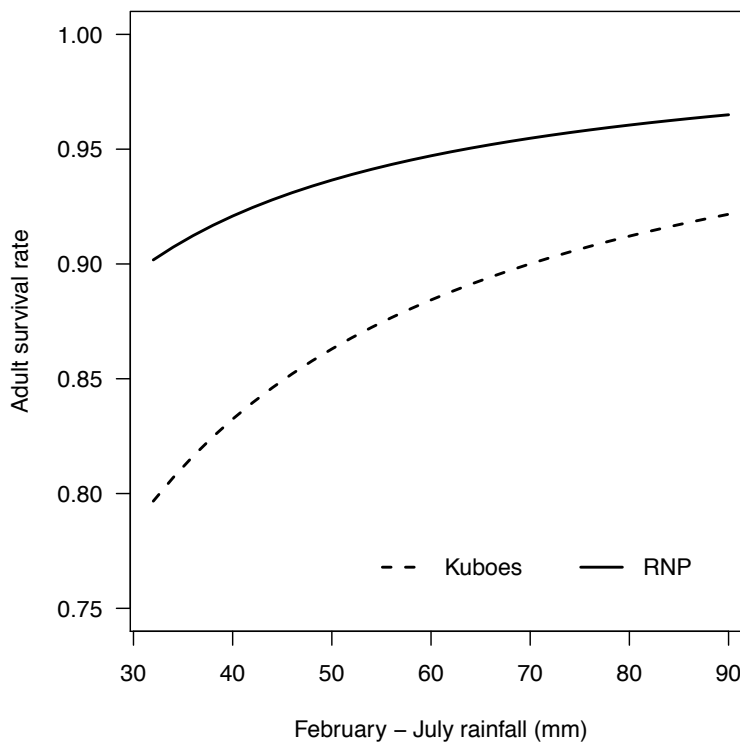


Figure 5.4: Comparison of adult survival rates over the dry season in Kuboes and the RNP in response to rainfall between February and August each year.

5.3.3 RNP-Paulshoek: long-term population dynamics

Livestock density was lower and more variable in the RNP than in Paulshoek, but given the high environmental variability of the RNP, was probably more stable than would be expected. The RNP is approximately ten times larger than Paulshoek (208 256 ha vs. 23 561 ha), but has on average only supported about twice as many animals as Paulshoek (5146 vs. 2423). Average livestock numbers relative to the total area of each study site were thus about four times lower in the RNP than in Paulshoek over the last 12 years (0.025 animals/ha vs. 0.103 animals/ha; figure 5.5). The attempt to correct these densities for relative forage availability - as approximated by FPAR - also suggests that animal density is on average lower in the RNP than in Paulshoek (0.0034 ± 0.0016 animals/FPAR vs. 0.0066 ± 0.0022 animals/FPAR). As indicated, the RNP estimate is likely to be an overestimate, because only that area of the RNP producing a detectable FPAR signal was considered.

Population variability was lower in Paulshoek (26.0 %) when compared to the PV of the total census figure obtained for the RNP in each year (33.2 %). However, the PV estimate for the 'resident' herds in the RNP was slightly lower (25.1 %) than that in Paulshoek. Considering only the more permanently RNP-based herds was an attempt to exclude the effects of movements of herds across the RNP border and the occasional failure to reach all herds in the park during each census fieldtrip. This analysis suggests that population variability in the RNP is probably slightly higher than in Paulshoek, but not markedly so. The coefficient of variation in annual rainfall from 2000 to 2009 was considerably higher in the RNP (54.2 %) than in Paulshoek (32.3 %).

The biomass prediction made using the Fritz & Duncan (1994) regression equation was very similar to the observed biomass in the total area of the RNP, but was slightly lower than predicted in Paulshoek (table 5.6). The attempt to adjust the RNP biomass estimate to reflect only the area that is accessible to herds produced a higher biomass estimate than what was predicted using the Fritz & Duncan (1994) regression equation.

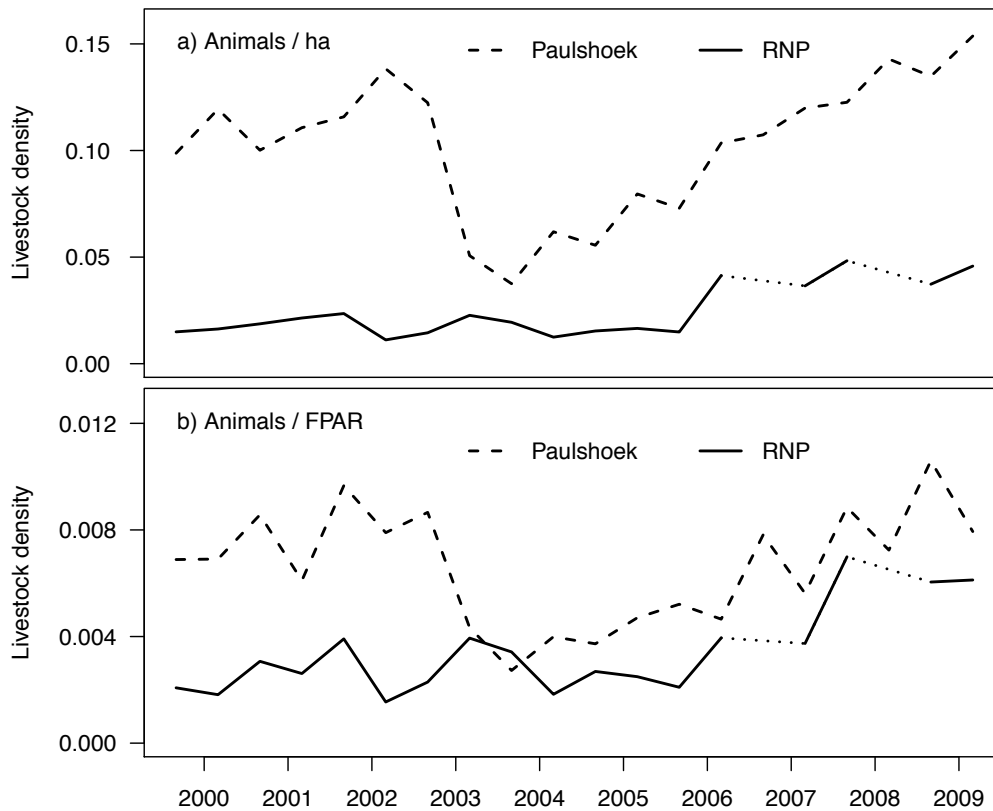


Figure 5.5: Total livestock density (goats and sheep) in Paulshoek and the RNP from 2000 to 2009, expressed a) relative to area (ha) and b) relative to an index of forage availability (FPAR).

Table 5.6: The predicted and observed livestock biomass in Paulshoek and the RNP. Predictions were made using the equation derived by Fritz & Duncan (1994) for medium soil nutrient systems.

Region	Predicted	Observed
Paulshoek	597 kg/km ²	463 kg/km ²
RNP _{total}	116 kg/km ²	111 kg/km ²
RNP _{used}		164 kg/km ²

5.4 Discussion

Ecological systems comprise a complex set of abiotic and biotic interactions. Within these complex systems, quantifying all relevant features that affect the dynamic interface between plants and large mammal herbivores is not possible. However, the structure of the landscape determines a systems endowment of key resources, and if this does determine herbivore population performance and abundance, then that should become apparent from comparison of contrasting systems. The key resource in the RNP is highly concentrated and readily identifiable, given the presence of the Orange River, but this is not the case in Kuboes and Paulshoek. The diffuse nature of the key resources in Kuboes and Paulshoek suggests that they are likely to be relatively smaller and more variable than the riparian zone in the RNP, but this was not quantified. It would however have been surprising if access to the Orange River key resource had not resulted in differences in goat population dynamics between Kuboes and the RNP, which otherwise appear to offer very similar environments.

A complicating factor in interpreting the results of the comparison between the RNP and Kuboes, in particular, is that the key resource is defined in dynamical terms. In these analyses, the goat population parameters that are being investigated (mass dynamics and vital rates) are responses to conditions that are measured over relatively short time periods. The potential danger of assessing short-term responses in a contrast of dynamics is that if one herbivore population were closer to equilibrium with its forage resource, then that population would be more sensitive to an environmental perturbation. However, a mitigating factor in the RNP-Kuboes comparison is the close proximity of the study sites, which effectively border one another. There is thus likely to be a high degree of environmental correlation between the systems, which should have a strong synchronising effect on the goat population dynamics in each region (Grenfell *et al.* 1998, Bjornstad *et al.* 1999, Koenig 1999). In the absence of census data for the Kuboes region, the analysis thus to some extent relies on the synchronising effect of similar climates. If both populations are in a similar state, then moderate or more substantial perturbations to each system should produce a clearly interpretable response.

The Paulshoek study site is situated 250 km SE of the RNP, and the synchronising effects of correlated environmental conditions on goat population dynamics, or Moran effect, is expected to be weaker (Bjornstad *et al.* 1999, Koenig 1999). Both study

sites are however largely influenced by the same general weather patterns. The population parameters that were compared between these two systems were measured over relatively long time-scales (10 - 12 years). They are thus expected to represent emergent properties of each system, and be less influenced by historical events. The consequence of differences in rainfall and floristics on the size and stability of the key resource in the RNP and Paulshoek were not directly quantified, but could be inferred from the population data.

The findings in both sets of comparative analyses suggest that the large and stable RNP key resource does have a discernable effect on herbivore population performance. In particular, the higher dry season survival rate of adult goats in the RNP than in Kuboes provides compelling evidence that access to the riparian key resource has an effect on goat population dynamics. The differences between the RNP and Paulshoek are less easy to interpret because of the differences in mean annual rainfall, but after allowing for that, livestock population densities in RNP appear to be more stable and possibly higher than observed in Paulshoek.

RNP-Kuboes: survival and mass

The higher dry season survival rate and less variable mass fluctuations of RNP adult goats suggest that the influence of a larger and more stable riparian key resource has been detected (survival: figure 5.4, mass: figure 5.3). If adult survival over the dry season is the key factor in both regions, then the significant difference in dry season survival rates between regions, by definition, indicates that the key resource is bigger in the RNP. This assessment may in some respects seem trivial, but the implications of being able to predict the size of the key factor by assessing which part of their resource base a herbivore population is coupled to are not.

The significant effect of rainfall on adult survival in both regions improves our understanding of how a seasonal bottleneck impacts a herbivore population. Rainfall during the mid- to late dry season (February to July) had a positive effect on survival in both regions. The mechanism of this effect is very likely to be the resultant plant growth response, which although not particularly substantial, should alleviate the pressure on the remaining forage reserves (figure 4.4). Splitting the dry season into the periods from February to April (mid-dry) and May to July (late dry) showed that late dry season rainfall had a significant effect on survival, but not mid-dry season

rainfall. This supports the evidence from chapter 3 that curtailing the length of the dry season has a greater impact on survival rates than that of moderating conditions during the dry season.

The higher variability of adult goat mass in Kuboes than in the RNP provides further clues as to how the nature of a key resource shapes population dynamics. Based on their key resource model, Illius & O'Connor (2000) suggest that higher variability in the key resource should result in higher variability in the key factor, and hence lower population sizes in otherwise equivalent systems. Dry season survival has been shown to depend on body condition (chapter 3), and thus greater variability in body condition should translate into greater variation in adult survival rates, the predicted key factor. The tautological point has once again been reached: a more variable key factor by definition means that the key resource is more variable. However, the fact that this could be predicted by an assessment of the landscape is again not a trivial finding.

As an extension, it is perhaps worth exploring how herbivore population dynamics might be predicted based on the floristic nature of the key resource. The key resource in the RNP appears to be dominated by well-established trees in the riparian zone. Although not quantified, the key resource in Kuboes is suspected to consist of growth along minor drainage lines and forage reserves in less accessible high-lying regions. How might stability be conferred through the floristic characteristics of the key resource? In this instance, the deeper rooting and general year-round availability of water to the riparian trees should result in more constant growth throughout the year. Thus, while a well-developed browse line might indicate severe depletion of accessible forage resources, this can be supplemented by fruits, flowers and green leaves that fall from above the browse line and become accessible in the litter layer. In contrast, if growth of the vegetation that comprises the key resource in Kuboes is more rainfall-dependent, then substantial variation in growth would be expected between years and within each dry season. In addition, if the growth form of the plants that form the key resource means that they are wholly within reach (in terms of height), then the lack of supplementary litter fall suggests that in a sense, depletion is more final. If this were to be the case, the greater variability in a herbivore population may not only reflect greater variability in rainfall, but also the floristic nature of its key resource. This highlights the difficulty in capturing the effects of environmental stochasticity on herbivore population dynamics (Saether 1997).

To return to the analyses, the variability in yearling and kid mass did not appear to differ significantly between regions. This was surprising, as the greater sensitivity of these life-stages to environmental effects would have been expected to produce a greater difference between regions than that observed in adults. One possible contributing factor may be the asymmetric forage deficit that arises as a consequence of the ability to reach the remaining forage reserves in the RNP riparian zone, to the detriment of smaller individuals. A second possibility is that kids are also supported by lactation during the dry season, which may buffer them against forage resource depletion at the expense of their mother's condition. Fryxell (1987) considered this to partially explain equal mortality in white-eared kob calves in a drought and a non-drought year, when adults showed a fourfold increase in mortality in the drought year.

RNP-Kuboes: fecundity parameters

There is little evidence from the analysis of fecundity parameters to suggest that the key resource in each region has a detectable influence on recruitment. Regional differences in birth rates were observed, but given the absence of a similar effect on pregnancy rates or neonate survival rates, and the absence of detailed information on the composition of the Kuboes key resource, it is hard to envisage how this difference could relate to differences in the key resource in each region. Rather, regional differences in genetic or population age-structure might account for this difference, but more detailed analyses would be required to test these (e.g. Brown *et al.* 1993, Albon *et al.* 2000). The present conclusion is that if the nature of the key resource does have an effect on population fecundity parameters, then that effect is likely to be subtle in comparison with the observed effect on mass dynamics and dry season survival.

The seasonal effect on neonate survival rate that was detected in the joint RNP-Kuboes analysis provides further insight into the effect of conditions at different stages of the year on goat population dynamics. The survival rate of neonates born in the wet season was markedly higher than those born in the mid or late dry season. This pattern is likely to reflect differences in the nutritional status of mothers, with the marked improvement in the forage resource during the wet season allowing them to better meet the high nutritional cost of lactation (Bauman & Currie 1980, Therrien *et al.* 2007).

RNP-Paulshoek: long-term dynamics

The Paulshoek region, 250 km SE of the RNP, has a higher and less variable annual rainfall (200 mm, CV = 32.3 %) than the RNP (80 mm, CV = 54.2 %). Regions with a higher annual rainfall, which leads to higher annual primary production, have been shown to support greater densities of large mammal herbivores (Coe *et al.* 1976, Fritz & Duncan 1994). Paulshoek would thus be expected to support a higher livestock density than the RNP, which was indeed found to be the case, whether expressed relative to the total area (± 4 times greater) or FPAR for the area producing a detectable signal (2+ times greater). The difference between these estimates largely reflects the smaller area of the RNP that was used in the FPAR based calculation, which was anticipated to be an overestimate of livestock/unit forage in the RNP, because forage existed elsewhere, but was not detected by the MODIS satellite. Paulshoek livestock densities are thus likely to be at least three times higher than in the RNP.

Livestock population variability (PV) for each region over the last 12 years was similar. PV in Paulshoek was estimated at 26.0 %, and although a higher estimate was obtained when considering the total RNP count (33.2 %), the PV for the eleven 'resident' herds (25.1 %) was slightly lower than that in Paulshoek. An *a priori* expectation of population variability for a given rainfall variability could not be found in the literature. However, given that rainfall variability is considerably higher in the RNP (54.2 % vs. 32.3 %), and yet PV is similar, it is concluded that population variability in the RNP is relatively lower than what would be expected. This lower population variability in the RNP was predicted *a priori*, based on the apparent difference in the nature of the key resource relative to the rest of the landscape in the RNP (larger and more stable) and Paulshoek (smaller and more variable).

A corollary of the greater stability of the livestock population in the RNP is that it should also be larger than what would otherwise be expected. This second prediction was tested using the regression equation for medium soil nutrient availability in Fritz & Duncan (1994). This set of regression equations was developed using census data from a wide variety of African systems with a rainfall range of approximately 200 - 1200 mm. Thus, for the RNP, the livestock biomass estimate was extrapolated beyond the range of the regression. No attempt was made to correct for differences arising from the effect of local variability in rainfall on the stability of each system, and estimates are thus considered to be for the average level of variability associated with

a particular annual rainfall value. The population density estimate for the RNP (117 kg/km²) was very similar to the observed average population density when considering the full area of the RNP (111 kg/km²). However, large areas of the RNP are comprised of steep and rocky terrain, and are effectively inaccessible to herds. Hendricks (2004) calculated that 67.9 % of the RNP was accessible to herds, based on records of all the stockposts that were used between 1995 and 2001. Livestock density was estimated at 164 kg/km² using this revised estimate of the area of the RNP that is accessible to herds. The livestock population density for Paulshoek (463 kg/km²) was lower than what was estimated (597 kg/km²), which would partially be attributable to donkeys and other large herbivores not being included in the calculations (Allsopp *et al.* 2007). Likewise, the RNP estimates do not include the gemsbok, springbok and cattle present in the park, and are also thus likely to be slight underestimates of the true large herbivore density. Goats and sheep do however make up the vast majority of the herbivore biomass in each region, and the predictions are thus considered to be a good first approximation of herbivore biomass in each region. Herbivore densities in the RNP thus appear to be slightly higher than would be expected, and densities in Paulshoek are probably lower than would be expected. This result agrees qualitatively with what would be anticipated based on the perceived differences in the key resource in each region. However, this assessment is by no means considered to be conclusive, but instead provides suggestive evidence for the effect of each key resource.

Summary

Herbivore population dynamics were predicted *a priori* based on the perceived nature of the key resource in three study regions. These predictions were supported in the first comparison between regions, as higher dry season adult survival rates and lower adult mass variability were observed in the system perceived to have a larger and more stable key resource. Fecundity parameters were not obviously different between these regions. In the second regional comparison, as predicted, long term population variability was relatively lower in the system perceived to have the larger and more stable key resource. The evidence suggesting that herbivore population size in this system was also larger than would be anticipated, in accordance with the prediction, was not considered to be conclusive.

6 Comment on the rangeland debate

'The single biggest problem in communication is the illusion that it has taken place' - George Bernard Shaw (unknown).

Unfortunately, this sentiment is symptomatic of the discussion of the processes shaping plant and animal dynamics in arid and semi-arid ecosystems. This dialogue has become known as the 'rangeland debate'. The rangeland debate began to build momentum in the early 1990's, arising from a critique from a social science and ecological perspective of the relevance for pastoralist societies of the traditional range management views that were rooted in commercial ranching. The origin of the debate is the paper by Ellis & Swift (1988) entitled: 'Stability of African pastoral ecosystems: Alternate paradigms and implications for development.' This paper, and the subsequent debate over its central proposition, has generated a series of commentary and review papers, which show little sign of drying up (e.g. Behnke *et al.* 1993, Scoones 1994, Sullivan 1996, Illius & O'Connor 1999, Cowling 2000, Sullivan & Rhode 2002, Briske *et al.* 2003, Vetter 2005, Gillson & Hoffman 2007, Derry & Boone 2010).

So what's all the fuss about? The rangeland debate ostensibly revolves around the relevant paradigm of rangeland function, and contrasts the respectively termed 'equilibrium' and 'nonequilibrium' paradigms. However, at times, the apparent implications of each paradigm for the livelihoods of pastoralists have obscured the discourse on the appropriateness of the ecological foundations of those implications. This highlights the importance of the issues at hand, as the involvement of a range of participants from researchers to end users - ecologists, stakeholders, managers, policy makers etc. - is only observed when a matter is relevant.

My objective here is to return to what should be at the core of the rangeland debate: understanding the ecological function of these rangelands. This is complicated by the lack of clarity in the meanings of three terms that are critical to the debate: equilibrium, disequilibrium and nonequilibrium. This is not a good start;

my intention is to as far as possible resist becoming embroiled in the semantics of the debate. Rather, I would like to show how these terms have been applied, while unpicking what I believe to be an underappreciated aspect of the ecological views held by each paradigm: the importance of recognising the spatial and temporal scale of each perspective. This analysis is based on the study presented by Ellis & Swift (1988), which I re-examine in order to gauge their view of the functioning of the ‘original’ nonequilibrium system, the Turkana District in northern Kenya. By doing so, I’d like to suggest that opinions are perhaps not as polarised as some might think. Herewith though, by necessity, are what I perceive to be the more relevant definitions of three terms used in the rangeland debate:

Equilibrium

Definition E1, range model definition: The plant community across the whole system has a single climax state achievable in the absence of grazing. A single continuum of Clementsian type successional stages exists, with grazing pushing the system away from the climax community, which otherwise moves steadily towards it. This is the ‘range succession model’ described in Westoby *et al.* (1989).

Definition E2, Lotka-Volterra definition: The plant community and the animal community are coupled by a functional mechanism (herbivory), which potentiates the existence of a negative feedback between the herbivore and the forage resource. Density-dependence is generally expressed in this context.

Disequilibrium

Definition DE1, disequilibrium: The situation where animal population dynamics do not match their resource dynamics perfectly due to perturbations to the system (e.g. environmental forcing) which cause the state variables (amount of forage or number of herbivores) of the system to not presently reflect the system’s inherent equilibrium. Due to the coupling between plants and animals (E2 above), the equilibrium is a moving attractor; the distance between the current state of the system and that moving attractor would be considered to be the extent of disequilibrium.

Nonequilibrium

Definition NE1, continuum nonequilibrium: A system in which perturbations to the system exacerbate disequilibrium past a point where the effects of herbivory on the plant community can easily be discerned, and herbivore mortality, when it occurs, appears to be density independent. This approach assesses the relationship between the system state variables in a correlative manner i.e. by regressing animal abundance against plant abundance. ‘Coupling’ (not in the sense used in E2) between herbivores and the forage resource can thus vary in strength (e.g. the r^2 of the regression). In this context, a continuum can exist from ‘equilibrium to nonequilibrium’, but could alternately be described as being the range from minor disequilibrium to major disequilibrium (DE1).

Definition NE2, binary nonequilibrium definition: The situation where a population is not coupled (in the sense of E2) to its environment. No correlation between state variables (i.e. herbivore numbers vs. forage availability) would be expected. Under this view, no continuum can exist from ‘equilibrium to nonequilibrium’, because they are systems with coupling (E2) and systems without coupling (E2), i.e. binary, not continuous. Note also that the term ‘nonequilibrium dynamics’ is an oxymoron under this definition ‘no-pattern patterns’.

Ellis & Swift (1988) present a study of pastoral dynamics in the arid to semi-arid Turkana District in Kenya. Their motivation ultimately stemmed from a desire to see the rangeland being managed in a manner most beneficial to the people who inhabit the region. People’s livelihoods were construed as being under threat, as outside attempts at managing Turkana and similar systems were perceived to be based on an inappropriate model of plant and animal dynamics. More particularly, they disputed the assumptions that 1) African pastoral ecosystems are potentially stable, 2) these stable systems are destabilised and degraded by pastoralists, and 3) alterations such as reducing livestock numbers and patterns of tenure could return these ecosystems to an equilibrial and more productive state. They express a justified dissatisfaction with the state of understanding of the ecology of these systems, resulting in improper management policy.

Ellis and Swift identify the prevailing management regime as being based on a simplistic Clementsian-style view of equilibrium dynamics. This view (E1) perceives

the current system-wide plant community as being positioned along a continuous and reversible successional sequence, determined by the grazing pressure or stocking rate in the region. They contend that two flawed assumptions were being made with regard to ecosystem function:

1. *'A critical assumption about equilibrial grazing systems is that plant growing conditions are invariant over time (pg 454)'*
2. *'Another fundamental assumption about the operation of equilibrial grazing systems is that herbivores play a major role in controlling plant biomass through consumption and offtake (pg 454).'*

The evidence that the first assumption does not hold is overwhelming, and would not be contested - rainfall varies dramatically both within and between years, temperatures fluctuate and plant growth is often highly seasonally pulsed. Hence, plant growing conditions are clearly highly variable in these systems and the first assumption must be rejected. An important point to note, as it reveals much of Ellis and Swift's perception of the type of systems that they are analysing, is their statement that: *'equilibrium is probably possible or at least approachable in systems with intra-seasonal and inter-annual variation in plant growth, provided that that variation is not too great (paraphrase, pg 454)'*. This shows that they recognise that plant growth conditions are never invariant, but that this does not necessarily cause a change in the functional relationship between herbivores and plants; it expresses the concept of disequilibrium.

The second assumption requires closer scrutiny, as it starts to deal with definition E2 of equilibrium - i.e. the existence of feedbacks in the plant-animal interaction. In their analysis, livestock are adjudged as unlikely to *'exert a major control on plant biomass'*, based on *'ecosystem-wide estimates of forage production and livestock consumption'*. The data they present support their conclusion; by their calculation livestock could only utilise 10 - 12 % of the total forage production in a good year. However, the spatial scale of the analysis requires unpacking. By using an ecosystem-wide spatial scale, a time step allowing animals to move across this full spatial scale is implied (in this analysis, annual). Thus, in this analysis, no distinction is made between the conditions experienced at different times of year, or the subsets of forage resources used at different times of the year.

Ellis and Swift's rejection of equilibrium dynamics is thus based on definition E1

- that animals do not exert a high enough grazing pressure to push the whole region's average vegetation back through earlier successional phases. Hence, reducing average stocking rates for the whole region won't result in the plant community of the whole region shifting towards a climax state. Although not clearly articulated, Ellis and Swift's discontent with the approach to rangeland management at the time was that the system was being managed at a single, large and homogenous spatial scale, and that seasonal variability was being ignored. Ellis and Swift then reject equilibrium as being a relevant process in rangelands, because it is not observed at this spatio-temporal definition of the system (i.e. ignoring seasonal variation).

In the following section of their paper, Ellis and Swift go on to discuss livestock dynamics in Turkana. At this point in their analysis, their analysis shifts to a new scale that recognises both spatial and seasonal variation in the system. In particular, focus falls on the role of the dry season. *'Despite the fact that Ngisonyoka livestock consume only a small proportion of the forage produced in a good year, livestock nutritional status and production rates closely track the seasonal dynamics of plant production'* (pg 455). This makes it apparent that while they have dismissed equilibrium as being relevant in their study system, it is only in the sense of definition E1 operating at a region-wide scale, and not in the sense of definition E2. This becomes clear in their statement that: *'We do not propose that there is no connection between livestock density and the degree of nutritional stress experienced during the annual dry period or during more extended droughts... there is potential for density dependent condition change [of the animal] during the dry season (pg 455)'*. Ellis and Swift thus clearly recognise the role of definition E2 of equilibrium as potentially being a factor in Turkana, i.e. Lotka-Volterra coupling (E2), but that the system is often far from the equilibrium moving attractor (disequilibrium, DE1).

The shift in scale at which the system is analysed makes a huge difference as to how dynamics are interpreted, and what processes are considered to be important. Plant-herbivore coupling (E2) is not evident at the scale of the whole region across the whole year, meaning that herbivores can't drive changes in vegetation back and forth along a Clementsian successional pathway (E1), at this whole system scale. However, when a seasonally defined subset of the system is assessed, the role of equilibrium (E2) is recognised as being important. The focus of much subsequent work has been to try and understand the consequences of 'Lotka-Volterra coupling' between herbivores and their forage resource largely being restricted to a spatio-temporally defined subset

of the system (in this instance the dry season, and dry season range), most notably that of Illius & O'Connor (1999, 2000). This work has frequently been perceived as being a direct and wholesale challenge to the findings of Ellis and Swift (e.g. Sullivan 1996), and to thus be firmly be on the side of the debate that argues the case of equilibrium.

Ellis and Swift's definition of equilibrium (E1) was not an appropriate model for the Turkana system, and as such, they proposed a new model for rangeland dynamics based on this system, which they called a nonequilibrium system. Their definition of a nonequilibrium system conforms to definition NE1 ('continuum equilibrium'), and is illustrated in figure 6 of their manuscript. This figure has frequently been reproduced in the literature to demonstrate conceptually what is meant by nonequilibrium in a rangeland context (e.g. Behnke & Scoones 1993, Briske *et al.* 2003).

In this schematic diagram (figure 6.1), the livestock population size is represented on the y-axis, and the forage resource (plants) is represented on the x-axis, reflecting the relevance of the one to the other. The animal population size is represented in apparently annual snapshots, linked by arrows showing the trajectory of animal population size relative to plant abundance. The size of the animal population increases during favourable periods, but never reaches the 'nominal carrying capacity' which would be prescribed by managers using the E1 range model. Nominal carrying capacity is plotted at one fixed animal population size, and is the number of animals that could be sustained if the total amount of primary production across the whole homogenous system were available at a steady supply throughout the year. This is the contention that Ellis and Swift aimed to dispel. The animal population never reaches 'nominal carrying capacity', as single year (minor) or multi-year (major) droughts reduce plant abundance and causing a decrease in the animal abundance. This cycle is repeated, with single year droughts occurring more frequently and causing smaller declines in population size than multi-year droughts. These single year droughts are also indicated to have an effect when the population size is high, but are not depicted as being a factor when the population size is small.

I have modified the original figure by plotting line A, which represents a hypothetical grazing pressure (number of animals/plant), to the left of which animal nutritional status starts to become compromised (not enough plants). This line represents E2, the Lotka-Volterra coupling between plant abundance and animal population size, and explains why crashes occur in drought years (not enough plants),

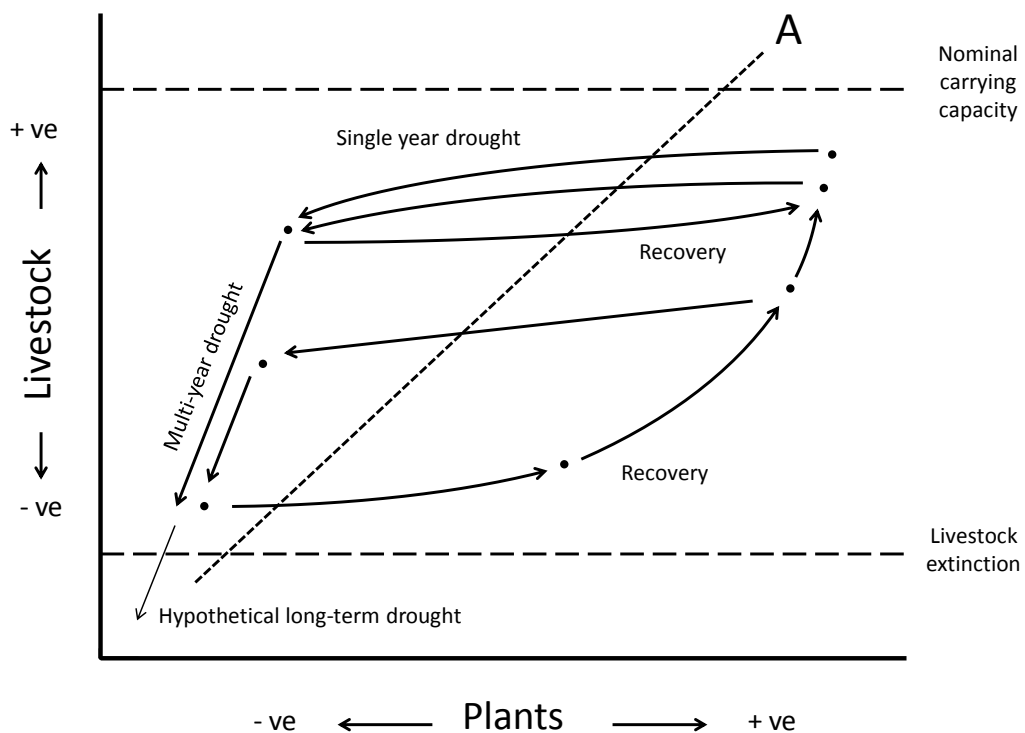


Figure 6.1: The conceptual model of nonequilibrium, redrawn from figure 6 in Ellis & Swift (1988). Line A has been added to indicate a hypothetical 'instantaneous carrying capacity' expressed as livestock/plants.

and why a crash is more likely when the population size is large (more plants are needed). It could be thought of as depicting 'instantaneous carrying capacity', and highlights the density-dependent functioning of the system. Finally, the x-axis is assumed to represent plants that are accessible to the animal population (e.g. within range from surface water or homestead), which is a requirement for the depicted relationship between livestock and plant abundance to exist. Animals are thus dying during droughts / the dry season (seasonal time scale) and from shortages in accessible forage / the dry season range (spatial scale).

The figure caption reads *'Turkana plant-livestock interactions under the influence of frequent drought perturbations'*. This is how Ellis and Swift perceived the archetypical nonequilibrium system to function. Populations build up under favourable conditions, but seasonal shortages of forage cause declines in the population, which happens more frequently when the population is large, and which are

more severe when the forage shortage persists for longer. All of these elements are consistent with a system being regulated by its key resource, complete with density-dependent mortality occurring during the season of plant dormancy (Illius & O'Connor 1999, 2000).

The nonequilibrium system described by Ellis and Swift is clearly a system that could reach equilibrium, but environmental variability keeps it in a state of disequilibrium (NE1, DE1). The high environmental stochasticity of Turkana means that the distance between the ratio of herbivores to available forage and the moving attractor equilibrium point will often be large. Nevertheless, when herbivore forage requirement exceeds forage abundance the herbivore population will exhibit a predictable response: it will decline, and how much it declines will be related to how severe the forage shortage is.

Ellis and Swift succeed in their stated purpose of displacing the idea that one prescribed fixed stocking rate could cause a system-wide change in the plant community. By calling this idea 'equilibrium', and refuting it, they reinvigorated research in this field, but inadvertently also caused a host of confusion. In terms of the benefits, this paper prompted the scientific community to engage with two important questions - 1) What drives plant community change in regions where grazing pressure is variable and usually weak (i.e. was Clementsian succession a reasonable model, Ellis and Swift argued not)?, and 2) How does spatio-temporal variability in a forage resource impact herbivore population dynamics (i.e. what were the consequences of plant-herbivore coupling being restricted to the dry season range during the dry season)?

The first question has been addressed by the state-and-transition model, formulated by Westoby *et al.* (1989), and the second by Illius & O'Connor (1999, 2000), in the form of the key resource model. The state-and-transition model agrees that a single, Clementsian-style successional pathway is inadequate in systems where many of the factors influencing plant growth are subject to variation, and emphasises the importance of event-driven change, especially the chance occurrence of extreme events. As a consequence, the potential for the existence of multiple stable states for vegetation communities is now recognised. These are separated by thresholds, breachable by sufficient perturbation of one or some permutation of system drivers or events. The key resource model predicts that animal populations are in long term

equilibrium with their dry season forage resources, while being largely uncoupled from their wet season forage resource. As such, the nature of the key resource becomes important to understanding herbivore population dynamics, which in turn shapes the effects that that herbivore population can have on the system.

The downside of Ellis and Swift's contribution is that it has resulted in confusion, which has irrationally allowed for the development of polarised standpoints. This has in some instances hindered research in this field by reducing the ability of researchers to communicate with one another. More importantly, however, the uncertainty caused by this communication breakdown has fed through to the end-user of the research. The lack of clarity in the rangeland debate, arising due to the ambiguity of terms at the very centre of the debate, has obscured the critical matter of understanding the ecological function of rangelands in stochastic environments, and hence the basis on which they can be conscientiously managed. Ellis and Swift's dismissal of the fundamental concept of 'equilibrium', because it is not useful at the spatial scale of the whole system and a temporal scale too great to capture seasonality, was rash. The problem was not the concept of equilibrium (E2), but the failure at the time to address the system at a relevant spatial and temporal scale. In order to explain the functioning of the Turkana system, as Ellis and Swift perceived it, the fundamental properties of Lotka-Volterra coupling are necessary (figure 6.1). What did need to change was the scale at which the system was addressed.

So where does that leave us? My impression is that everyone agrees that the range model (E1) is inappropriate in seasonally variable plant-herbivore systems. There has also been little to suggest that either side of the debate believes that herbivores don't eat plants (NE2). There would thus seem to be universal agreement that there is true Lotka-Volterra coupling between herbivores and plants, and that this is likely to be restricted to the subset of forage resources available in the dry season. At the one end of the debate the system is said to be 'equilibrial' because this coupling exists, and at the other end of the debate the system is said to be 'non-equilibrial' because this coupling, although not disputed, is difficult to detect when environmental stochasticity is high (e.g. rainfall CV > 33 %, Ellis & Galvin 1994). The debate - if there really is one - should thus be concerned with the implications of this agreement on the fundamental ecological function of rangelands i.e. seasonally restricted coupling between herbivores and their forage resource.

Ellis and Swift concluded that because the correlation between the state variables of the system (herbivore and plant abundance) was weak, that the impacts of herbivores on the plant community could be dismissed. This has been countered by the key resource model (Illius & O'Connor 2000), which shows that because coupling is restricted to only a subset of the system, climatic variability can increase the range of defoliation intensity by herbivores, producing occasional defoliation episodes of high intensity. Hence, their argument is that the impacts of herbivory could not be dismissed in variable ecosystems simply because of a poor correlation between herbivore numbers and plant abundance. Rather, at a simplistic level, if one of the points in that correlation is at a high number of herbivores and a low number of plants, then herbivory matters. This argument has not been countered, but on occasions it has been dismissed, because of the misperception that it advocates a return to the range succession model (E1, e.g. Sullivan & Rhode 2002).

In conclusion, given the agreement that Lotka-Volterra coupling (E2) exists over a part of the plant-herbivore system, research should be focussed on understanding its consequences. There is undisputed evidence that herbivory can have a negative impact on the plant community in variable rangelands. This needs to be communicated to end-users. This communication would be greatly facilitated by consistent terminology, but given the circumstances, the messenger may just have to be ignored. The message, however, must be delivered.

7 General discussion

Illius & O'Connor (1999, 2000) presented a hypothesis of how plant-herbivore dynamics function. This hypothesis was originally framed in an African rangeland context, in response to the claim that equilibrium concepts were not relevant to plant-herbivore systems when environmental stochasticity is high (Ellis & Swift 1988). However, this work went further than addressing whether equilibrium concepts could be dismissed, as it sought to identify when and where they were likely to be important, and considered the consequences of this. Illius & O'Connor (1999) picked up on work by, amongst others, Ian Scoones (e.g. Scoones 1991, 1995), which showed the importance of key resources to herbivore dynamics in highly variable African systems. The idea that the dry season is important in water-limited systems was thus not new - that had been shown in many previous studies (e.g. Western 1975, Fryxell 1987, Ellis & Swift 1988). What was new however, was the recognition of just how important the dry season and the key resources identified by Ian Scoones in fact were for understanding plant-herbivore systems in this African context. These consequences will be discussed later, but one example is an improved understanding of how grazing might impact the plant community in a seasonally variable environment (e.g. Illius & O'Connor 2000).

The idea that herbivore populations are closely coupled with the resources accessible in the dry season also implies that they are to some extent uncoupled from resources elsewhere in the system, assuming that resources in the growing season are more abundant than applies in the dry season. The key resource model showed that increasing the area of the wet season range by two orders of magnitude had little, but not zero, effect on animal population size (Illius & O'Connor 2000). This lack of dynamical coupling between consumers and their resources can reasonably be defined as nonequilibrium. Thus, the idea of nonequilibrium being possible in these systems is a corollary of having demonstrated that equilibrating forces are in existence but are largely restricted to a limited part of the system. By convincingly arguing the case for herbivores being in equilibrium with their key resource, Illius & O'Connor (1999,

2000) provided a unified framework in which the nonequilibrium ideas of Ellis & Swift (1988) could actually exist. The critical component of this framework was to first recognise that equilibrium was restricted to a subset of the total suite of resources: the potential for equilibrium does not follow from a demonstration of nonequilibrium existing over parts of the system.

The Richtersveld National Park

The purpose of this study was to identify the key resource of the goat population in the Richtersveld National Park. The key resource is the resource that determines the size of the key factor: the coupling between resource and vital rate is intrinsic to the definition. The analytical approach taken in this study was to try and detect this coupling by modelling variation in population vital rates as a response to potentially influential environmental factors. The environmental factors found to influence population vital rates were then used to assess which parts of the resource base could be considered to be the key resource.

Season plays a dramatic role in determining the fortunes of the RNP goat population, predominantly through its impact on the body condition of individuals. This suggests that this population is regulated from the bottom-up by food limitation during parts of the year (Sinclair 1975). In an arid African landscape, Illius & O'Connor (1999) predict that this food limitation would lead to coupling with the forage resources available in the dry season, with the corollary that the goat population is not dynamically coupled to its wet season forage resource. This would appear to be the case in the RNP.

Hairston *et al.* (1960), seeking to explain why there was apparently an excess of vegetation over that required by herbivores, predicted that the herbivore trophic level would generally be top-down regulated. This is unlikely to be the case in the RNP, as goats show clear coupling to their dry season forage resource. The virtual absence of large predators in the RNP rules out their role in a top-down regulation of the goat population, but the potential role of parasites and disease were not investigated. Parasites and disease would however be expected to have greatest impact when goats are in poor body condition, which occurs due to food limitation in the dry season (e.g. Grenfell 1992).

Dry season

The dry season is the critical period of the year for goats in the RNP, as has been widely observed in other water-limited plant-herbivore systems (e.g. Caughley *et al.* 1985, Fryxell 1987, Ellis & Swift 1988, Mduma *et al.* 1999). Goat body condition declines over this period, but remains sensitive to changes in environmental conditions. During this period, a density-dependent negative feedback becomes established between goat mass, the proxy for body condition, and the forage resource. A density-dependent decline in the body condition of impala has been recorded in Zimbabwe (Gaidet & Gaillard 2008), but as noted by these authors, evidence for this is scarce in these systems.

Forage depletion in the riparian zone was negatively related to goat density, but depletion rates differed with height in the profile and between species. Browse is depleted from the bottom-up, leading to asymmetric competition for the remaining forage reserves that favours larger individuals. This effect contributes to the greater relative decline in body mass of kids and yearlings when compared to adult goats. Feeding height stratification and the formation of a browse line due to greater dry season defoliation pressure is a frequently observed but seemingly little studied phenomenon (e.g. de Garine-Wichatitsky *et al.* 2004, Makhabu 2005). This study would appear to be the first to link the effect of the formation of a browse line to intraspecific competition between life-stages that results in differences in body condition. Browse depletion also varies amongst species, with species known to be preferred by goats showing higher rates of depletion, as would be expected (Owen-Smith & Cooper 1987). This is predicted to have consequences for the species composition of the tree community, which over the long term should favour species of lower preference to goats, and might partly explain the current abundance of *Tamarix usenoides* in the riparian zone.

Rainfall during the dry season has a positive effect on both plant growth and goat body condition. Browse regrowth is detectable approximately a month after a rainfall event, with goat body condition showing signs of improving at a similar time lag. Early winter rainfall, which signals an end to the dry season, appears to be better for goat body condition than a substantial mid-season rainfall event occurring during an otherwise longer dry season. Fryxell (1987) also suggests that the length of the dry season is critical, as per capita mortality rate of white-eared kob increased

exponentially as the dry season progressed.

The 2009 dry season lacked both mid-dry season rainfall and an early end to the dry season. Herd movements between stockposts in the riparian zone were more frequent in this year, which was interpreted as an indication that resources were limiting (Fretwell & Lucas 1969). Herds spent more time in the riparian zone in 2009 than in the other two years in the study period, regardless of browsing pressure on the riparian forage resource being highest in this year. Hendricks *et al.* (2005b) report that herds hardly left the riparian zone during the 1998 - 1999 drought in the Richtersveld. This increased reliance on the riparian zone during unfavourable periods, despite the negative feedback of a depleted forage resource on goat body condition that leads to a higher mortality rate, is compelling evidence that the population is bottom-up limited by the dry season forage resource.

Wet season

The relief of the wet season in the RNP is dramatic in contrast to the strain of enduring the dry season (figure 7.1). Goat body condition in all life-stages improved throughout the wet season, and evidence of limitation during this period was scarce. Adult body condition in the early and mid wet season was density-dependent, but the time lag of this effect suggests that it largely reflects slower recovery after a more intense dry season bottleneck, which is exacerbated by the high energy requirements of lactation (Bauman & Currie 1980, Therrien *et al.* 2007). Kid mass was negatively affected by density throughout the wet season, but this was not evident in yearlings. The extent of mass gain did not appear to be closely related to conditions in the current wet season, as although the 'wet season condition' of individuals was poorest the worst wet season (2009), it was highest in the wet season of intermediate quality (2008).

Body condition carryover effects between seasons were difficult to untangle because of the small sample size of years to compare. Goats were at their heaviest in the study period at the end of the 2008 wet season, but were lightest in the subsequent 2009 dry season, which was also the most severe dry season (figure 4.11). However, the ranking of dry season mass in 2007 and 2008 was the same as the ranking of conditions in the preceding wet seasons. A beneficial carryover effect of better mass gain in the plant growth season on condition and hence survival in the subsequent period of plant dormancy has been shown in caribou (Crete & Huot 1993) and elk



Figure 7.1. Rooilepel, the wet season range, in the dry season.

(Cook *et al.* 2004). However, based on the short series of years in this study period, it would seem that the carryover effect of mass from the wet season to the dry season is slight, and would confer a negligible benefit to individuals in a severe dry season.

The evidence for coupling of the goat population with the wet season forage resource is much less convincing than for the more intensively studied dry season range. The extent of mass gain did not match wet season quality, and the evidence for carryover effects was similarly limited. The most important role of the wet season would thus seem to be to end the dry season, as the dry season has the dominant influence over the RNP goat population.

Survival

Survival rates were lower when goats were under greater nutritional stress, which strongly emphasises the importance of the dry season to population dynamics. Food limitation in the dry season has been directly linked to mortality in white-eared kob (Fryxell 1987) and wildebeest (Mduma *et al.* 1999), but has been suggested to be

important in many other studies (e.g. Dunham 1994, Georgiadis *et al.* 2003, Knoop & Owen-Smith 2006, Gaidet & Gaillard 2008). Adult goat survival to the end of the dry season was directly related to change in body condition over the mid-dry season. Although density effects on adult survival were not detected, they should theoretically exist because mass loss was density-dependent. The detection of density-dependence in adult survival is uncommon in large mammal studies, and should ideally take the age-structure of the population into account (Festa-Bianchet *et al.* 2003). Survival over the dry season, as would be predicted by Illius & O'Connor (1999), is potentially the key factor driving the RNP goat population, and work is required to test this further.

Fecundity

Recruitment rates also seem to be strongly influenced by conditions in the dry season. Gestation occurs mainly over the dry season which, based on the time lag of the density effect on pregnancy rate (0 - 2 months) and birth rate (0 - 3 months), suggests that conditions in the dry season are important to the overall fecundity rate. Density was considered to be a reasonable proxy for nutritional stress due to the demonstrated density-dependent link between mass and the dry season forage resource.

Pregnancy rates were highest in the year with mid-dry season rainfall, rather than the year with the shorter dry season. Forage regrowth following this mid-season rainfall event is likely to have coincided with the period of peak rate of foetal growth, and thus resulted in more pregnancies coming to term, particularly in first-time breeders (e.g. Clutton-Brock *et al.* 1997, Keech *et al.* 2000, Johnstone-Yellin *et al.* 2009, Wilson *et al.* 2009). Conditions during pregnancy have been shown to be important for the mass at birth and subsequent survival of offspring in a number of species, including roe deer (Gaillard *et al.* 1997), bighorn sheep (Festa-Bianchet *et al.* 1998) and mountain goats (Hamel *et al.* 2010). The sensitivity of pregnancy and birth rates to dry season conditions thus would appear to be an important factor determining recruitment in each year.

Neonate survival rates did not differ between years in the RNP, which suggests that the adequacy of nutrition during lactation was generally sufficient (Landete-Castillejos *et al.* 2003, Therrien *et al.* 2008). Thus, dry season conditions would appear to determine the number and probably the mass of offspring born in each year

(e.g. Hamel *et al.* 2010), but their chance of survival is little affected by conditions in a particular year (wet season adequacy). This pattern has been observed in roe deer, where fawns are able to compensate for a poor start to life by the adequacy of nutrition during the plant growth season (Pelliccioni *et al.* 2004, Toigo *et al.* 2006). However, survival over the subsequent plant-dormancy season is body condition-dependent (Gaillard *et al.* 1993). Further analysis of the marked goat data is required to assess this effect in the RNP.

Neonate survival rates showed little response to environmental factors, but were higher closer to the river, possibly due to the availability of shade in the heat of the day. The inclusion of the Kuboes data allowed for a seasonal effect on neonate survival rates to be detected, with higher survival rates in the wet season. Although it is not possible to assess the absolute adequacy of nutrition for lactation, it would seem clear that forage reserves are far superior in the wet season, as would be expected. The conditions both pre- and post-partum are likely to be important determining recruitment in the RNP, as has been demonstrated in many other species e.g. Soay sheep (Forchhammer *et al.* 2001), bighorn sheep (Portier *et al.* 1998) and roe deer (Gaillard *et al.* 1997). However, the evidence from this study suggests that conditions during pregnancy, i.e. mainly the dry season, have a greater effect on recruitment.

Key factor

The balance of evidence suggests that coupling between goats and their forage resource is closest in the dry season (figure 7.2). During the dry season, goat body condition is sensitive to variation in the condition of the forage resource, and has definite consequences for both survival and fecundity. Further work is required to identify which of these parameters would strictly be considered to be the key factor (e.g. Coulson *et al.* 2005). Mduma *et al.* (1999) found neonate survival and dry season calf mortality to both be important factors shaping blue wildebeest population dynamics in the Serengeti, but conclude that adult survival is the most important parameter determining population size. It is possible that the key factor determining population growth rate could also change over time. This has been shown for red deer, where recruitment parameters were most influential during periods of population expansion, but adult survival over the plant dormancy season was more important during stable phases in the population trajectory (Albon *et al.* 2000). Gaillard *et al.*



Figure 7.2. *Aloe dichotoma*, or kokerboom, in the Richtersveld National Park.

(2000) suggest that the relatively lower effect of recruitment parameters on large herbivore population growth rates may be compensated for by higher inter-annual variability in these rates. Thus, although perturbations of adult survival rates may have a greater effect on population trajectories, they occur too infrequently to dominate the population growth signal.

Survival and fecundity are both likely to be important in the RNP, but which of these should be considered the key factor is beyond the scope of this study. The availability of both a 15 year census record and three years of vital rate estimates from the marked individuals provides an ideal opportunity for further analyses in this regard, e.g. using the retrospective matrix method (Coulson *et al.* 2005). However, despite not being able to isolate the key factor in this study, it is clear that both survival and fecundity rates are linked to the dry season forage resource. The RNP goat population thus provides another example of an African herbivore population that conforms to the food limitation hypothesis (Sinclair 1975). The conclusion drawn from this study is that the riparian forage resource forms the key resource in the RNP. However, the effect of this key resource is not limited to determining the size of the

key factor of the RNP goat population, as it also exerts a significant influence on other vital rates of the population.

Study site comparisons

The comparison between the RNP and the adjacent Kuboes rangeland was based on the idea that, lacking access to the Orange River, there must be more limited dry season resources in Kuboes. Similarly, the Paulshoek rangeland also lacks an obvious large dry season resource, although it has a considerably higher rainfall than the RNP and Kuboes. The RNP was thus predicted to have a relatively higher and more stable livestock population than either of these rangelands, if the positive effect of higher rainfall on herbivore biomass was accounted for in Paulshoek (Coe *et al.* 1976, Fritz & Duncan 1994). There was some evidence to support this prediction in both comparisons, but both sets of results are provisional on a number of assumptions regarding the demography of each population. The analyses are thus considered to provide a first assessment of how an understanding of a region's key resource could be used to understand its plant-herbivore dynamics.

One lesson from these analyses is how the dynamical definition of the key resource complicates the process of identifying it. Resources that are critical in a severe year may be less heavily utilised in a moderate year, thus obscuring their importance. In order to identify the key resource, the scale of enquiry needs to be taken into account. For example, in the RNP, migration to the riparian zone represents a regional scale decision, but choosing where to be based within the riparian zone and which species to eat both represent finer scales of selection within the ecological hierarchy (e.g. Senft *et al.* 1987). Identifying the riparian zone as the RNP key resource thus represents a regional to landscape scale of enquiry, which is facilitated by it being highly spatially concentrated. However, within the riparian zone, a species which was not heavily utilised during the study period e.g. *Tamarix usenoides*, may become more important if it is all that remains in a severe drought.

Identifying the key resource in Kuboes and Paulshoek is complicated by its diffuse nature, which may mean that regional or landscape scale decisions are less useful in identifying it. There is undoubtedly a seasonal difference in the forage resource that is used in these two regions (pers. obs.; Samuels *et al.* 2007), but if seasonal ranges overlap to a large degree, then a detailed knowledge of diet selection

and grazing preferences may be required to identify the key resource at a useful scale. The fine-scale impacts of grazing have been the focus of much research in Paulshoek (e.g. Todd & Hoffman 1999, Riginos & Hoffman 2003, Todd 2006, Anderson & Hoffman 2007, Richardson *et al.* 2007), which provides a good base for future work to integrate this knowledge into identifying the areas and species which are critical in this landscape. By focussing attention on this subset of resources, a key resource-based understanding of system dynamics should emerge. Given the wealth of livestock population data in Paulshoek, there is thus an excellent opportunity for future collaboration to more thoroughly compare how the respective key resources shape livestock dynamics in the RNP and Paulshoek.

Beyond Namaqualand

The idea of bottom-up food limitation through a key resource is implicit in much of the herbivore population dynamics literature. However, the explicit recognition that herbivore dynamics are primarily linked to only a subset of their forage resources should allow for further benefit to be derived from previous studies, by re-examining their findings. A good example of this is the frequently detected correlations between rainfall and different populations in African multi-species herbivore assemblages e.g. in the Kruger National Park (Ogutu & Owen-Smith 2005, Owen-Smith *et al.* 2005) and in the Mara-Serengeti ecosystem (Ogutu *et al.* 2008). Predation is an important component of these systems, but understanding the bottom-up effects of rainfall on the forage resource cannot be ignored. The objective here is not to review the findings of these studies, but rather to suggest that the best-fit correlation between a specific rainfall time-lag and the survival rates of a particular species should now be taken a step further. If late wet season rainfall is found to be important, is that because it is improving the dry season forage resource, or does it perhaps shorten the dry season? Are browsers and grazers similarly affected by rainfall? Does a potentially larger and more stable key resource explain the high abundance of impala, which is a mixed-feeder, in the Kruger National Park? The dietary constraints of a herbivorous species determine what part of the plant community can be considered to be the forage resource. Thus, by assessing the effect of e.g. late wet season rainfall, on that component of the plant community, a mechanistic understanding of population dynamics could be approached, rather than a correlative understanding. This would

also assist in understanding predation in these systems, which is perceived to respond to the body condition of prey species (Owen-Smith 2008).

The work by Coe *et al.* (1976) and Fritz & Duncan (1994), which considers the effect of rainfall and nutrient status of a region on the herbivore biomass it could support, could similarly be extended. Re-classifying each system included in the original regressions, by considering its landscape structure, would be expected to reveal continent wide-trends in the effect of key resources. For any given combination of rainfall and soil nutrient availability, a higher herbivore biomass will be sustained in the presence of a larger and/or more stable key resource (e.g. RNP vs. Kuboes in this study). Once again, attempting to capture more directly the mechanistic link between herbivores and abiotic parameters of the environment should improve the accuracy of our ability to predict the herbivore population dynamics in a system.

Conservation

Herbivores in most 'wild' ecosystems are spatially constrained - either directly by fences, or through conflicts in landscape use (e.g. Ben-Shahar 1993, Ogotu *et al.* 2010, Shrader *et al.* 2010). Regulating the abundance and distribution of herbivore populations within these landscapes has become an important objective for managers, who need to prioritise the conservation of biodiversity in general and threatened species more particularly. Water is a useful tool for manipulating herbivore populations (e.g. Gaylard *et al.* 2003, Smit *et al.* 2007, Chamaille-Jammes *et al.* 2007), but the mechanisms that make it a useful tool are not always explicitly recognised. In water-limited systems, the provision of additional drinking water can allow herbivores to access greater forage resources in the dry season (Redfern *et al.* 2003), thus increasing the size of the key resource. However, not all species respond equally to the provision of artificial water, with the distributions of grazer species being found to be influenced by artificial water points, but not browsers (Smit *et al.* 2007).

The provision of artificial water points in the northern Kruger National Park led to an increase in the local plains-game populations, with a concomitant increase in the predator population. This influx of predators, as well as increased competition for forage resources, are both predicted to have caused the sharp decline in the numbers of roan antelope in this region, a localised and high conservation priority species (Harrington *et al.* 1999). A better understanding of the foraging ecology of this

species, as well as the consequences of manipulating the key resource of other species, may have allowed these consequences to have been better anticipated (e.g. Knoop & Owen-Smith 2006). Similarly, a better understanding of the effect of essentially homogenising the accessibility of the landscape, through the provision of artificial water points, would have ameliorated the impacts of the drought described by Walker *et al.* (1987). In particular, the heavy impact on the forage resource across the entire landscape might have been avoided if: a) parts of the landscape were inaccessible, and b) population sizes were smaller prior to the drought.

Pastoral systems

A primary objective of rangeland scientists is to stabilise the household economies of pastoralists in developing nations, to enable them to cope with the uncertainty of the environment (e.g. Behnke *et al.* 1993). Various approaches to dealing with high environmental variability have been suggested, including opportunistic stocking regimes through judicious timing of livestock sales and purchases (e.g. Illius *et al.* 1998, Campbell *et al.* 2000), supplementary feeding during droughts (Vetter 2005) and mobility patterns that allow for underutilised forage reserves to be accessed during droughts (e.g. Butt *et al.* 2009). These strategies and others will likely have been met with varying success, in response to both the series of climatic events and the landscape structure of the systems under which they might have been assessed. While we can't change the weather, a sound understanding of how these variables impact herbivore population dynamics is important for deciding what we can in fact do. A better appreciation of the role of key resources in stochastic pastoral systems should allow for the identification of situations where system instability is due to poor management, but also situations where instability is inevitable. Understanding the ecology of these systems is critical to the formation of management policies in both these situations (figure 7.3).

Perspective

Much of what we know about long-term herbivore population dynamics is based on temperate northern hemisphere studies. The physiology of large herbivores in tropical African systems is unlikely to differ substantially, and these studies are thus relevant to



Figure 7.3. Pastoralism in an arid and variable environment: an RNP stockpost

understanding plant-herbivore dynamics in these systems. It is of interest though that the idea of a herbivore population being wholly uncoupled from its resource would originate in an African study system (Ellis & Swift 1988). The characteristics of the plant growth season may be important in explaining this. The seasonal distinction in temperate systems, where many of the long-term studies have been carried out, is largely based on temperature (referred to as summer and winter). However, in a general African context, the distinction is based on water availability (referred to as wet season and dry season). These generalisations are likely to have been formulated based on the important abiotic factors that limit plant growth in the respective systems. In temperate systems, the plant growth season (summer) is a consequence of the reliable trajectory of the earth around the sun, with a slight tilt. Waiting for the wet season can be much less predictable: the appropriate time of the year may have arrived, but the rains may not. The potential impacts of a failed plant growth season on plant-herbivore dynamics are immense, and the greater potential for this in a semi-arid African landscapes, may partly account for the role of key resources having been recognised in this context (e.g. Scoones 1995, Illius & O'Connor 1999).

Conclusion

For every herbivore population, by definition, a key resource must exist. The strength of the idea is that it demands that the mechanistic relationship between herbivores and their forage resource is addressed. Identification of the key resource of a herbivore population allows for the impact of perturbations to the system to be assessed, both through their direct effects on individuals, and through their impacts via the key resource. The key resource thus provides a valuable basis for understanding herbivore population dynamics in a variable world.

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