Foal Survival and Resource Ecology of Lactating Grevy's Zebra (*Equus grevyi*) Females

Elizabeth Tupper

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ABSTRACT

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In this thesis, I first investigate factors affecting survival of Grevy's zebra (*Equus grevyi*) foals and then analyze the landscape use patterns of lactating females and their foals as they pertain to resource availability during the dry season. Monitoring population vital rates of endangered species is essential for understanding population dynamics and designing appropriate conservation strategies. For the endangered Grevy's zebra, low foal survival has been implicated as a major factor driving population declines. This study employed cheap, non-invasive sight-resight methodology to regularly survey Grevy's zebra foals at a wildlife conservancy in central Kenya. Using Program MARK, I then created models to investigate how survival changes as foals age, as well as how it is impacted by rainfall and resource availability. Foal survival to 1 year is less than 30%, with lowest survival rates within the first three months after birth and also around weaning. Even in this arid-adapted equid, rainfall appears to influence foal survival through its relationship with resource availability, while general trends suggest that predation is less important in driving patterns of foal survival. Although estimates of foal survival were lower than those reported in any previous study on equid populations, its impact on population size relative to other demographic parameters remains unknown.

The dry season is a critical period for African ungulate survival, as resources decrease substantially in quantity and quality. For hindgut fermenting grazers such as zebra, grass quantity is typically considered more important than quality in determining foraging decisions and resulting spatial patterns of grazing. However, differences in forage quality may be important for late gestation and early lactation females due to their higher energetic and nutritional demands. In this study, I used monthly survey data to identify areas frequently used by lactating female Grevy’s zebra and their foals during multiple dry seasons. I then collected grass in these and control areas to determine if landscape use patterns are driven by spatial variation in grass nutrient content. The results of this study support the hypothesis that lactating Grevy’s zebra selectively forage in areas of high grass quality during the dry season. Levels of potassium (K), sodium (Na), phosphorus (P), and crude protein (related to percent nitrogen), as well as the ratio of calcium to phosphorus (Ca:P) appear to be particularly important in influencing landscape use patterns of lactating zebras during the dry season.

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CHAPTER 1:
General introduction to Grevy's zebra (*Equus grevyi)* ecology and the Lewa Wildlife Conservancy population

Introduction

The endangered Grevy's zebra (*Equus grevyi*) is the largest wild member of the *Equidae* family. Although once found in five East African countries, this species is now restricted to central-northern Kenya and a few small, isolated regions in Ethiopia (Figure 1.1). Grevy's zebra, like many endangered large mammals, are found at relatively low densities over large areas, making accurate population monitoring challenging (Moehlman et al. 2008; Parker et al. 2010). The current global population is estimated to have between 2,000 and 2,500 individuals, following a decline from about 15,000 individuals in the late 1970s (Moehlman et al. 2008). The majority of this population is now concentrated toward the southern end of the species' range in the Samburu and Laikipia Districts of Kenya (Williams 2002).

Grevy's zebra biology

Grevy's zebra are typically found in arid and semi-arid grass and shrubland habitats with permanent water sources (Klingel 1974; Williams 2002) and have many physiological and social adaptations to living in arid environments (Rubenstein 1989; Becker and Ginsberg 1990). Like many other ungulates, they exhibit slight sexual size dimorphism, with females weighing about 385 kg and males about 430 kg (Kingdon 1997). Grevy's zebra are hind-gut fermenters and considered bulk grazers, although they have been found to consume browse (up to 30% of their diet) under stressful environmental conditions such as drought (Ginsberg 1987) and in areas suffering from overgrazing (Moehlman et al. 2008). Adult males and non-lactating females may go two to five days without drinking, but lactating females can only tolerate one to two days without water (Becker and Ginsberg 1990; Rowen 1992).

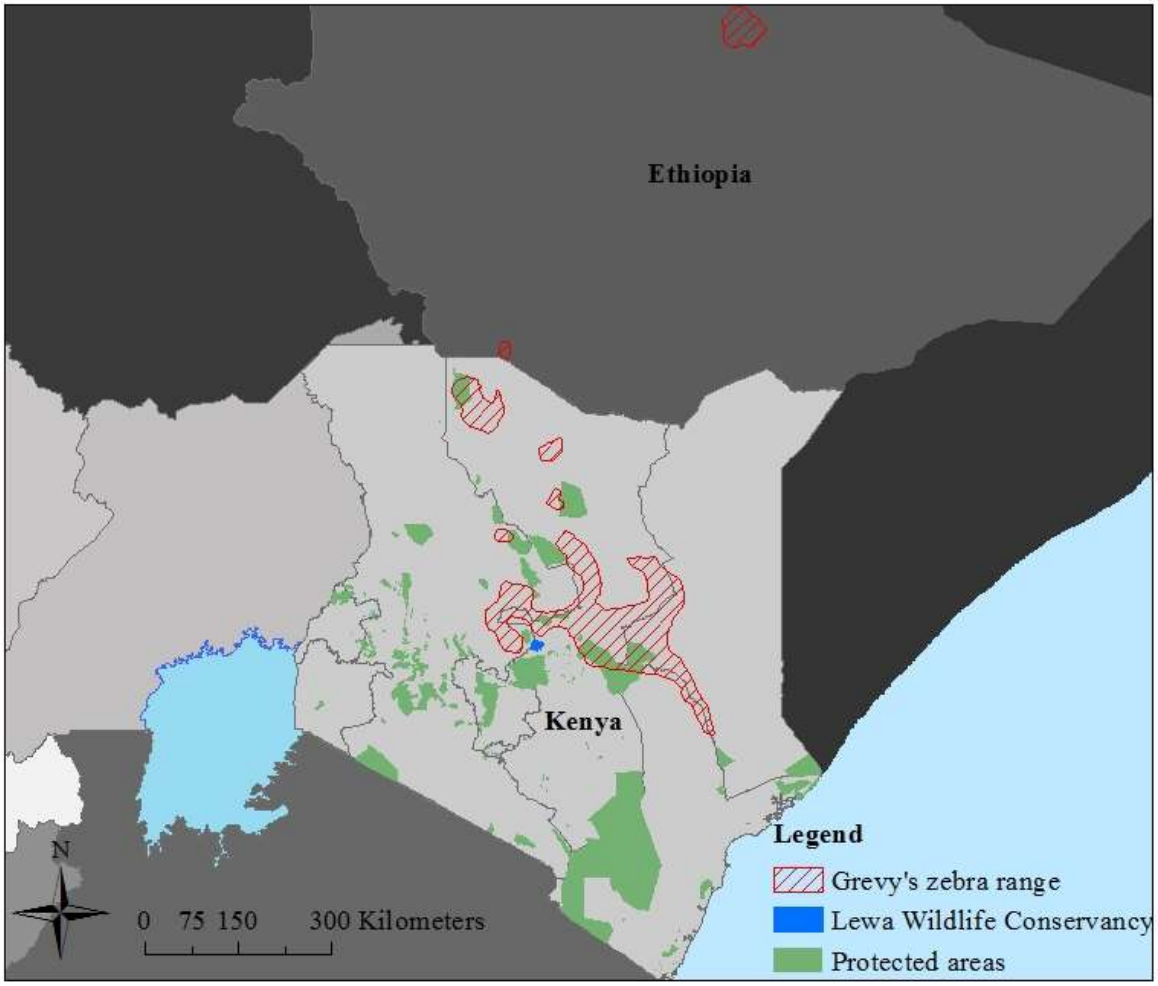

Figure 1.1. Map showing the current range of Grevy's zebra (*Equus grevyi*) in East Africa. Data on range was downloaded from the International Union for Conservation of Nature and Natural Resources (IUCN, www.iucnredlist.org/technical-documents/spatial-data). Data on protected areas in Kenya was downloaded from the World Database on Protected Areas (WDPA, www.wdpa.org)

Breeding males are solitary and defend territories of 2 to 12 km^2 (Klingel 1974; Ginsberg 1989). These males exhibit resource defense polygyny, attracting females based on the water and food resources found within their territories (Rubenstein 1986; Ginsberg 1989). Lactating females form relatively stable groups, while bachelor males and non-lactating females form less stable groups characterized by temporary associations (Rubenstein 1986; Ginsberg 1989; Sundaresan et al. 2007a). These fission-fusion groups average between 3 and 10 individuals (Nelson and Williams 2003) and generally include individuals of the same reproductive class (Klingel 1974; Rubenstein 1986).

The stable groups formed by lactating females typically consist of three to four pairs of females and their foals (Rubenstein 1986; Ginsberg 1989). Compared to non-lactating females, these groups move less frequently and congregate closer to water sources (Rubenstein 1986; Ginsberg 1989; Sundaresan et al. 2007b). Becker and Ginsberg (1990) report that lactating females with young foals (<3 months old) generally remain on male territories within 2 km of a water source in protected areas, whereas other females will move up to 15 km away in order to find better grazing areas. Outside of protected areas where livestock are often congregated adjacent to water sources, however, lactating females may move up to 13 km from water to find acceptable forage (Nelson and Williams 2003).

Males become reproductively mature around 3 years of age, but do not establish territories until they are 6-7 years old (Rowen and Williams 2000). Females, on the other hand, become reproductively mature around 3.5 years old. Condition-dependent estrus causes breeding to be dependent on rainfall patterns (Williams 1998) and can result in anoestrus during periods of low resource availability following drought (Ginsberg 1987). Peak birthing periods in this species have been suggested to follow rainy/dry season cycles (Rowen and Williams 2000), but the highly variable rainfall patterns of their environments causes a lack of specific, consistent birthing season (Figure 1.2). Gestation lasts about 13.5 months (387-428 days), after which females give birth to a single foal (Ginsberg 1989; Iaderosa 1983). The period of peak lactation in females lasts for about 3 months after a foal's birth, and is followed by a mid-lactation period during which foals rely less on milk and begin to drink water (Ginsberg 1989). Foals begin weaning at around 6 months, are completely weaned by 11.5 months, and are considered independent after about 12 months (Ginsberg 1989; Rowen 1992).

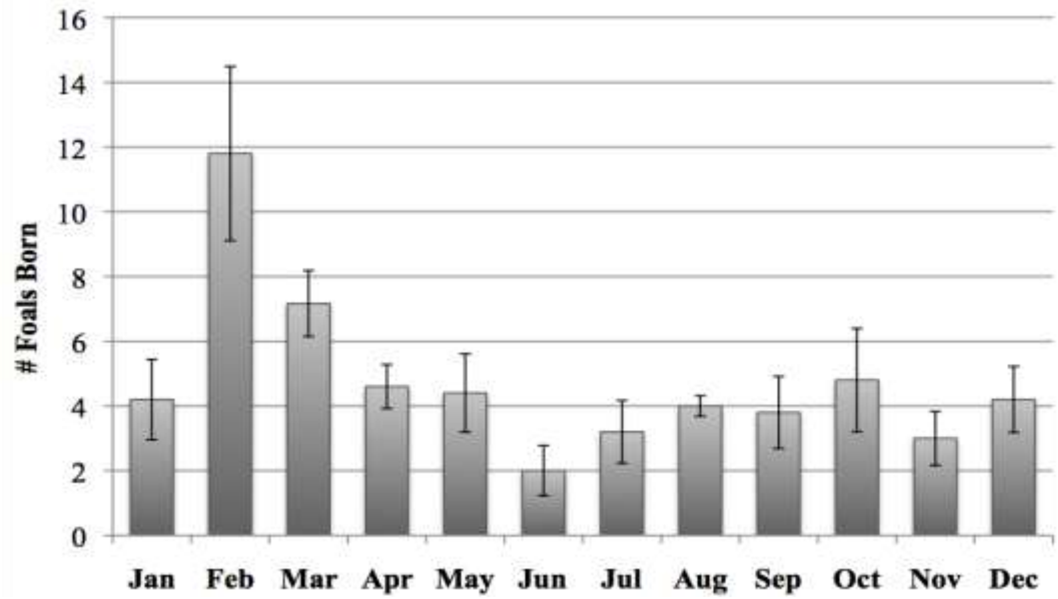

Figure 1.2. Mean number of Grevy's zebra births per month for the 5-year period between 1/2003 and 12/2007 at the Lewa Wildlife Conservancy. Bars represent ± 1 standard error. Note that birth months were estimated based on records for each foal identified in monthly surveys (see Chapter 2 for details about survey methodology).

Other basic biological and demographic characteristics remain unknown for this species, highlighting the need for continued research. Reliable information on age-specific survival, fecundity, and interbirth intervals is lacking, which makes accurately modeling population dynamics and projecting population growth rates difficult. Grevy's zebra exist throughout areas that are heterogeneous in land cover and use type, and therefore may show important differences in demography and dynamics between populations (Williams 1998, 2002). Adding to the need for additional research, therefore, is the fact that the majority of information presented here was collected from a single well-studied population that has largely dissipated since the most recent study (Nelson and Williams 2003; SR Sundaresan, personal communication).

Threats to Grevy's zebra

The Grevy's zebra was first classified as endangered by the IUCN in 1986, a status which has not changed (Moehlman et al. 2008), and has been listed in Appendix I of CITES since 1979. Historically, Grevy's zebra were hunted extensively for their skins (Rowen and Williams 2000). Following a hunting ban imposed by the Kenyan government beginning in 1977 and the CITES listing in 1979, rates of hunting for skin export declined dramatically. Since then, hunting Grevy's zebra for meat and medicinal purposes has become a greater threat (KWS 2008). Grevy's zebra are also facing population fragmentation and isolation, which may increase vulnerability to stochastic events such as drought (Rowen and Williams 2000). Various diseases have been a threat to Grevy's zebra, especially where livestock are abundant and during periods of drought (KWS 2008). Between December 2005 and March 2006, there was an anthrax outbreak in southern Samburu District that killed at least 53 individuals and led to a massive effort to vaccinate nearby populations (Muoria et al 2007).

Other threats to Grevy’s zebra today involve reduced access to water and quality grazing areas. Upstream water extraction for irrigation has led to lower water availability for Grevy’s zebra throughout much of their remaining range. This threat is especially dire for the Ewaso Ng’iro River, which supplies water to the core remaining habitat of Grevy’s zebra in Kenya, including the Lewa Wildlife Conservancy (KWS 2008). Additionally, Grevy’s zebra coexist with pastoralists and livestock throughout the majority of their current range, resulting in increased competition for resources (Williams 1998, 2002; KWS 2008). This competition has caused changes in Grevy’s zebra behavior and poses significant threats, especially during the dry season when resources are scarce. For instance, Williams (1998) found that Grevy’s zebra drank at night rather than during the day in non-reserve areas where livestock grazing occurred, leaving adults and their foals at greater risk of predation.

Conservation Initiatives

There have been numerous conservation efforts initiated throughout Ethiopia and Kenya that focus on the Grevy’s zebra. Organizations such as the Grevy’s Zebra Trust and Northern Rangelands Trust focus on community involvement in conservation and several private conservancies and ranches contribute to research and protection of the species. Together, with members of the African Wildlife Foundation and Kenya Wildlife Service, members of these institutions formed the Grevy’s Zebra Task Force in 2004 with the goal of coordinating conservation efforts. This task force compiled a “Conservation and Management Strategy” for the species that includes nine strategic objectives focused on mitigating threats to Grevy's zebra and engaging with communities to ensure sustainable conservation strategies.

The Lewa Wildlife Conservancy's Grevy's zebra population

Despite undergoing a substantial range reduction, the Grevy's zebra has extended its range southward in Kenya and now inhabits the Laikipia Plateau and nearby Lewa Wildlife Conservancy (Williams 2002, Figure 1.1). The Lewa Wildlife Conservancy (LWC) is a 209 km^2 private reserve in central Kenya (center point: 0°06'N, 37°21'E) that consists primarily of open grassland, bushed grassland with *Acacia*-dominated woody vegetation, and riverine woodland. The conservancy sits at the southern edge of the current Grevy's zebra range in central Kenya (see Figure 1.1). The Grevy's zebra is one of LWC's two flagship conservation species, the other being the black rhino (*Diceros bicornis*), and managers hope to be able to help re-stock parts of the zebra's former range with individuals from the conservancy's population.

As in all semi-arid savannas, ecology at LWC is heavily influenced by rainfall patterns. Average annual rainfall on LWC was about 500 mm between 2002 and 2009 (Figure 1.3), although this ranged substantially from 286 mm in 2005 to 769 mm 2006. Rain falls primarily during two periods (Mar-Apr, Oct-Dec) which are separated by a long dry season lasting about 4.5 months. Actual rainfall is often irregular in time and distribution with low predictability. It is not uncommon for the conservancy to receive no rain at all during the months of the long dry season (mid May-Sep). When it does rain during this period, rainfall is often light and locally distributed in just a small area of the conservancy.

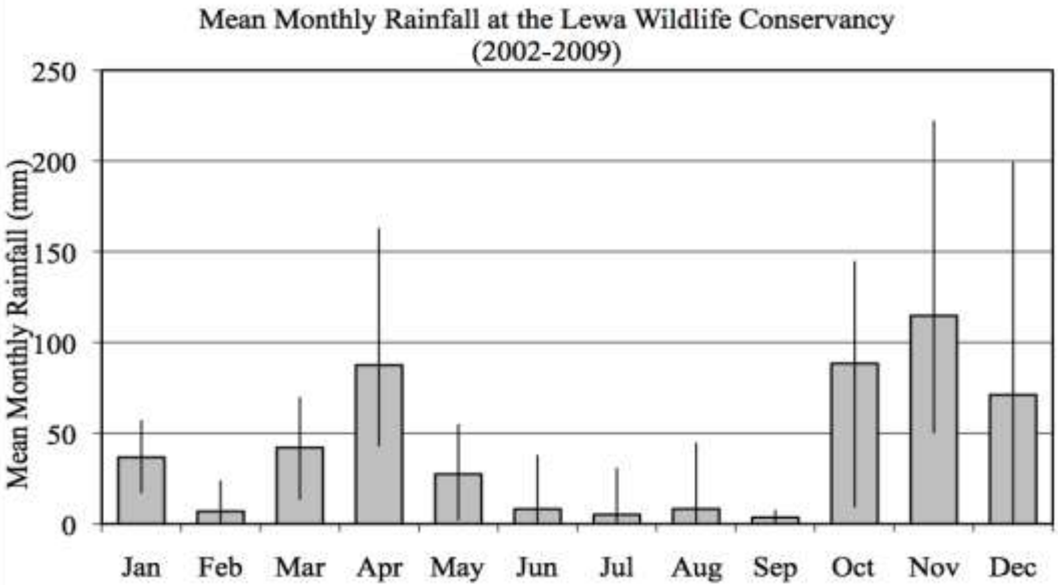

Figure 1.3. Mean monthly rainfall at the Lewa Wildlife Conservancy (2002-2009). Bars indicate the minimum and maximum monthly rainfall during this period. Average annual rainfall for this period was 499 mm, ranging from 286 mm in 2005 to 769 mm in 2006.

Historically a marginal area for Grevy's zebra, there are currently about 350 individual Grevy's zebra inhabiting LWC, comprising about 15-20% of the global population. LWC is considered a critical conservation area for this species for several reasons (Williams 2002). First, LWC allows almost no domestic grazing within its borders, so competition with livestock is practically nonexistent. Second, the conservancy has reliable water sources, even during the long dry season (Figure 1.4). Third, the Grevy's zebra is a top conservation priority for LWC, and its staff and donors are devoted to studying and protecting the population. The Lewa Wildlife Conservancy therefore provides critical breeding habitat and represents a core conservation region that is crucial for the long-term survival of the species (Nelson and Williams 2003; KWS 2008).

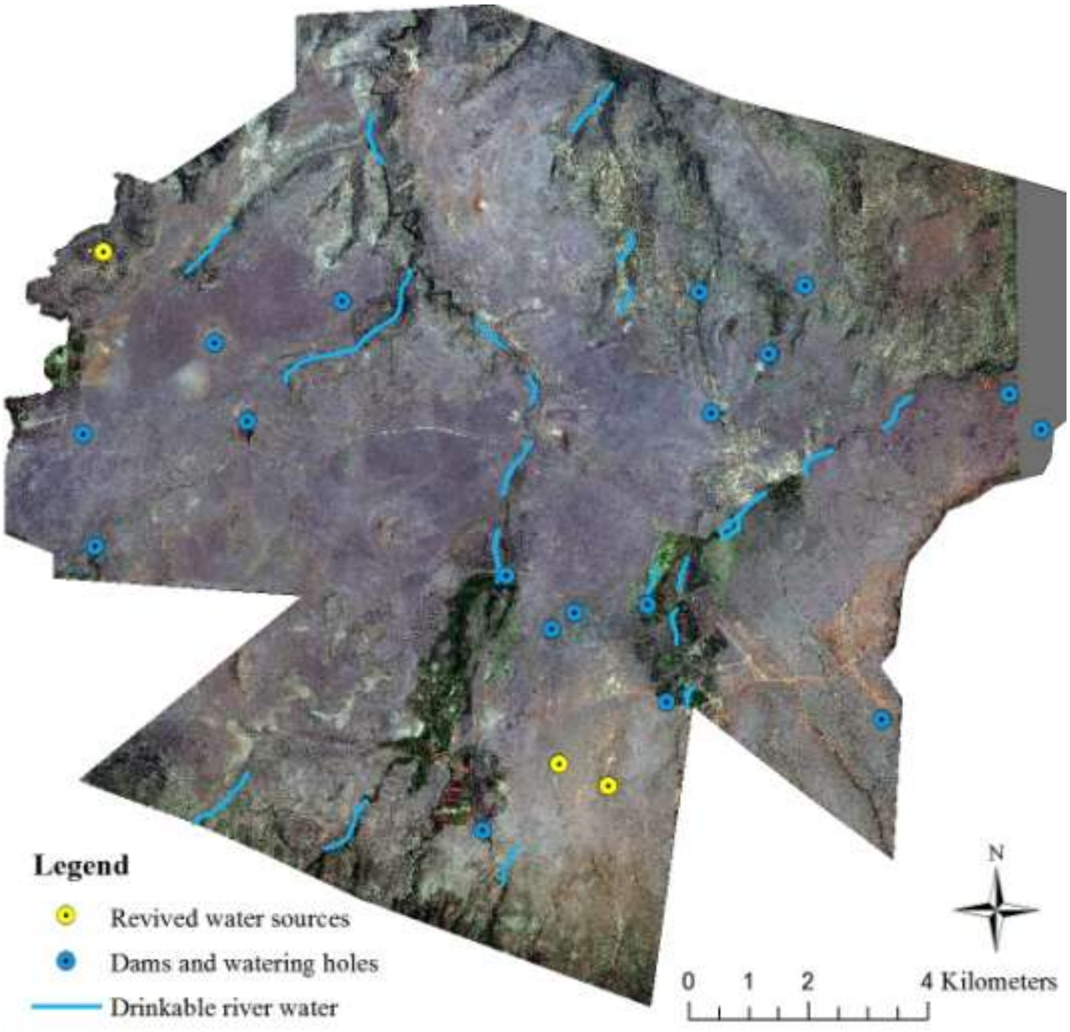

Figure 1.4. Map showing the distribution of drinkable water sources for Grevy's zebra during the dry season, including three dams that were revived in 2009. See methods section of Chapter 3 for definition and identification of drinkable water sources.

Although the Lewa Wildlife Conservancy remains an important region for Grevy's zebra and currently supports one of the largest subpopulations, its Grevy's zebra numbers have decreased substantially in the past ten years. Since 2001, when the number of Grevy's zebra peaked at 556 individuals, the population has undergone a reduction in size of almost 40% (Figure 1.5). Although its causes are uncertain, several hypotheses have been proposed to explain this population decline. First, plains zebra (*Equus quagga*, formerly *Equus burchelli*) occur in high numbers on the conservancy. With similar diets and body size, they are likely an important source of interspecific competition for Grevy's zebra and have been shown to be competitively dominant over Grevy's zebra (Rubenstein 2010). As an arid-adapted species, the Grevy's zebra is less restricted by water needs than most other resident grazing species. Perhaps paradoxically, the abundance and recent addition of permanent water sources at LWC in 2009 may benefit plains zebra and other species at the expense of Grevy's zebra by further increasing interspecific competition. The conservancy's plains zebra population has grown relatively rapidly in the past few years, while the Grevy's zebra population has declined, and interspecific competition may be a substantial impediment to increasing or even maintaining Grevy's zebra numbers in the region (Rubenstein 2010; see Figure 1.5).

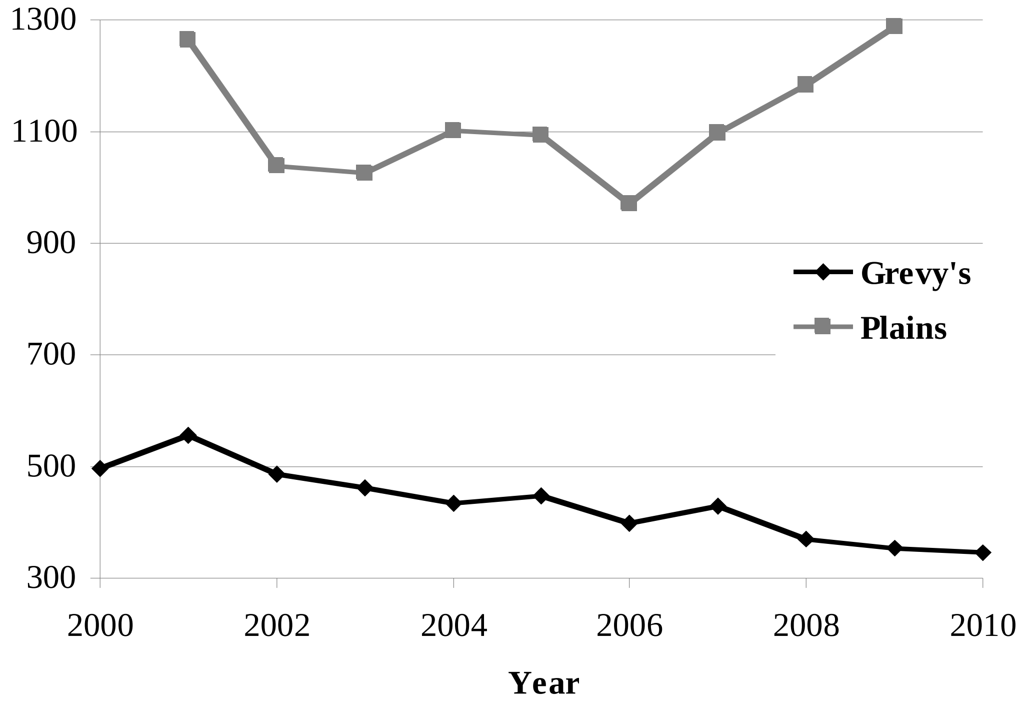

Figure 1.5. Yearly population estimates of Grevy's zebra (*Equus grevyi*) and plains zebra (*Equus quagga*) at the Lewa Wildlife Conservancy. Estimates were derived from ground and aerial counts conducted at the beginning of each year (Jan-Mar).

Another possible factor contributing to the decline of LWC's Grevy's zebra population is predation. There are currently 20 lions (*Panthera leo*) on Lewa (10 per 100 km^2), although the number of lions has varied substantially since they first appeared in the region in 1999 (Figure 1.6). Grevy's zebra are the preferred prey of lions on Lewa (Rubenstein 2010), and predation is typically considered the major threat to Grevy's zebra on the conservancy (KWS 2008). Evidence suggests that adding artificial water sources may attract lions by increasing overall prey biomass, leading to devastating impacts on preferred prey species (Harrington et al. 1999). Thus, the installation of new water sources on Lewa may potentially increase predation risk for Grevy's zebra in addition to potentially increasing interspecific competition.

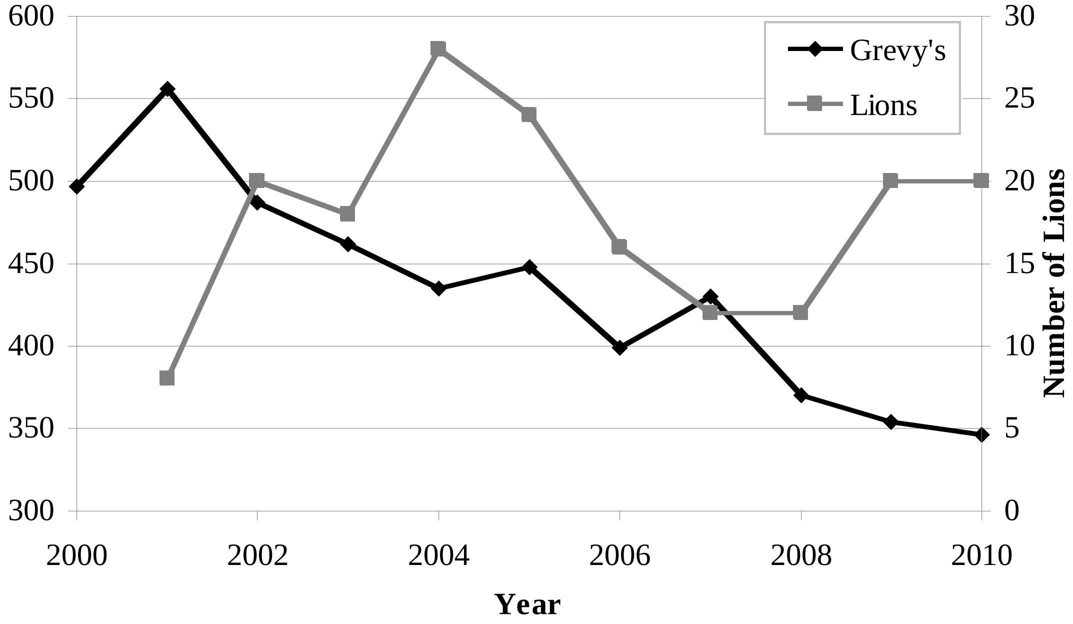

Figure 1.6. Number of individual Grevy's zebra (*Equus grevyi*) and lions *(Panthera leo*) recorded on the Lewa Wildlife conservancy durring annual census counts.

Thesis overview

In this thesis project, I first investigate factors affecting Grevy's zebra foal survival, a demographic parameter that has been implicated as a major factor driving population declines in this species. Specifically, I examine rates of foal survival in relation to foal age and resource availability and explore the potential role of predation in driving survival patterns. I then investigate the landscape use of lactating females and their foals as it pertains to resource availability during the dry season. Throughout these chapters, potential conservation implications are discussed, and recommendations made where appropriate.

CHAPTER 2:
Factors influencing Grevy's zebra (*Equus grevyi*) foal survival at the Lewa Wildlife Conservancy, Kenya

Abstract

Monitoring population vital rates of endangered species is essential for understanding population dynamics and designing appropriate conservation strategies that target the factors responsible for declines. Obtaining reliable estimates of these parameters may be difficult for large-bodied, wide-ranging species, and determining the influence of bottom-up and top-down processes on vital rates is particularly challenging. For the endangered Grevy's zebra (*Equus grevyi*), low foal survival has been implicated as a primary factor responsible for declining populations, yet there are no current efforts underway to monitor population vital rates. This study employed cheap, non-invasive sight-resight methodology to regularly survey foals at a wildlife conservancy in central Kenya. Using Program MARK, I then created models to investigate how survival changes as foals age, as well as how it is impacted by rainfall and resource availability. Foal survival to 1 year is less than 30%, with lowest survival rates within the first three months after birth and also around weaning. Even in this arid-adapted equid, rainfall influences foal survival through its relationship with resource availability. Although predator data were too sparse to include in the MARK models, general trends suggest that predation is less important than resource availability in driving patterns of foal survival. As estimates of foal survival were lower than those reported in any previous study on equid populations, it is likely a key factor contributing to population declines. However, its impact relative to other demographic parameters such as subadult and adult survival, as well as

fecundity, is unknown. Although this study serves as an important first step in understanding the population dynamics of this endangered species, future research should focus on determining other population vital rates to allow for more reliable population.

Introduction

Patterns of survival in large ungulates

Understanding the factors that influence the population dynamics of endangered species is essential for developing successful conservation strategies. Determining population vital rates, including survival and reproduction parameters, is particularly important as it allows us to target factors responsible for population declines (Morris and Doak 2002; Johnson et al. 2010). Large ungulates typically have consistently high adult survival rates (>0.90 until senescence) and lower, fluctuating juvenile survival rates (Linnell et al. 1995; Gaillard et al. 1998, 2000; Owen-Smith 1990, 2005). Although some authors argue that changes in adult survival rates will lead to proportionally greater changes in population sizes (Gaillard 1998, 2000; Eberhardt 2002), others argue that adult survival rates are usually so stable in ungulate populations that changes in juvenile survival rates are more likely the cause of population fluctuations (Owen-Smith and Mason 2005).

The dynamics of tropical ungulate populations are generally less well understood than those of temperate populations (Owen-Smith and Mason 2005), in part because tropical ecosystems have a higher number of predator and prey species and are consequently more complex (Mills and Shenk 1992; Owen-Smith 2005). In arid and semi-arid African savannas, general population trends suggest that large ungulate populations are regulated by bottom-up processes related to resource availability (Bell 1982; East 1984; Sinclair 1974; Sinclair et al. 1985; Owen-Smith 1990; Mills et al. 1995; Mduma et al. 1999; Illius and O'Connor 2000; Georgiadis et al. 2003; but see Sinclair 1979; Gasaway et al. 1996). Much of the variation in survival rates among young ungulates is attributed to climatic variation, which controls resource availability and impacts survival via direct and indirect pathways (Owen-Smith 1990; Pascual and Hilborn 1995; Mduma et al. 1999). For instance, mortality may increase directly though starvation or indirectly through the effects of poor maternal health on juvenile survival (Sinclair 1975; Fritz and Loison 2002; Owen-Smith 2005).

On the other hand, top-down processes such as predation and disease may also be important drivers of mortality. Predation pressure is often greater for young ungulates than adults (Linnell et al 1995; Fritz and Loison 2006; but see Mills and Shenk 1992; Grange et al. 2004), and may increase during periods of resource scarcity when poor health causes individuals to become more vulnerable (Mech 2007). However, in African savannas, predation may also increase during the resource-abundant wet season due to increases in vegetation that provide cover for stalking predators such as lions (Smuts 1978; van Orsdol 1984, Mills et al. 1995, Funston et al. 2001).

Considered together, the effects of bottom-up and top-down forces on survival and overall population dynamics are difficult to tease apart (Owen-Smith et al. 2005), and may vary substantially between species and populations. For instance, nonmigratory plains zebra (*Equus quagga*, formerly *E. burchelli*) in the Serengeti appear to be limited by predation (Sinclair 1979), whereas Laikipia zebra populations appear to be limited by resource availability (Georgiadis et al. 2003). The effects of these processes may also vary temporally in seasonal environments, in which both resource availability (McNaughton and Georgiadis 1986) and species-specific predation pressure (Owen-Smith 2008) have been shown to change significantly. Although complex, understanding how bottom-up and top-down processes act independently and interact to affect vital rates and population trajectories is important as it will ultimately allow us to devise more effective conservation strategies.

Determining vital rates in an endangered equid population

The population sizes of large endangered herbivores are often difficult to monitor (Parker et al. 2010), and accurately measuring demographic parameters within these populations can be even more challenging (Johnson et al. 2010). Because of this, past studies investigating the effects of environmental variables on African ungulate demographic parameters have used general census counts or count ratios (e.g. young:female) and typically consider only annual impacts over large time scales (Owen-Smith 2000; Durnham et al. 2003, 2004; Ogutu and Owen-Smith 2005; Ogutu et al. 2006, 2008, 2011). However, mark-recapture studies that repeatedly sample individually identifiable animals yield more reliable survival estimates than analyses of count ratios or age structures (Caughley 1974; Bonenfant et al. 2005) and are recommended for assessing the influence of environmental variables on populations (Lebreton et al. 1993; Grosbois et al. 2008). These mark-recapture studies typically involve capturing, marking, releasing, and then recapturing animals periodically through sampling events after the initial release (Jolly 1965; Seber 1965). Originally used to estimate population size, these methods have now been applied to measure a range of population parameters, including survival and recruitment (Cormack 1964; Pradel 1996)

To date, most work on equid population dynamics has focused on the abundant plains zebra, while little is known about population vital rates and dynamics of the endangered Grevy's zebra, a species which is undergoing population declines throughout much of its range (Moehlman et al. 2008). The information that is available comes from several studies (Klingel 1974; Rubenstein 1986; Ginsberg 1987, 1989; Rowen 1992; Williams 1998) focusing on a single population that has largely dissipated since the last detailed study took place over a decade ago (SR Sundaresan, personal communication). Critical information such as longevity, inter-birth intervals, and age-specific fecundity and survival is still unknown, even for this heavily studied population (Williams 2002), making it difficult to evaluate population health and accurately project population growth.

Low foal survival and subsequent recruitment rates have been hypothesized as a major factor perpetuating population declines in Grevy's zebra populations (Williams 2002), and targeting foal survivorship is one of the key strategies suggested for increasing Grevy's zebra numbers by the Grevy's Zebra Task Force (KWS 2008), a group formed in 2004 to coordinate conservation efforts for the species. Despite widespread action aimed at conserving Grevy's zebra across Kenya, however, there are no efforts currently underway that attempt to monitor their population vital rates. Most work involves building community support for Grevy's zebra conservation or monitoring the movements of collared individuals.

In this paper, I use repeated surveys of Grevy's zebra foals together with data on rainfall and lion abundance to estimate how bottom-up and top-down processes impact foal survival. This is the only project to my knowledge that attempts a rigorous survival estimation and then goes further to attempt to understand the mechanisms driving the observed patterns. This information can then be used to help guide conservation decisions aimed at increasing recruitment and maintaining population sizes (Cordingley et al. 2009; KWS 2008).

Methods

Study area

The Lewa Wildlife Conservancy (LWC) is a 209 km^2 private reserve in central Kenya (center point: 0°06'N, 37°21'E; Figure 1.1). It is completely fenced except for several gaps intended to allow for elephant movement. The landscape consists primarily of open grassland, bushed grassland with *Acacia*-dominated woody vegetation, and riverine woodland. Mean annual rainfall was about 500 mm between 2002 and 2009, ranging from 286 mm in 2005 to 769 mm in 2006 (see Figure 1.3).

Sight-resight foal surveys

This study uses a variation of mark-resight methodology (Cormack 1964; Arnason et al. 1991) to determine survival rates among foals. Mark-resight designs have the same advantages of traditional mark-recapture studies but are usually less field-intensive, less disruptive, and cheaper because individuals do not need to be physically captured for sampling (Minta and Mangel 1989; McClintock and White 2009). These advantages were greater in this case as initial marking was unnecessary because natural stripe patterns permit easy identification of individual animals.

Since February 2003, members of the LWC Research and Monitoring Department have conducted monthly “foal patrols” in which they drive a set route around the entire conservancy to survey for Grevy’s zebra foals. Because foals are not always easily visible from the road, the survey team also uses sighting information from LWC’s Security Department to increase the likelihood that a foal will be recorded on a given survey date. Each day, there are 24 security guards patrolling 12 blocks (each a few square kilometers) of the conservancy who are able to provide the survey team with additional information about foal locations. If the survey team does not see a foal from the road in a location where one was spotted by security, the team will drive off of the set path in order to locate and record the foal.

Once a foal is sighted, its location is recorded using a GPS device, and its age, sex, and total group size are noted. Age is estimated as 0-3 months, 3-6 months, 6-12 months, or >1 year (yearling) based on the individual’s body size and brown/black stripe pattern (following Rowen 1992). A photograph of each foal and its mother is then taken for later identification, which is achieved using the unique stripe pattern on the mother’s right rear thigh. This pattern is coded, yielding an identification label for each female (Figure 2.1). Foals were later assigned their own unique identification numbers based on survey histories in order to differentiate foals of the same female. This identification method has an accuracy rate of about 98% (Ginsberg 1987) and has been used successfully in many studies (e.g. Ginsberg 1989; Becker and Ginsberg 1990; Rowen 1992; Wisbey 1995; Williams 1998; Nelson and Williams 2003).

Rainfall

Between January 2002 and December 2004, rainfall data were collected at a single central location on the conservancy. In January 2005, 13 rain gauges were set up throughout the conservancy, and all future rainfall values are monthly averages from all gauges combined.

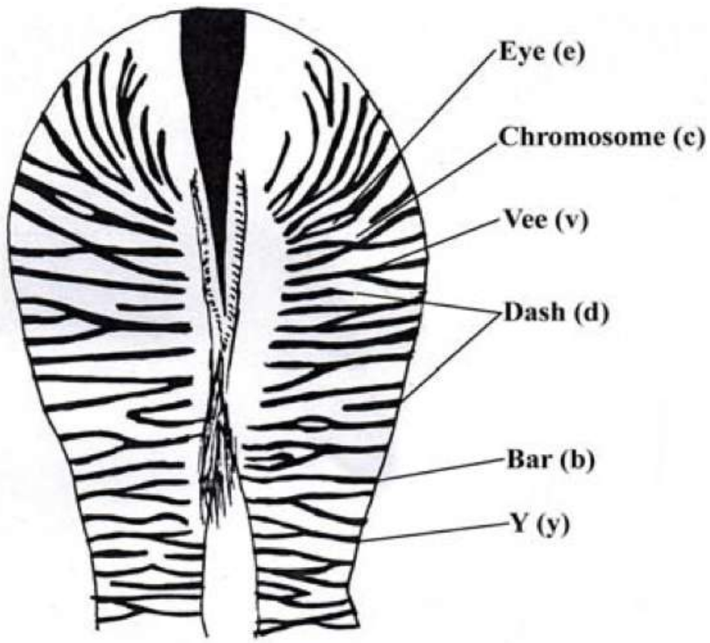

Figure 2.1. Coding convention for Grevy's zebra stripe patterns. Stripes are classified as one of six shapes: Y, Bar, Vee, Chromosome, Eye, and Dash. The zebra pictured here would have the code 'vvedcvdybbybdeyybvyyb.' From Nelson and Williams (2003).

Lion census data

Lions are the major predator of Grevy's zebra at LWC, responsible for >90% of predation-related deaths (Geoffrey Chege, unpublished data). To investigate the role of predation on foal survival, I also examined general trends in lion numbers in relation to foal survival estimates. Lion numbers were determined from annual census counts, which are carried out by the LWC Research and Monitoring Department using a combination of ground and aerial census methods. The low temporal resolution of this data prohibited its inclusion in the modeling process described below.

Survival analyses

Program MARK

Using the survey data described above, I estimated survival of foals by age class and as a function of rainfall using the software Program MARK 6.0 (White and Burnham 1999). Program MARK uses maximum likelihood estimation to determine survival and recapture probabilities based on encounter histories from mark-recapture datasets. Apparent survival (ϕ) represents the probability of survival between one interval and the next and recapture probability (p) represents the probability that an individual alive in the population will be encountered on a given sampling occasion. Because data were too sparse to build a model that included both rainfall as a covariate and age structure, I estimated the effects of age and resource availability in two separate modeling designs that contained encounter histories with different combinations of the observation data.

Assumptions

The basic Cormack-Jolly-Seber (CJS) model requires that a number of assumptions are met, specifically:

(1) All individuals have the same probability of recapture
(2) All individuals have the same probability of surviving from one sampling occasion to the next
(3) Marks are not lost or overlooked
(4) All sampling events are instantaneous and animals are released immediately

I assume that assumption 3 was met as zebras cannot lose their marks and photographing them ensures that marks are not missed or overlooked. Because the sampling design does not involve capturing or handling animals, assumption 4 was also met. Assumptions 1 and 2, on the other hand, are typically more problematic and often violated due to emigration and differences in age and sex. In order to evaluate lack of model fit caused by violating these first two assumptions, I used goodness of fit (GOF) testing to determine the variance inflation factor ($\hat{c}$), a measure that quantifies the amount of overdispersion and then allows for model correction. This was done by using Program MARK's built-in median $\hat{c}$ GOF test.

Model selection

After adjusting the fit using the estimated $\hat{c}$ value calculated in MARK, model selection was based on the quasi Akaike's Information Criterion ($QAIC_c$). This criterion incorporates both model fit and number of parameters, reflecting the reduced precision of both highly parameterized and overly simplistic models (Pryde et al. 2005). Models with $QAIC_c$ values less than 2.0 are considered to be strongly supported (Burnham and Anderson 2002), and increasing differences in $QAIC_c$ between the best model and alternative models represent decreasing support. Models with $\Delta QAIC_c$ values greater than 10 are considered completely unsupported by the data.

Model 1: Survival by age class

For the age class survival analysis, I constructed encounter histories according to single sampling occasions, resulting in a total of 1117 sightings of 323 foals collected during 59 occasions over the course of 6 years (2003-2008). When a survey of the conservancy was not completed in a single day, I pooled data from multiple days and treated them as a single occasion. Because the interval between sampling occasions was not equal, I calculated the intervals as a fraction of 1 month. To then investigate how survival varies with age, I constructed a time-since-marking (TSM) model. This type of model is a variation of the standard Cormack-Jolly-Seber (CJS) model that takes into account variation in survival probabilities relative to when individuals are first marked.

I split the foals into two groups based on the age at which they were first encountered: 0-3 months (N=265) and 3-6 months (N=58). Individuals that were first encountered and recorded in age classes 6-12 months (N=10) or yearling (N=4) were excluded from the analyses due to the greater degree of uncertainty associated with their initial age estimates. Because the exact age of each foal when first marked was not specifically known, I grouped all individuals into the beginning of the age class they were first recorded in to build the TSM model. For instance, all animals first recorded in the 0-3 month old age class were essentially treated as if they were first encountered when they were <1 month old.

Individual zebras often have a series of zeros in their encounter histories after they reach about a year old, regardless of whether they are alive or not, because they are simply no longer recorded during surveys. Because there is no way for Program MARK to differentiate between mortality and non-recording, a yearling (12+ months) class was included in every model to absorb the effect of foals "aging out" of the survey records. This class was always assigned its own parameters, but these survival and recapture estimates for yearlings were unreliable and therefore discarded. However, including this class in the models avoids underestimation of foal survival and ensures the accuracy of the <1 year estimates.

I created a set of candidate models that considered variation in survival and recapture probabilities with age. These survival and recapture estimates can either change or remain constant over time, the latter of which requires fewer overall parameters (Jolly 1982). Notation follows that suggested by Lebreton et al. (1992) and used in Cooch and White (2009). The subscript "*t*" represents time-dependent estimates, whereas the subscript "." represents estimates that are constant through time. TSM models are noted by showing the number of age classes (i.e. a3 = 3 age classes), followed by the model structure for each age class separated by a backslash (see Table 2.1 for descriptions of age classes and table 2.2 for model notation examples). Because ϕ and p do not necessarily follow the same pattern of variation with age, I included models in which age class structures differed between these parameters.

Notation	Age class structure
a2	<1 year, 12+ months
a3	0-5, 6-11, 12+ months
a4	0-2, 3-5, 6-11, 12+ months
a5	0-2, 3-5, 6-8, 9-11, 12+ months
a7	0-1, 2-3, 4-5, 6-7, 8-9, 10-11, 12+ months
a13	0, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12+ months

Table 2.1. Description of age class structures used in models. All estimates given for 12+ month (yearling) classes were excluded from subsequent analyses.

Model	Description
ϕ(a2-./.)p(a2-./.)	2 age classes for both ϕ and p; constant survival and recapture probabilities in each class.
ϕ(a2-t/.)p(a2-./.)	2 age classes for both ϕ and p; time-dependent survival for first age class, constant survival for second class, constant capture probabilities for each class.
ϕ(a5-./././.)p(a2-./.)	5 age classes for ϕ and 2 for p estimates; all estimates constant for each class. Assumes age-structured survival rates but constant recapture probabilities for foals <1 year old.

Table 2.2. Examples of model notation with descriptions.

Attempts to run both bootstrap and median-$\hat{c}$ GOF tests failed for the most basic time-dependent model without an age structure for foals <1 year old. This suggests inadequate fit and indicates that the data are too sparse to use a time-dependent model as the general model (Cooch and White 2009). This is not surprising, as the number of foals on the conservancy at any one point in time is relatively low. Due to this lack of fit, I subsequently removed the remaining time-dependent models from the candidate set and used the next most parameterized model that adequately fit the data [ϕ(a13-./././././././././././.)*p*(a7-./././././.)] as the general model. The median $\hat{c}$ test for this model yielded a value of 1.0154, suggesting slight overdispersion. This value was used for adjustments.

Model 2: Incorporating rainfall as a covariate

To investigate whether foal survival is related to resource availability, I built several models that constrained survival estimates to be a linear function of rainfall and compared these to unconstrained models. Before constraints can be added, it is important that the underlying general model adequately fits the data. Because the underlying model in this case must be time-dependent and time-dependent models using monthly intervals did not provide adequate fit, I chose to pool data into three-month intervals and create a new time-dependent model. If an individual was recorded at least once during any survey within the three-month period it was considered seen (“captured”) for that occasion. This resulted in a total of 817 foal observations of 323 foals over 24 sampling occasions in 6 years. Pooling data prevented the inclusion of age structure in the model because it increased the uncertainty associated with age estimates. A “throwaway” age class was still included in all models as in the age-structured model described above, and transition into this class was calculated conservatively based on the earliest possible time a given individual could move into that class. This ensured that survival estimates were not underestimated due to non-recording. The median $\hat{c}$ value of the general model [ϕ(a2-t/.)p(a2-./.)] that was used for adjustments was 1.0272.

The candidate model set for this analysis uses the same notation as the last, but models constrained by rainfall data are noted as such. Because the effects of rainfall on abundance have been shown to lag in time for plains zebra and other ungulates (Ogutu et al. 2008; Owen-Smith et al. 2005), I also included models that incorporated moving three-month averages of past rainfall. These models are noted as “rainlag” plus the time in months in which the three-month rainfall window is moved back in time. Following Owen-Smith et al. (2005), a standardized version of rainfall was included in case proportional variation in rainfall was more important than absolute differences in rainfall. Standardization was performed by dividing the average monthly rainfall of the three-month interval by total average monthly rainfall and then $\log_e$ transforming the result. Models that include standardized rainfall values are noted by “st.”

Results

Age class analysis

The best model was that which included 5 age classes (0-2, 3-5, 6-8, 9-11, 12+ months) for both survival and recapture estimates. The model that contained no age structure during the first year of a foal’s life [ϕ(a2-./.)p(a2-./.)] essentially received no support ($\Delta QAIC_c$=40.63), which strongly suggests that foal survival is not constant throughout the first year after birth. The top-ranking model yielded monthly survival rates that were lowest in the first 3 months after birth at 86%, with a total survival in this age class (i.e. to about age 4 months) of 64%. Monthly survival then increases slightly to 92% during the following 3 months before decreasing to 88% when foals are 6 to 8 months old. The fourth age class had the highest monthly survival with 96%. Using these estimates from the top-ranked model, the total estimate of Grevy's zebra foal survival to one year is 30%.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Qdev
ϕ(a5-././././.)*p*(a5-././././.)	3291.17	0.00	0.34	1.00	2446.40
ϕ(a5-././././.)*p*(a4-./././.)	3291.32	0.15	0.32	0.93	2448.59
ϕ(a7-././././././.)*p*(a5-././././.)	3292.75	1.58	0.15	0.45	2443.90
ϕ(a3-././.)*p*(a3-././.)	3295.11	3.94	0.05	0.14	2458.47
ϕ(a7-././././././.)*p*(a7-././././././.)	3295.85	4.68	0.03	0.10	2442.90

Table 2.3. The top five ranking time-since-marking models using $QAIC_c$ for rank determination. All models have constant survival and recapture probabilities per age class, but not between age classes. Time-dependence in survival and recapture probabilities is not included in any of the models, with only the structure of age classes differing between models.

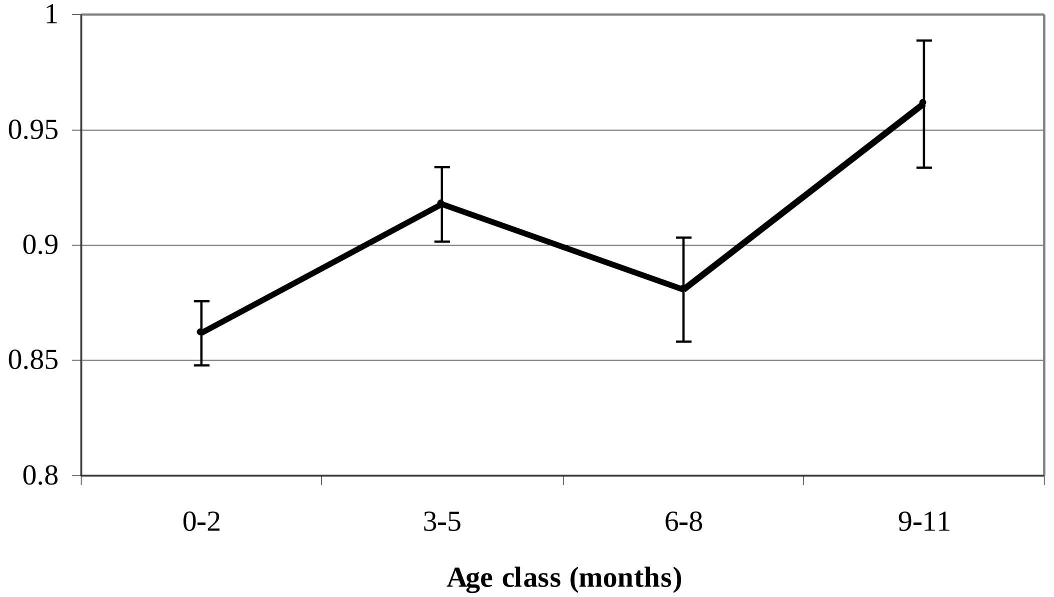

Figure 2.2. Monthly survival estimates from the top ranked model with 5 age classes, where error bars represent ± 1 SE. The fifth class is excluded from this figure as it was only used to absorb the influence of foals "aging out" of the dataset. Monthly survival estimates for each class are: 0-2 months = 0.86, 3-5 months = 0.92, 6-8 months = 0.88, 9-11 months= 0.96. Survival to one year is calculated as follows: $0.86^3 \times 0.92^3 \times 0.88^3 \times 0.96^3 = 0.300$.

Rainfall analysis

The top-ranked model was one that included a standardized average rainfall lagged by two months. This means, for instance, that survival estimates from Apr-May corresponded to rainfall averaged from Feb-Apr. The unconstrained model that only considered time-dependent survival with no effect of rainfall received little support ($\Delta QAIC_c$=4.50). In general, the models including standardized rainfall values performed better than those with absolute rainfall values, accounting for 3 of the top 5 models and suggesting that proportional differences in rainfall may account for variation in survival better than absolute differences.

Model	**QAICc**	**ΔQAICc**	**QAICc Weights**	**Model Likelihood**	**QDeviance**
ϕ(a2-rainlag2_st/.)*p*(a2-./.)	1500.50	0.00	0.40	1.00	664.56
ϕ(a2-rainlag3_st/.)*p*(a2-./.)	1502.41	1.91	0.15	0.39	666.46
ϕ(a2-rainlag3.)*p*(a2-./.)	1503.49	2.99	0.09	0.22	667.54
ϕ(a2-rainlag4_st/.)*p*(a2-./.)	1503.90	3.40	0.07	0.18	667.96
ϕ(a2-rainlag2/.)*p*(a2-./.)	1504.00	3.50	0.07	0.17	668.06

Table 2.4. The top 5 models from a candidate set that included a general, unconstrained model and 10 models that were constrained as functions of rainfall or standardized rainfall (see Methods section).

Survival and mortality (1-ϕ) estimates show a clear seasonal trend (Figures 2.3, 2.4), with mortality each year peaking around the end of the dry season (August-September) and reaching relative minima around February-March following the usual heavy rains of November-January. Yearly survival estimates for this model were lower than in the age class model as a result of the conservative estimation of transition into the yearling age class, resulting in possible exclusion of older foals with higher survival rates (see previous section). These estimates are therefore more likely representative of patterns of survival to weaning (10 months) rather than 1 year.

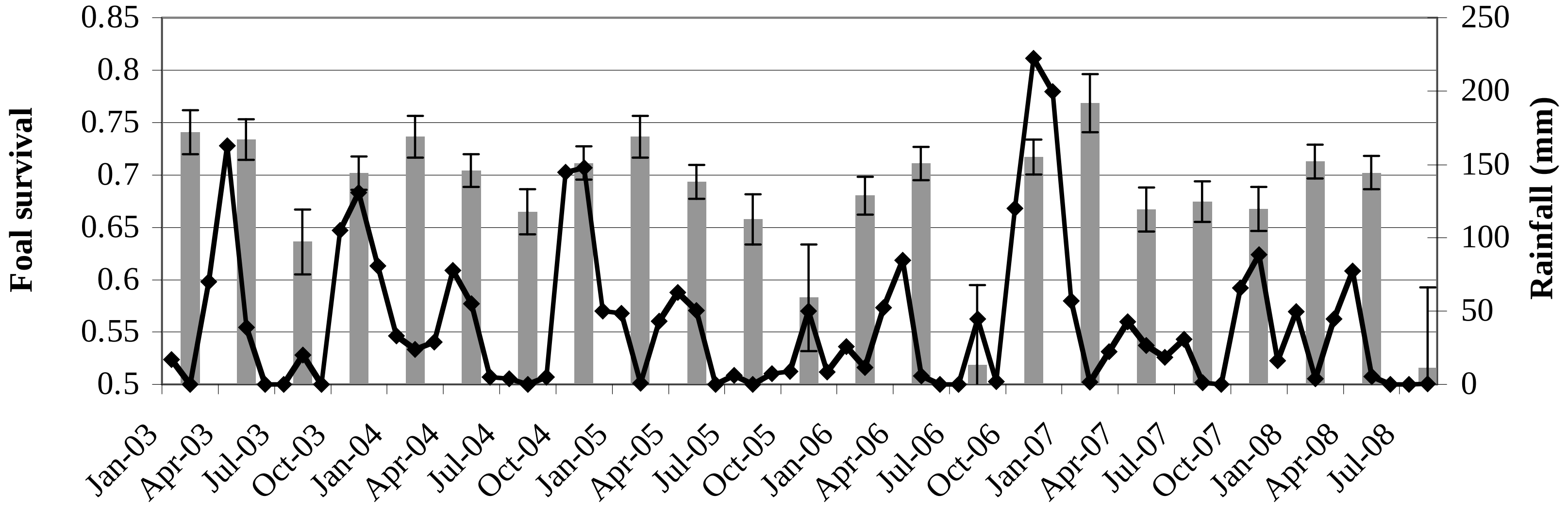

Figure 2.3. Survival estimates (columns ± 1 SE) for each three-month interval and average monthly rainfall (line) from Jan 2003 through Aug 2008.

Predator abundance

The number of lions at the conservancy grew from 18 to 28 between February 2003 and March 2004, and then fell to 12 by March 2007 (Figure 2.4). This represents a range of lion density between 0.057 and 0.134 lions/km^2 during the study period. Despite the number of lions decreasing by more than half, foal mortality rates did not show a clear pattern of decline.

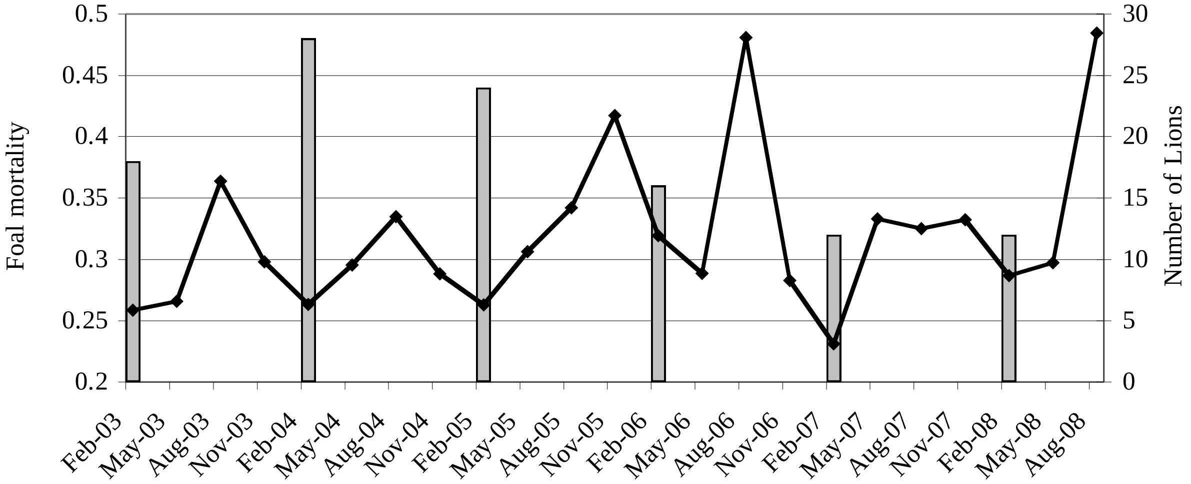

Figure 2.4. Number of lions recorded at the Lewa Wildlife Conservancy during annual censuses (columns) and estimated three-month *mortality* rates (1-ϕ; line) from Jan 2003 through Aug 2008. Mortality was calculated based on survival estimates from the top-ranked rainfall model [ϕ(a2-rainlag2_st/.)*p*(a2-./.)].

Discussion

Overall and age-specific foal survival in Grevy's zebra at the Lewa Wildlife Conservancy

The estimated survival rate of 30% to 1 year in this population is lower than that recorded in any previous study of Grevy's zebra or plains zebra (*Equus quagga*, formerly *E. burchelli*). This figure likely represents an overestimate as foal surveys were carried out monthly and individuals dying within the first month after birth may have never been initially recorded. A study of naturalized horses (*Equus caballus*) found that "virtually all" foals died within the first few days after birth (Monard et al. 1997). If this pattern holds true for Grevy's zebra, the survival estimate produced in this study could substantially overestimate survival.

Survival is not constant during the first year of a foal's life, but is lowest during the first three months after birth and at the start of weaning when foals are 6-8 months old. These results are consistent with those of a previous study on Grevy's zebra (Rowen 1992) and suggest that weaning is a particularly stressful period of foal development. Although the effect of weaning on survival in other ungulates is unknown, weaning may be more stressful for Grevy's zebra foals than foals of other equids because it occurs earlier (Becker and Ginsberg 1990).

Compared to other equid populations, foal survival in Lewa Wildlife Conservancy's Grevy's zebra population is low. The survival estimates of 30% to 1 year and 33% to weaning are substantially lower than those found in two previous studies of a nearby Grevy's zebra population, in which estimates ranged from 61% (Williams 1998) to 90% (Rowen 1992) survival to weaning for resident zebra foals. Grange et al. (2004) compared vital rates of a relatively stable plains zebra population to those of rapidly growing wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer*) populations in the Serengeti. Estimating foal survival from population structure data, they performed a series of modeling exercises and concluded that the low first-year zebra survival rate of 0.389 was the only major difference between populations and was the key parameter responsible for limiting the zebra population. Lewa's foal survival rate is even lower than that recorded for this Serengeti zebra population, and therefore likely plays a key role in the continuing decline of this population. However, lack of additional data prohibits us from comparing the impact of this parameter on population trends relative to other demographic parameters such as adult survival and fecundity.

Investigating the effects of resource availability and predation on foal survival

Rainfall and resource availability

The results of this study demonstrate that rainfall strongly influences foal survival through its relationship with forage quantity and quality. Survival showed a clear seasonal trend, in which it was lowest at the end of the long dry season and highest at the end of the rainiest three months. The best model included a short time lag between rainfall and its effects on survival estimates, a pattern that is consistent with previous studies on plains zebra foal abundance (Ogutu et al. 2008) and which may represent the delayed impact of rainfall on vegetation, the lagged impact of changes in forage quality on foal health, or a combination of both. Animals typically build up fat reserves during the growing season to sustain themselves throughout the dry season; they therefore typically have the best body conditions at the end of the rains and worst body condition at the end of the long dry season (Sinclair 1975; Ginsberg 1987). Foals store proportionally less body fat that adults and are thus more susceptible to changes in resource availability (Owen-Smith 1990; Pascual and Hilborn 1995; Mduma et al. 1999). This study suggests that a similar lagged pattern appears following the end of the long dry season as foals remain in poor bodily condition until they can rebuild sufficient fat reserves after undergoing the stress caused by the decreased quantity and quality of forage during the dry season (Sinclair 1975, 1977; McNaughton and Georgiadis 1986; Mduma et al. 1999).

Despite the importance of wet season rainfall in building fat reserves, previous studies considering annual survival rates have suggested that dry season rainfall may be more important than wet season or overall rainfall in driving patterns of adult and juvenile survival in ungulates (Pascual and Hilborn 1995; Pascual et al. 1997; Mduma et al. 1999; Durnham et al. 2003; Ogutu and Owen-Smith 2003; Owen-Smith et al. 2005). Although our data did not span enough time to analyze this directly, several factors suggest this may also be the case for Grevy's zebra. First, the dry season peak in mortality is depressed in August-September 2007 (Figure 2.4), which could be attributed to the fact that rainfall during the typically dry months of June and July was about five times higher than average that year. The opposite effect was seen in 2005, when the heavy October rains that typically end the dry season failed, causing a later, heightened peak in foal mortality (Figure 2.4). Second, a previous study of Grevy's zebra that yielded survival rates of almost 90% (Rowen 1992) was carried out in an area that received overall less annual rainfall (361 mm compared to 500 mm at LWC, this study), but had more than twice as much dry season rainfall on average compared to this study (~50 mm compared to 24 mm, respectively).

Predation

Grange and Duncan (2006) suggest that equids such as zebra are more sensitive to top-down processes than bovids because they are less sensitive to changes in forage quality. In this study, it was not possible to quantify the effect of predation or a possible interactive effect of predation and rainfall on foal survival because the lion abundance data were too sparse to include in any models. That said, the general trend of decreasing lion numbers between Feb 2004 and Aug 2008 (dropping from 28 to 12 individuals) was not met by an overall decreasing trend in mortality estimates (Figure 2.4), a pattern which would have been present if predation were directly suppressing survival or having an additive effect with rainfall. This ultimately suggests that predation pressure may not be as important in driving foal mortality as resource availability.

A comparison with Rowen's (1992) study of Grevy's zebra foal survival further supports this inference. She estimated that there were about 25 lions in her main study area of 293 km^2 (0.085 lions/km^2). The 209 km^2 Lewa Wildlife Conservancy averaged 18.3 lions over the course of the current study period, resulting in a comparable mean lion density (0.088 lions/km^2). With a greater density of Grevy's zebra at LWC, we might expect greater lion depredation there, but this is unlikely to account for the 63% lower survival rates in the LWC population. Overall, although a lack of detailed data on predator numbers limits my conclusions, these general trends suggest that resource availability plays a larger role in influencing foal survival than predation.

Conservation and Management implications

The Lewa Wildlife Conservancy is typically considered an important breeding and foaling area for Grevy's zebra (Nelson and Williams 2003; KWS 2008), and the low foal survival rates demonstrated in this study therefore raise serious conservation concerns for this endangered species. Although this low foal survival is undoubtedly contributing to the roughly 40% decline in the LWC Grevy's zebra population during the past decade (2001-2011, see chapter 1), it is not clear from this analysis if it is the key demographic parameter driving this pattern. Other studies on vertebrate populations have suggested that changes in adult survival tend to be more important in driving population declines than changes in juvenile rates (Gaillard 1998, 2000; Eberhardt 2002) and we will not understand the relative influence of foal survival until we have adequate measures of other parameters. Future research should therefore focus on determining subadult and adult survival rates and the factors that most strongly influence them. Because zebra of different reproductive states have different nutritional demands and may face different levels of predation (Owen-Smith 2008), it would be ideal to also investigate sex-based differences in survival. Finally, in order to reliably model population dynamics and subsequently perform a sensitivity analysis, we will also need to collect data on age-specific fecundity and interbirth intervals.

Because both bottom-up and top-down processes determine vital rates, we must understand their impact in order to target the factors driving population trends. The results of this study suggest that, at least for foals, bottom-up processes may be a more critical management concern than top-down ones. Measuring the effects of predation on vital rates is difficult, and will require the collection of finer-grain data on predator abundance as well as age-specific predation patterns. Because so little is still known about Grevy’s zebra population vital rates, this study can only be seen as a first step in gathering accurate information that will allow us to better understand the population dynamics of this species.

CHAPTER 3:
Landscape use patterns of lactating female Grevy's zebra (*Equus grevyi*) and their foals in relation to grass mineral content

Abstract

The dry season is a critical period for African ungulate survival in semi-arid savanna ecosystems because resources decrease substantially in quantity and quality. Females who are pregnant or nursing withstand additional stress during this period due to their increased demands for water, energy, and nutrients. For non-ruminant, hindgut fermenters such as zebra, forage biomass is typically considered more important than quality in determining foraging decisions and resulting spatial patterns of grazing. However, existing evidence suggests that this assumption may be invalid and some studies show that lactating female zebra fail to meet their energetic and nutritional requirements during the dry season. As forage quality may therefore be more important to zebra of this reproductive state, this study investigated whether differences in forage quality influence the spatial distribution of lactating Grevys zebra (*Equus grevyi*) and their foals during the dry season on a reserve in central Kenya. I used monthly survey data to identify areas frequently used by lactating female Grevy's zebra and their foals during multiple dry seasons. I then collected grass in these and control areas to determine if landscape use patterns are driven by spatial differences in grass nutrient content. The results of this study support the hypothesis that lactating Grevy's zebra selectively forage in areas of high grass quality during the dry season. Levels of potassium (K), sodium (Na), phosphorus (P), and crude protein (related to percent nitrogen), as well as the ratio

of calcium to phosphorus (Ca:P) appear to be particularly important in influencing landscape use patterns of lactating zebras during the dry season.

Introduction

Large herbivore foraging and the importance of resource quantity and quality

The relationship between animals and their food resources is the foundation for optimal foraging theory, which is broadly concerned with how animals can maximize energy gain in a heterogeneous environment where resources are patchily distributed (MacArthur and Pianka 1966; Stephens and Krebs 1986). As a modification to this theory, it is now widely recognized that animals must also balance nutritional requirements in addition to obtaining enough energy for maintenance (Seagle and McNaughton 1992). Foraging decisions change seasonally, as well as according to various constraints such as predation risk, water availability, and an individual’s physical state, social surroundings, and knowledge of alternative foraging options (Ydenberg et al. 2007). For large herbivores, the distribution of forage resources plays a key role in determining spatial patterns of landscape use (McNaughton 1988). In general, these patterns are the result of differences in abiotic and biotic factors of the environment, as well as complex foraging behaviors that differ among species and individuals (Bailey and Provenza 2008).

The ability of herbivores to extract nutrients from their food also plays a role in their foraging decisions and ability to satisfy nutritional demands. Herbivores have adapted well to consuming nutrient-poor food sources by evolving efficient digestive systems and excellent abilities to perceive and regulate nutrients in their diets (Janis

1976). Despite suggestions that they are in direct competition with each other, medium-sized grazers with different gut morphologies (i.e. ruminants and hindgut fermenters) persist alongside each other in many habitats. To explain this, it has been hypothesized that ruminants exploit medium-quality forage resources while hindgut fermenters persist on low-quality food sources, thereby avoiding direct competition with each other. (Alexander 1952; Bell 1971; Janis 1976; Foose 1982; but see Duncan et al. 1990). While ruminants face intake rate restrictions due to their digestive anatomy, hindgut fermenters are capable of higher passage rates (Foose 1982) and are therefore thought to consume greater quantities of food when its quality is low (Duncan et al. 1990). However, Shrader et al. (2006) provide evidence against this assumption by demonstrating that the non-ruminant white rhinoceros (*Ceratotherium simum)* does not increase consumption rates to make up for the decrease in forage quality during the dry season.

Studies on African grazers in general (most of which are ruminants) or ruminants specifically have shown that spatial patterns of grazing and ungulate density are primarily controlled by differences in forage nutritional quality rather than abundance (McNaughton 1988, Scoones 1995; Ellis and Swift 1988; Grant and Scholes 2006; Wilmshurst et al. 2000; Shrader et al. 2006). However, because forage quality is typically considered less important than quantity for hindgut fermenters such as equids, studies on these species have stressed the importance of forage biomass (Janis 1976; Rubenstein 1986*;* Berger 1986; Bell 1971*;* Ginsberg 1987; Williams 1998). Teasing apart the relative influence of forage quantity and quality on non-ruminant distributions has been difficult and evidence so far has been mixed, probably in part due to the number of different metrics that have been used as a proxy for forage quality. Studies that measure nutrient content directly typically consider only the macrominerals nitrogen (N) and phosphorus (P), despite the fact that microminerals have been shown to be important in determining wild herbivore distribution (Belovsky 1978; McNaughton 1988, Seagle and McNaughton 1992; Grant and Scholes 2006; Ben-Shahar and Coe 1992).

The dry season: Importance for limiting populations

Most studies on foraging behavior and distribution have taken place during the wet season, even though both forage quantity and quality are lower and more patchily distributed during the dry season. During this time, drinkable water becomes scarce and vegetation essentially becomes unsuitable for consumption (Sinclair 1975). The dry season is therefore a critical period for African ungulate survival (McNaughton and Georgiadis 1986) and plays an important role in limiting herbivore populations (Sinclair 1975). In particularly heterogeneous, mineral-poor landscapes such as semi-arid African savannas, herbivore populations are limited by the availability of forage in key resource areas or “hotspots” that contain high quality forage (Ellis and Swift 1988; Scoones 1995; McNaughton and Georgiadis 1986; Illius and O’Connor 1999; Augustine et al. 2003). Herbivore body condition has been shown to decrease substantially during the dry season, and it has been suggested that nutritional deficiencies endured during this period leave animals more susceptible to disease, predation, parasites, and ultimately death (McNaughton and Georgiadis 1986).

The dry season is especially hard on pregnant and lactating females because they have higher energetic and nutritional requirements compared to non-reproductive females and males (NRC 2007; Ginsberg 1987; McNaughton 1990; Anderson et al. 2007; Prins and van Lengevelde 2008). A study of plains zebra (*Equus quagga*) in Ethiopia demonstrated that lactating females actually fail to meet their nutritional and energy requirements during the dry season, which has repercussions for their overall physical health and the health of their foals (Abaturov et al. 1995). Poor maternal nutrition during the dry season has been implicated as one of the main drivers of foal mortality in zebra populations in South Africa (Owen-Smith et al. 2005) and suggests that the availability of high quality forage for pregnant and lactating zebra may be an important factor influencing population dynamics.

Nutritional ecology and distribution of lactating Grevy's zebra

While nutrition is widely recognized as an important aspect of individual health, applications of nutritional ecology to conservation and management of wild populations have remained largely unexplored (Parker et al. 2009). In order to protect endangered species in the wild, we must understand their resource needs and the ability of their current habitats to adequately supply those resources. In addition, we must understand how those resources are distributed throughout their ranges and how this influences population distribution and dynamics (Grant and Scholes 2006). In a previous study on Grevy's zebra (*Equus grevyi)*, Sundaresan et al. (2007c) found that lactating females were more frequently sighted in areas of short green grass and medium-dense bush than were non-lactating females and males. In contrast to Ginsberg (1989), who suggested that proximity to water drove female spatial decisions, Sundaresan et al. suggest that lactating females may be preferentially choosing areas with nutrient-rich grasses, despite the increased risk of foal predation in these areas as a result of lower visibility caused by dense bush.

This tradeoff between forage nutritional quality and predation risk has been shown to occur in parturient female caribou (*Rangifer tarandus*; Gustine et al. 2006), and may have significant implications for predation-related foal mortality. On the other hand, maternal health also influences foal health (Mech et al. 1991) and poor foal nutrition has been shown to make young ungulates more susceptible to predation (Mech 2007), so the benefits of foraging in nutrient-rich areas may outweigh the risks associated with predation.

The current study investigates whether differences in forage quality are influencing the landscape use patterns of lactating Grevy's zebra females and their foals during the dry season in an environment where water is abundant. Although several studies have shown a relationship between forage mineral content and grazer distribution during the wet season (McNaughton 1988; Seagle and McNaughton 1990), none have focused on hindgut fermenters or the dry season specifically.

In this study, I identify areas that lactating females and their foals used consistently during multiple dry seasons at the Lewa Wildlife Conservancy (LWC), Kenya. I then tested the null hypothesis that the degree of use of particular areas is independent of grass mineral content. Although localized rainfall can temporarily alter available foliar nutrient content, general spatial patterns of grass quality are relatively consistent from year-to-year as a result of its relationship to underlying bedrock composition, topography, and soil nutrient availability (Bowell and Ansah 1993; Illius and O'Connor 2000; Seagle and McNaughton 1992; S.J. McNaughton, personal communication). In addition to shedding light on the landscape use patterns of a hindgut fermenting species in relation to forage mineral content, the results of this study will provide insight into resource availability in a critical habitat area for Grevy's zebra. Several different strategies exist for managing forage quality in rangelands, some more compatible with current land uses at LWC than others, and these should be explored in order to figure out the best conservation approaches in this area.

Methods

Study Area

The Lewa Wildlife Conservancy (LWC) is a 209 km^2 private reserve in central Kenya (center point: 0°06'N, 37°21'E; Figure 1.1). The landscape consists primarily of open grassland, bushed grassland with *Acacia*-dominated woody vegetation, and riverine woodland. Mean annual rainfall was about 500 mm between 2002 and 2009 (see Figure 1.3). Four grass species dominate the landscape: *Pennisetum stramineum, P. mezianum, Themeda triandra*, and *Cynadon dactylon*, with *P. stramineum* being the most prevalent.

Foal Patrol: Surveying the conservancy for foals

Foal/female location data were obtained from the "foal patrol" survey dataset. Surveying methodology is described in detail in Chapter 2. Because this study focuses specifically on dry season nutritional resources, I considered only foal/female sightings that occurred between June 1 and September 31 of each year. Although May is typically a dry month, I considered the start of the dry season to be June to account for the time needed for ephemeral water sources to dry up. Therefore, I am defining the "dry season" as June-September for the purposes of this study. Additionally, I limited the analysis to early- and mid- lactation females with foals less than 6 months old, as their nutritional requirements are higher than females with older foals (NRC 2007) and they have been shown to have similar spatial distributions compared to zebra of other reproductive states (Ginsberg 1989).

Determination of high-use and control areas

I used kernel density estimation to create a dry season utilization distribution map for females with foals less than 6 months old using the Hawth's tools extension for ArcGIS (Beyer 2004; www.spatialecology.com). Kernel density estimation is a method that creates a probability density estimate using a kernel function to produce a smoothed multi-dimensional representation of spatial data. For each data point, a smoothed kernel (bump) is used to represent the probability density function, with the surface value being greatest directly at each point and decreasing to zero as the distance from the point increases (Silverman 1986). These kernels are then summed in order to determine the probability density function throughout the entire study area (Horne and Garton 2006). The resulting probability density function is heavily influenced by the choice of the kernel function parameters, in particular the bandwidth (also called h value, smoothing factor, search radius), which determines the distance around each point considered in calculations.

The most widely recommended procedure for choosing a bandwidth value is the least-squared cross validation (LSCV) method (Kernohan et al. 2001; Gitzen and Millspaugh 2003). However, LSCV is known to produce low bandwidth values, resulting in undersmoothing and a utilization distribution that is broken into small fragments or "islands" that misrepresent how animals actually use the landscape (Kie et al. 1996; Blundell et al. 2001; Kernohan et al. 2001; Amstrup et al. 2004). Although LSCV is widely used, several authors have suggested that the bandwidth determination method used should depend on the nature of the study (Kernohan et al. 2001; Fieberg 2007). It should be noted that most of the current literature focuses on bandwidth selection for home range analyses and therefore was not necessarily directly applicable to this study in which high and low use areas were the focus. Using LSCV to create kernel densities for the Foal Patrol dataset resulted in undersmoothing and a utilization distribution that made little sense when typical Grevy's zebra movement was considered. I therefore rejected this method of bandwidth selection and used ArcGIS 9.3's default method, which uses the smallest width or height of the input layer divided by 30. This resulted in a bandwidth of 375 m, which I used consistently for all evaluations of habitat utilization to reduce bias in results and ensure comparability.

Using the utilization distribution for the dry season, I identified areas of highest and lowest use by foals and lactating females. Typically, studies of animal space use delineate the home range using the 95% volume contour, the "core" area using the 50% volume contour, and the "highest-use" areas with the 25% volume contour (Worton 1989; White and Garrott 1990; Seaman and Powell 1996; Gitzen et al. 2006). Following these studies, I used the 25% volume contour line to represent areas of highest use, but I also created a new category, which I call "low use" that describes areas falling within the 75% and 95% volume contour lines. Contour lines were determined using Hawth's tools. The resulting layer represented a map of high and low use areas of females and their foals during the dry season (Figure 2.1).

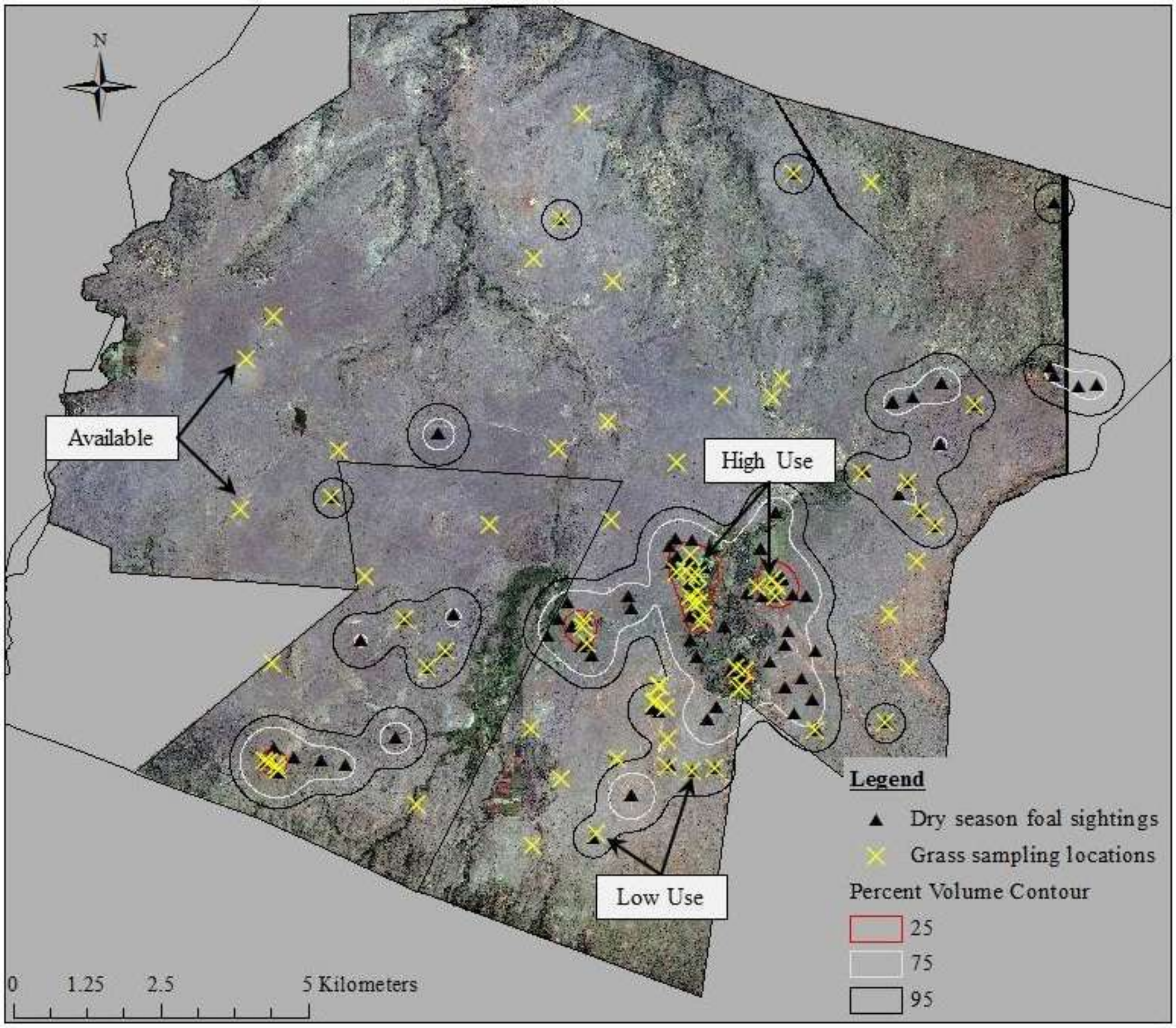

Figure 3.1. Map showing locations of lactating females with foals less than 6 months old, percent volume contours from the utilization distribution created through kernel density estimation, and the locations at which grass samples were collected for nutrient analysis.

Grass sample collection

Between 9 August and 23 August 2010, I collected 75 grass samples from areas of high (N=26) and low use (N=23), as well as from random points in the larger "available" landscape (N=26). Grass samples from high use areas were collected at locations within the 25% volume contour, using specific GPS locations from the Foal Patrol dataset when possible. The number of samples taken in each specific high use area was roughly proportional to the number of foal sightings per separate area (with the exception of one area that was slightly underrepresented due to repeated accessibility problems). Low use samples were collected at specific isolated foal sightings outside of the 75% volume contour lines but within the 95% volume contour that typically denotes the edge of the home range. I also collected 26 samples from the larger “available” landscape, generally defined as any grassed area that does not fall on a steep slope. “Available” sampling locations were chosen using a random point generator from Hawth’s Tools extension for ArcGIS (Beyer, 2004; www.spatialecology.com). I had originally intended to control for the effects of grass growth stage on nutrient content by only collecting brown or brown-green grass. However, this was not possible at some of the sampling locations because only greener grass was present (see vegetation characteristics section below).

I collected samples by choosing a center point (usually the specific GPS location from the foal patrol dataset or random point generation), pulling grass using a motion that simulated a zebra bite, and then repeating this at two other locations 15 m in random opposite directions from the center point. Collected grass was placed into a paper sample bag (provided by Crop Nutrition Laboratory Services; www.cropnuts.com) with punched holes to allow for drying. The samples, although almost all completely dry, were allowed to dry out of direct sunlight for at least one week and then sent to a lab (Crop Nutrition Laboratory Services, Nairobi, Kenya; www.cropnuts.com) where the dry combustion method was used to determine levels of 11 macro- and micro- minerals (B, Ca, Cu, Fe, K, Mg, Mn, N, Na, P, Zn). Boron (B) was excluded from later analyses because it is not one of the fourteen identified essential mineral elements for equids (Cunha 1991), and was only included in the analysis package as it is an important mineral for plants. The crude protein of grass samples was estimated following standard procedure by multiplying %N by 6.25.

Vegetation characteristics

While in the field, I categorized grass greenness and estimated grass height to provide coarse information about growth stage and forage quantity, respectively. Grass greenness was categorized as Brown, Brown-Green, Green-Brown, or Green (following Sundaresan et al. 2007c). I recorded grass height as a range because it varied considerably due to the patchy distribution (tufts) of grass at small spatial scales, but used the maximum height in statistical analyses to serve as a crude measure of grass quantity. It should be noted that this does not take into account the percent of grass cover or grass density. However, there were only a few areas that had sparse or extremely patchy ground cover, and all of these had extremely short grass.

Distance to water

I calculated the distance from each foal sighting and grass sampling location to the closest drinkable water source using the ArcGIS “Near” tool. Drinkable water sources such as dams, waterholes, and rivers were identified during a meeting with members of the Lewa Research and Monitoring Department. Our identification scheme was conservative in how we defined “drinkable,” and generally including only open water sources where Grevy's zebra have been seen drinking during the dry season by members of the Research and Monitoring Department.

Statistical analyses

All statistics were done using R (Version 2.12.2011-02-22; R Core Development Team, www.R-project.org). For vegetation characteristics, I used one-way ANOVAs to determine if nutrient concentrations differed among grasses of different color categories. To analyze the landscape use patterns of zebra, I combined the data from low use and available samples into a single control group because there was no significant difference between them and doing so allowed me to use a more straightforward statistical model for analysis (following McNaughton 1988). To compare how explanatory variables influenced the degree of zebra use, I used logistic regression models. Like all other generalized linear models, logistic regression models estimate unknown parameters using maximum likelihood techniques, but use a logit link function. Because many of the variables were highly correlated with each other, I used both multiple and simple logistic regression to present the results. For the multiple logistic regression analysis, I used the function *bestglm* (McLeod and Xu 2010) to evaluate all possible models and select the best one based on the Akaike's Information Criterion (AIC) value. I then compared the mineral concentrations of control and high use areas with those required in feed for the congeneric horse (*Equus ferus caballus*).

Results

Vegetation characteristics

A greater percentage of high use sampling locations contained green-brown or green grass (31% and 4% of total high use samples, respectively) compared to low use sampling locations (Figure 3.2). All of these samples were collected directly adjacent to swampy areas or rivers except one, which was in an area dominated by *Cynadon dactylon* – a species that has been shown to remain green throughout periods of little rain (Ginsberg 1987). The majority (71%) of all samples consisted of entirely brown grass, reflecting the low soil water availability of the dry season. As expected, the concentrations of most (6 of 10) nutrients were significantly related to grass color, suggesting a relationship between grass quality and growth stage and providing support for the use of grass greenness as a coarse indicator of grass quality for these specific minerals (Table 3.1).

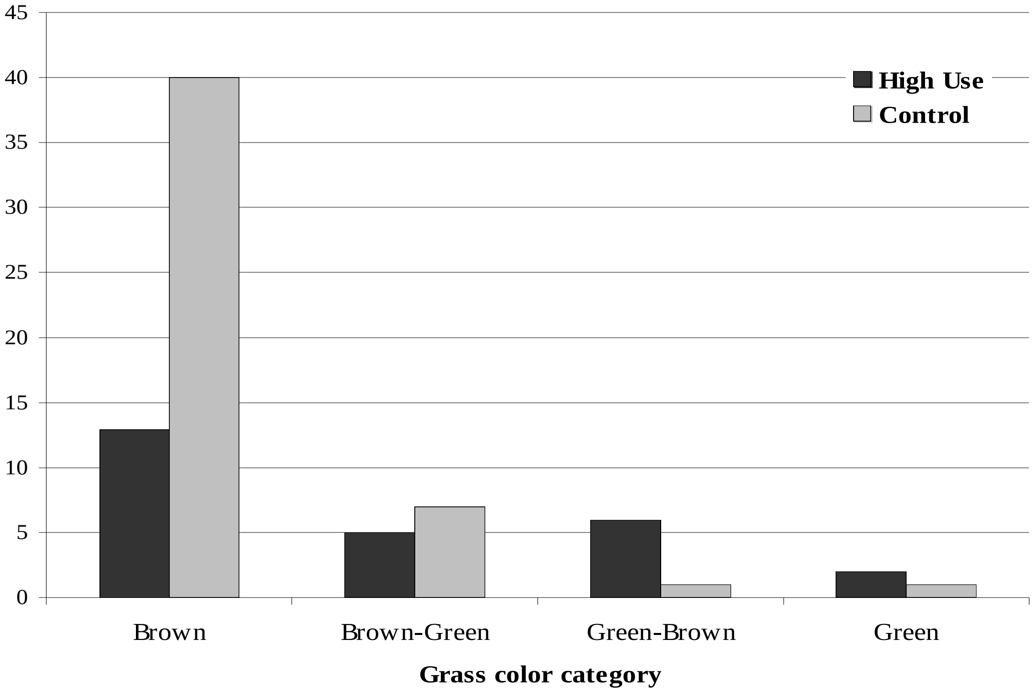

Figure 3.2. Number of high use and control samples collected in each grass greenness category.

	Grass Greenness Category				
	Brown	*Brown-Green*	*Green-Brown*	*Green*	*F-Value*
K (%)	**0.24**	**0.47**	**0.89**	**1.29**	**55.9**
P (%)	**0.12**	**0.17**	**0.26**	**0.28**	**24.7**
N (%)	**0.91**	**1.15**	**1.33**	**2.01**	**20.2**
Na (ppm)	**241.6**	**267.0**	***424.3****	**401.7**	**13.6**
Mn (ppm)	**45.8**	**60.4**	***114.6***	**82.3**	**16.1**
Mg (%)	**0.13**	**0.17**	***0.22***	**0.21**	**16.0**

Sample sizes: B=53, BG=12, GB=7, G=3; df=3 for all tests

*Represents the mean after 3 outliers were removed; mean with outliers =1185 ppm

Table 3.1. Mean nutrient concentrations as a function of grass greenness. Table shows only significant results (all p<0.0001) of one-way ANOVA tests. Concentrations of Fe, Zn, Cu, and Ca were not significantly different between grass color categories at the p<0.05 level.

Grass nutritional quality and zebra landscape use

The best predictive model determined using multiple logistic regression incorporated Cu, Fe, K, Mn, and Zn concentrations, although only %K was significant at the $p<0.05$ level (Table 2.3). Because multicollinearity may be influencing the incorporation of certain variables (Figure 2.2), especially those highly correlated with %K, I also present the results of simple logistic regression models (Table 2.4).

Deviance Residuals				
Min	1Q	Median	3Q	Max
-1.7524	-0.6111	-0.4185	0.2575	2.2633
Coefficients				
	Estimate	Std. Error	Wald z	Pr(>|z|)
(Intercept)	1.66	2.045	0.812	0.417
Cu_ppm	-0.271	0.196	-1.384	0.166
Fe_ppm	-0.003	0.002	-1.746	0.081
K_perc	**4.903**	**1.818**	**2.697**	**0.007**
Mn_ppm	0.054	0.033	1.637	0.102
Zn_ppm	-0.114	0.069	-1.647	0.1
Residual deviance: 61.607 on 69 df				

Table 3.2. Results of best predictive model determined using the *bestglm* function to evaluate all possible multiple logistic regression models. (see methods). Significant variables ($p<0.05$) are in bold.

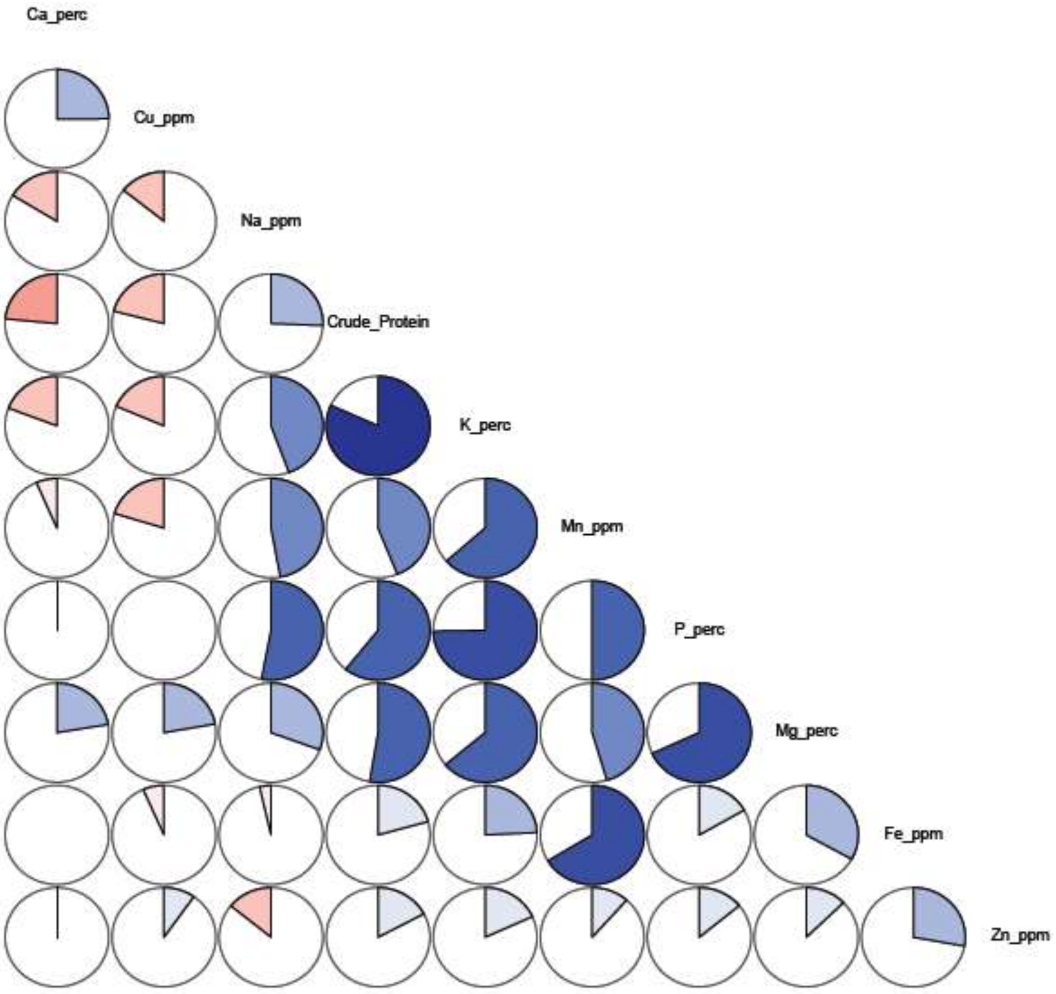

Figure 3.3 Correlogram of correlations among nutrient concentrations. Red and blue coloration reflect negative and positive correlations, respectively. The magnitude of the correlation between variables is represented by the portion of each circle that is filled and the darkness of shading.

Simple linear regression models for each explanatory variable considered (nutrients or maximum grass height) showed that there were significant differences in levels of grass K, N, P, Mg, Mn, and Na between high use and control areas (Table 2.3). Because grass growth stage can influence the availability of nutrients (Table 2.2), I also considered only brown and brown-green grass samples collected in control and high use areas. When all green-brown and green samples were dropped from the analysis, only four explanatory variables remained significant at P<0.05: %K (p=0.004), %Mg (p=0.02), %N (p=0.03) and %P (p=0.04). All of these nutrients were highly correlated with each other (Figure 2.2).

Variable	Estimate	Std Error	Wald z	P value
K	**4.357**	**1.195**	**3.65**	**0.0003**
N	**2.628**	**0.859**	**3.06**	**0.0022**
Mg	**17.078**	**5.801**	**2.94**	**0.0032**
P	**11.497**	**3.975**	**2.89**	**0.0038**
Na	**0.011**	**0.004**	**2.67**	**0.008**
Mn	**0.029**	**0.011**	**2.66**	**0.008**
Cu	**-0.303**	**0.153**	**-1.98**	**0.047**
Zn	-0.063	0.048	-1.31	0.19
Ca	-0.339	1.365	-0.25	0.80
Max Ht.	0.004	0.016	0.23	0.82
Fe	0.000	0.001	0.10	0.92

(a) Simple logistic regression models for each variable when grass samples from all greenness categories were considered. Significant variables (p<0.05) are in bold. N=75.

Variable	**Estimate**	**Std Error**	**Wald z**	**P value**
K	**4.817**	**1.674**	**2.88**	**0.004**
Mg	**17.058**	**7.303**	**2.34**	**0.020**
N	**2.306**	**1.062**	**2.17**	**0.030**
P	**11.316**	**5.514**	**2.05**	**0.040**
Na	*0.007*	*0.005*	*1.51*	*0.132*
Zn	-0.066	0.055	-1.20	0.230
Max.Ht	0.042	0.042	0.99	0.323
Cu	*-0.145*	*0.160*	*-0.91*	*0.362*
Fe	-0.001	0.001	-0.90	0.367
Mn	*0.011*	*0.016*	*0.72*	*0.473*
Ca	0.715	1.522	0.47	0.638

(b) Results when analysis was restricted to only grass samples that were classified into the Brown and Brown-Green color categories. Significant variables (p<0.05) are in bold. Explanatory variables that are significant at the p<0.05 level when all greenness categories are considered but which become non-significant in this analysis are in italics. Total N=66; 48 control, 18 high use.

Table 3.3 (a,b). Results of simple logistic regression for each independent variable with use category (Control or High) as response variable and nutrient concentrations and height as explanatory variables.

Grass nutrient concentrations compared to those required by horses

Comparing the available nutrient content in grasses at the Lewa Wildlife Conservancy with those suggested for the congeneric species *Equus ferus caballus* (domestic horse) provides more insight into what specific nutrients may be driving habitat use patterns for lactating Grevy's zebra (Table 2.5, Figure 2.3). Iron (Fe), magnesium (Mg), and manganese (Mn) were found in sufficient quantities in both low and high use areas and are therefore unlikely to influence spatial grazing patterns. Calcium (Ca), copper (Cu) and zinc (Zn) concentrations were lower in the grasses of high use areas than control areas, and are therefore also unlikely to be contributing to the observed landscape use patterns.

One or more of the remaining five factors in Table 2.5 likely contributes to landscape use patterns of lactating female Grevy's zebra and their foals. These include levels of K, Na, P, N (representative of crude protein), as well as the Ca:P ratio. All of these nutrients were below required levels in the grasses of both low and high use areas except for K, which was sufficient only in high use areas. The Ca:P ratio is extremely high in both high use and control areas, surpassing the maximum tolerable level (5:1) for adult horses in the control areas. Teasing apart the relative influences of each of these variables on grazing decisions is difficult, as they are all correlated with each other (Figure 2.2)

Nutrient	Requirement	% of requirement Low Use	 High Use	Difference in % requirement (High use - low use)
Ca:P	1.53	352	289	-64
Crude protein (%)	13.20	43	52	8.9
K (%)	0.42	57	96	38
Na (ppm)	1000	24	27	3
P (%)	0.34	35	44	9.2
Cu (ppm)	10	90	85	-5
Fe (ppm)	50	1460	1278	-182
Zn (ppm)	40	52	47	-5
Ca (%)	0.52	122	126	4
Mg (%)	0.10	131	158	27
Mn (ppm)	40	119	127	9

(a) Grass samples from all greenness categories.

Nutrient	Requirement	% of requirement Low Use	 High Use	Difference in % requirement (High use - low use)
Ca:P	1.53	333	227	-105.9
Crude protein (%)	13.20	44	58	14.3
K (%)	0.42	63	144	82
Na (ppm)	1000	24	53	28
P (%)	0.34	37	53	16.4
Ca (%)	0.52	123	121	-2
Cu (ppm)	10	91	81	-10
Zn (ppm)	40	52	47	-4
Fe (ppm)	50.00	1437	1459	22
Mg (%)	0	137	172	35
Mn (ppm)	40.00	118	181	63

(b) Only brown and brown-green samples

Table 3.4 (a,b). Mean nutrient content of grasses in low and high use areas compared to required concentrations in feed for the congeneric domestic horse (*Equus ferus caballus*). Dark gray shading represents nutrients for which both low and high use areas contain adequate amounts of that nutrient. Light gray shading represents areas for which the nutrient content decreases from low use to high use areas. Feed requirements are from Cunha (1991) and NRC (2007) and reflect information for 500 kg lactating females.

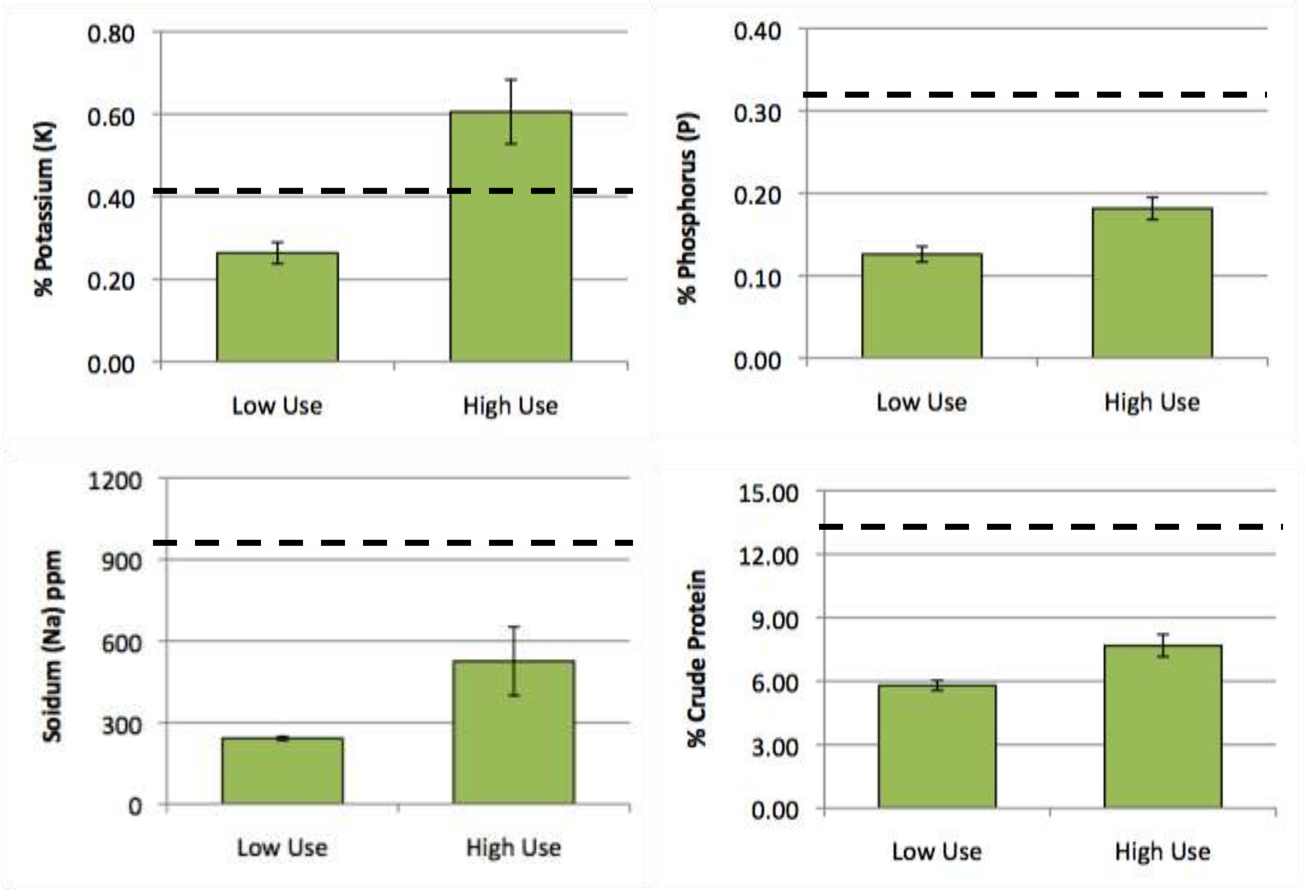

Figure 3.4. Nutrient or crude protein concentration compared between high-use and control areas, with the concentrations required for maintenance in grass fed to lactating horses (dotted lines; data from Cunha 1991 and NRC 2007).

Discussion

Relationship between Grevy's zebra landscape use and forage nutritional content

The dry season is a critical period for African ungulate survival in semi-arid savanna ecosystems. Females who are pregnant or nursing withstand additional stress during the dry period due to their increased demands for water, energy, and nutrients. Hindgut fermenters such as the Grevy's zebra (*Equus grevyi*) are often assumed to increase intake rates in the dry season to compensate for decreases in food quality and therefore increase nutritional intake. However, few studies have tested this assumption and existing evidence suggests this compensation mechanism does not occur (Shrader et al. 2006). Other compensation methods, such as increasing grazing time, have also been shown to be absent among lactating Grevy's zebra during the dry season (Ginsberg 1987). These lactating zebra may therefore be finding alternative ways to meet their energetic and nutritional requirements. The results of this study support the hypothesis that lactating Grevy's zebra selectively forage in areas of high grass quality during the dry season.

Levels of potassium (K), sodium (Na), phosphorus (P), and crude protein (related to % nitrogen), as well as the ratio of calcium to phosphorus (Ca:P) appear to be particularly important in influencing landscape use patterns of lactating zebras during the dry season. All of these minerals except K have been demonstrated to be important in influencing the grazing patterns of herbivores in general and ruminants more specifically at various spatial scales (McNaughton 1988, 1990; Grant and Scholes 2006; Seagle and McNaughton 1992; Ben-Shahar and Coe 1992). When growth stage is held relatively constant by considering only brown and brown-green grass, zebra still showed preferences for areas of higher K, Mg, N and P. This highlights the importance of these specific minerals in influencing the spatial distribution and foraging patterns of lactating zebra and demonstrates that Grevy's zebra are particularly adept at perceiving differences in grass quality despite being bulk grazers that have adapted to eat low-quality forage.

Although the results of the multiple regression analysis suggest that grass K is the only significant variable, it is difficult to draw conclusions about the relative influence of each mineral due to the high degree mutlicollinearity between minerals. Other studies have downplayed the potential importance of K (McNaughton 1988), but its role in influencing foraging patterns of lactating females and their foals should not be written off. Mammalian milk typically contains a large amount of K and may be important for these females (NRC 2007). Additionally, foals require feed with greater concentrations of K (0.6%; Jarrige and Martin-Rosset 1981) than lactating females, and even grass in the high use sites did not meet their requirements.

P and Na have been widely recognized as necessary minerals for sustaining pregnancy and lactation (Murray 1993, 1995; McNaughton 1990), and may be especially important in driving the foraging patterns of lactating females in this study. One specific high use area in this study had particularly high levels of forage Na, despite being less rich in other nutrients (including N, P, K) compared to the remaining high use sites. This area may be used consistently by lactating females in order to obtain greater amounts of this specific nutrient. The Ca:P ratio of grasses at LWC was surprisingly high, exceeding those suggested as maximums for nursing foals (1.5:1) and weanling (2:1) horses, and far exceeding those suggested as optimum ratios for foals and lactating females (Cunha 1991). High Ca:P ratios have been shown to be acceptable when P concentrations in feed are adequate (Jordan et al. 1975), which was not the case at LWC. Because the Ca:P ratio decreases from low to high use areas, we might conclude that they are foraging in certain areas to reduce the effects of high Ca:P ratios on foals, however, this may simply reflect selective foraging in areas of greater grass P concentrations.

Consistent with studies of other species (Abaturov et al. 1995), it appears as though lactating female Grevy’s zebra are not meeting their nutritional requirements during the dry season. The trend of decreasing body condition with dry season progression is well-documented across species (see McNaughton and Georgiadis 1986), but Ginsberg (1987) showed that lactating Grevy's zebra females are found in worse body condition than non-lactating and pregnant females during the dry season and therefore may be getting hit particularly hard during periods of low rainfall. This has important implications for foal survival (Mech et al. 1991). A study of plains zebra showed that foal survival was correlated with rainfall during the dry season prior to birth, leading the authors to suggest that maternal nutritional status was having substantial impacts on the ability of foals to survive (Owen-Smith et al. 2005). Similarly, poor foal health as a results of poor maternal health can leave infants at greater risk to predation (Mech 2007) and disease, and may be contributing to low foal survival rates (30%, see Chapter 2) in this population.

Impact of water availability on distribution

The availability of water sources is widely recognized as an important factor influencing the distribution of ungulates, especially during the dry season and for lactating females. For Grevy's zebra specifically, it has been shown to be a primary factor influencing the distribution and movements of lactating females (Ginsberg 1989). However, the Lewa Wildlife Conservancy has an abundance of available water (see Figure 1.3) and it is probably not a critical factor determining landscape use patterns among females there (Sundaresan et al. 2007b). A previous study found that early-lactation female Grevy's zebra typically remain within 2 km and mid-lactation females within 2.5 km of a permanent safe water source (Ginsberg 1989). However, another study found females up to 5 km away from drinkable water in a protected area, with no effect of female reproductive class (lactating versus non-lactating; Williams 1998). The majority of grass sampling locations in both high and low use areas in the current study were well within these distances. Out of 75 sampling locations, only four were more than 2.0 km from water and of these, only one was more than 2.5 km from water. Furthermore, three of these were low use sites where lactating females had actually been recorded during the dry season, suggesting these distances are within distance constraints related to water. Water availability is therefore unlikely to play a major role in limiting the possible distribution of females and foals on LWC.

Revisiting the quantity versus quality debate

Forage quantity is usually considered to be more important than quality for bulk grazers such as the Grevy’s zebra. However, the coarse measure of grass quantity used in this study (maximum height) showed no relationship with the habitat use patterns of lactating females. There is typically a tradeoff between plant quality and plant biomass, where tall vegetation is of poorer quality (Newman 2007) and this tall grass simply may not provide lactating females with adequate amounts of nutrients at normal intake rates. This pattern is supported by previous studies on grazers (Wilmshurst et al. 2000) and on Grevy’s zebra specifically; for instance, Ginsberg (1987) found that non-reproductive females were found in high grass biomass areas during the dry season more than expected based on the abundance of such areas in the study region, while lactating females typically preferred medium-low to medium biomass areas. Williams (1998) found a positive relationship between grass abundance and habitat use for Grevy’s zebra of all reproductive states, but only outside of protected areas where grass abundance is lower overall due to the presence of livestock; this pattern dissolved inside of a protected areas where early and mid-lactation females were found more often in areas of low grass abundance.

Ginsberg (1987) recognized the tradeoff between forage quality and quantity in East African savannas but suggested that the differences in grass quality would have to be large to offset differences in quantity and subsequently impact the foraging patterns of Grevy's zebra. This study shows that, at least at LWC, relatively large differences in forage quality do exist throughout the landscape during the dry season. Areas of high grass biomass may be particularly low in quality at LWC because it has a problem with undergrazing. Some areas of the landscape are consistently underutilized, causing certain grass species (primarily *Pennisetum stramineum*) to become moribund during the dry season. Grass in this state becomes extremely high in fiber and is typically avoided by herbivores. Therefore, despite this grass being present in large quantities, it is practically useless to grazers and results in a functional habitat size that is much smaller than the actual size of the conservancy.

New grass growth and green biomass tend to become concentrated in only a few areas during the dry season (Ginsberg 1987). In this study, high use areas contained proportionally more green grass samples, suggesting that lactating zebras selectively utilize these consistently green grass areas to obtain more nutrient-rich forage. Although we might expect grazers to only forage on these small, rare patches of nutritious green grass during the dry season, lactating females also forage in areas of brown and brown-green grass. Green grass is typically shorter than brown grass in semi-arid savannas (Duncan 1983; Shrader et al. 2006), a trend which was present in this study (B= 40.83, BG=37.46, GB= 43.17, G=27.09 cm). Similar to other grazers, lactating zebra my not be able to sustain themselves on rare patches of high quality, green forage because it is only available in low quantities, resulting in an inability to maintain normal food intake rates (Duncan 1983; Shrader et al. 2006).

Two other factors may be contributing to the use of brown and brown-green grass areas by Grevy's zebra. The first is interference competition, which increases when grass biomass is lower (Rubenstein 1986, horses). The large number of plains zebra at LWC may be especially important as they have competitive advantage over Grevy's zebra (Rubenstein 2010). Second, predation risk may also limit the use of highly nutritious green grass patches. Several studies have found that lion predation often occurs near water sources (Schaller 1972; Packer 1986; Williams 1998). In this study, many of the consistently green or green-brown grass areas were next to the swamp or rivers, where lions may hunt more frequently. Furthermore, several of these areas have relatively thick vegetation, which leads to increased predation risk due to lower visibility. The landscape use patterns of lactating zebra presented in this study may therefore represent the tradeoff between satisfying nutritional requirements and avoiding areas with high predation risk.

Conclusions and future directions

As in the Serengeti, there appear to be localized areas at the Lewa Wildlife Conservancy that act as crucial habitat for fulfilling the nutritional needs of lactating females (McNaughton and Banyikwa 1995). Although not possible for this study due to time and logistical constraints, two other factors should be considered to further test the hypothesis that lactating females are selectively foraging on high quality grasses during the dry season. First, it would be ideal if long-term dry season habitat use patterns of lactating females could be compared to those of non-lactating females. This would help tease apart the relative influence of grass quality and quantity in influencing spatial patterns of foraging among animals of different reproductive states. Such long-term data on non-lactating females have not yet been collected at LWC. Second, this study should be repeated during the wet season to see if these patterns are indeed seasonal. Habitat utilization maps for lactating females show that high use areas during the wet season (determined from same survey dataset) do not overlap with those of the dry season. This indicates that their primary foraging areas do vary seasonally. Even core areas (within 50% volume contours) barely overlap between seasons. Williams (1998) suggests that resource distribution is more important in influencing space use of Grevy's zebra when resources are limiting, but that other factors such as predators or forage-maturation may determine space use during periods such as the wet season when resources are not limiting. This may explain the different patterns of landscape use evident from the survey data, and could be tested by repeating a study similar to this one during the wet season.

Overall, this study suggests that where water is not limiting, dry season forage quality may be more important than previously thought for hindgut fermenters, especially females in the first six months of lactation. The nutritional needs of these females may be even greater than assumed in this study as the majority of these females are also likely pregnant (see Rowen 1992). Whether or not the relationship between forage quality and degree of landscape use holds true for non-reproductive equids will need to be tested, although previous studies suggest that it may not (Ginsberg 1989; Williams 1998; Sundaresan et al. 2007c). Similarly, it is unclear from this study whether or not this relationship will be similar during the wet season. Although previous studies of total herbivore distribution have provided support for such a relationship (McNaughton 1988, etc), it may not prove significant for an arid-adapted hindgut fermenter such as the Grevy's zebra.

The results of this study have important implications for managing wild rangelands. The functional dry season habitat for grazers at Lewa may be substantially smaller than the actual size of the conservancy due to the large areas of extremely poor quality grass. This may ultimately be limiting populations of grazers, including the flagship Grevy's zebra, and methods of increasing range quality and grazing uniformity should be explored.

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